Evo-Devo — Of Course, But Which One? Some Comments on Chomsky's Analogies between the Biolinguistic Approach and Evo-Devo

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In some recent papers, Chomsky has suggested some non-trivial analogies between the biolinguistic approach and evolutionary developmental biology (Evo-Devo). In this paper, the point is made that those analogies should be handled with caution. The reason is that the Evo-Devo version chosen by Chomsky in order to build the analogies fully assumes a gene-centric perspective. Although providing genes with a special power fits in well with the Principles-and-Parameters model, it does not agree at all with the reduction of the power attributed to genes that the Minimalist Program has placed on the agenda. Nevertheless, other Evo-Devo approaches exist that seem more accurate than the particular version adopted by Chomsky — approaches therefore which are more promising for fulfilling the minimalist biolinguistic approach.

Keywords: evolutionary developmental biology; gene-centrism; Minimalist Program; Principles-and-Parameters Theory

1. Introduction

From its origins, Generative Grammar has compellingly argued that language is biologically seated. Therefore, Chomsky has repeatedly claimed that linguistics should be thought of as a branch of biology (apart from Chomsky 1980, see e.g. Chomsky 1975: 123, 1986: 27, 2000: 90, 2005: 2 for wide discussion). To be more precise, as Freidin & Vergnaud (2001: 648) put it, a branch of theoretical developmental biology, because a core concern of Generative Grammar is to explain language growth in the individual.

Within this context, Chomsky has recently pointed out (see Chomsky 2007, 2008, 2010) non-trivial analogies between the biolinguistic approach (henceforth, BA) and evolutionary developmental biology (Evo-Devo). Our paper makes the point that Chomsky's analogies should be handled with caution. As Hall & Olson

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(2003: xv) write, "no unified theory of evodevo exists". This means that the Evo-Devo perspective, according to which "[e]volution is biased by development" (Raff 2000: 78), can be implemented through different theories and assumptions. Chomsky's analogies between the BA and Evo-Devo raise the problem that they are based on an Evo-Devo theory which is directly linked to developmental genetics and which, accordingly, takes genes to have a core or special power, as represented by Carroll (2005). To our mind, Chomsky's analogies may be accurate as regards Principles-and-Parameters Theory (henceforth, PPT), but they do not sit properly with a truly minimalist BA. Therefore, for those analogies to be sustained, we suggest that the need exists to consider other Evo-Devo theories which reject gene-centrism or primacy of the genes.

2. Chomsky's Analogies

According to Chomsky (2010: 45), there are "some analogies between 'the Evo Devo revolution' in biology and ideas that have been lurking in the background of biolinguistics since its origins [...]". The first one refers to the PPT.¹ In that model, the principles of Universal Grammar (henceforth, UG), or linguistic geno-type, were considered to be 'open', in such a way that enabled a narrow range of parametric variation. The setting of a principle P in the parameters A or B was considered to be triggered by the linguistic environment the learner is exposed to (Turkish, Spanish, etc.). Thus, grammars are the result of fixing the same principles in different positions. This view has been nicely expressed by means of the well-known 'switch metaphor':

We may think of the language faculty as a complex and intricate network of some sort associated with a switch box consisting of an array of switches that can be in one of two positions. [...]. The fixed network is the system of principles of universal grammar; the switches are the parameters to be fixed by experience.

(Chomsky 1988: 62–63)

In the same vein, Evo-Devo has shown that "the same regulatory genes were shared by animals with different body plans (for example, insects and vertebrates)" (Raff 2000: 75). Minor changes in regulatory mechanisms produce very different results on the surface (see Carroll 2005 for a wide discussion).² In fact, Chomsky (2007: 3) points out that PPT "was also suggested by major developments in general biology, specifically François Jacob's account of how slight changes in the hierarchy and timing of regulatory mechanisms might yield great superficial differences — a butterfly or an elephant, and so on" (see also Chomsky 2010: 49). For obvious reasons, that model "seemed natural for language as well; slight changes in parameter settings might yield superficial variety,

¹ Anyway, that analogy is not new; it can be traced back to Chomsky (1980: 66–67), although at that time the label 'Evo-Devo' had not yet been coined.

² Carroll (2005: 111) also adopts the switch metaphor; he speaks of genetic switches, the switches controlling how genes are used, and which are crucial in the models of genetic expression and regulation. Thus, the same genes/linguistic principles are arranged differently in different organisms/languages.

through interaction of invariant principles with parameter choices" (Chomsky 2007: 3).³

That situation meant the discovery, both in biology and in linguistics, of deep homologies among organisms on one side, and among languages on the other. Such a discovery reversed the traditional assumption of an "endless variation" (Boeckx 2009: 88) held by both disciplines. As regards language, Joos's (1957: 96) claim that languages "can differ from each other without limit and in unpredictable ways" is well known. Generative Grammar showed that assumption to be untenable. In biology, the prevailing assumption was very similar; as Mayr (1963: 609) put it, "[m]uch that has been learned about gene physiology makes it evident that the search for homologous genes is quite futile except in very close relatives". That is, different genes for different animals. As Carroll (2005: 9) points out, "[f]or more than a century, biologists had assumed that different types of animals were genetically constructed in completely different ways". Evo-Devo has shown, in the same vein as PPT, that such a contention was unjustified.

Chomsky's (2010) second analogy between the BA and Evo-Devo has to do with third factor conditions, that is, "[p]rinciples not specific to the faculty of language" (Chomsky 2005: 6). According to Chomsky (2007: 3), "some of the third factor principles have the flavor of the constraints that enter into all facets of growth and evolution, and that are now being explored intensively in the evodevo revolution" (see also Chomsky 2010: 51). Therefore, Evo-Devo discoveries point to "architectural constraints that limit adaptive scope and channel evolutionary patterns" (Chomsky 2010: 51).

Chomsky (2010: 45) asserts that "the analogies have been suggestive in the past, and might prove to be more than that in the years ahead". This assertion suggests that both analogies apply to any stage of the BA, that is, both to the PPT and to the Minimalist Program (henceforth, MP). We contend, though, that whereas the first analogy is applicable to PPT, none of them can aptly characterize the minimalist BA. The reason is that the Evo-Devo approach referred to by Chomsky is a strictly gene-centered theory, and gene-centrism is explicitly rejected by MP. To sum up, we will aim to show that the Evo-Devo version derived from developmental genetics is not an accurate analogy for the BA which MP has brought to the fore.

3. On the Status of Evo-Devo

The so-called Modern Synthesis (and the Neo-Darwinism which emerged from it) was undoubtedly a fundamental hallmark in biology: It gave rise to modern biology. However, some of their effects were clearly undesirable. One of them was gene-centrism (for criticism, see Goodwin 1994, Oyama 1985, Moore 2001, and our discussion below). Another undesirable outcome of Modern Synthesis

³ Chomsky (1981: 3–4) already made the same point: "[T]he languages that are determined by fixing their values one way or another will appear to be quite diverse" (see also Chomsky 1980: 66).

(and Neo-Darwinism) was to ignore development or, at least, leave it aside, thus favouring the dissociation between phylogeny and ontogeny (a wide consensus exists on this topic; see Griffiths & Gray 2001: 195, Robert *et al.* 2001: 954, Weber & Depew 2001: 239, Wimsatt 2001: 219; Robert 2002: 592, Gilbert 2003: 470–471, Gilbert & Burian 2003: 68–69, Carroll 2005: 6–8, and Jablonka & Lamb 2005: 27; for an in-depth analysis of the causes, see Robert 2004 and Amundson 2007). Two reasons underlie that dissociation: First, since Modern Synthesis, population genetics has become the core discipline of Evolutionary Biology (Wimsatt 2001: 219). Population genetics studies the gradual change of genetic frequencies at the population level. Therefore, the definition of evolution within Modern Synthesis as a process affecting populations, not individuals, led to a non-developmentalist theory (Moore 2001: 167). Second, since Modern Synthesis, it has been considered (as pointed out above) that development involved different explanations for different animals (see Carroll 2005: 6).

This disagreement between evolution and development has been reversed by Evo-Devo, which has bridged the gap between both levels in such a way that evolution is accounted for by means of developmental factors. Indeed, Gould (2002: chap. 10) defines Evo-Devo as the evolution of development. More concretely, Evo-Devo aims "to unveil how developmental processes and mechanisms become modified during evolution" (Baguñá & García Fernández 2003: 705).⁴ It is for that reason that, according to Fodor & Piattelli-Palmarini (2010: 30), Evo-Devo has made it possible to turn around Dobzhansky's (1973) claim that "nothing in biology makes sense except in the light of evolution"; as Fodor & Piattelli-Palmarini put it, Evo-Devo "tells us that it's the other way around: nothing in evolution makes sense except in the light of developmental biology".

However, it should be noted that Evo-Devo is a general perspective, rather than a specific theory or model. This means that any theory which reliably links evolution and development will be an Evo-Devo theory, no matter how concretely that relation will be implemented and approached. Accordingly, Hall & Olson (2003: xv) argue, as stated above, that "no unified theory of evodevo exists", whereas Robert (2002: 597) makes the same point: "Like any field of biology, evo-devo commands a diverse range of theoretical perspectives and experimental approaches". Indeed, Balari & Lorenzo (2009: 7) characterize at least three types of different (and even conflicting) Evo-Devo theories: (i) those assuming the 'genetic program' metaphor, (ii) those which extend the metaphor beyond genes and assume a developmental program, and (iii) those which completely abandon the idea of 'program', and take development to be the outcome of a developmental system. To sum up, all those approaches share "the idea that evolution is strongly constrained by the very same factors that strongly constrain the development of individuals" (Balari & Lorenzo 2009: 3); however, each concrete approach implements the same idea very differently.

Most of the disagreements among the several implementations of Evo-Devo are to do with one of the main problems theoretical biology is concerned

⁴ In the opinion of Robert *et al.* (2001: 956), the general objective of Evo-Devo can be deconstructed as follows: (i) the relationship between embryonic development and evolution; (ii) how changes in developmental processes affect evolutionary change, and (iii) how development itself has evolved (see also Hall 2000: 177).

with, that is, to integrate developmental biology within genetics and evolutionary theory, as pointed out by Weber & Depew (2001: 239)⁵:

The field has been left to contestations between molecular reductionists, who assume that the problem of development is simply the problem of turning structural genes on and off, and those who identify in one way or another with the contemporary 'developmentalist challenge', who are confident that what genes do is far from the whole story.

Let us note that the geneticist Evo-Devo approach (henceforth, Evo-Devo_{GEN}), finely represented by Carroll (2005), still assumes the primacy of genes which characterized Neo-Darwinism.⁶ And it should also be noted that this Evo-Devo_{GEN} is the approach taken by Chomsky in order to build the analogies with the BA (indeed, Chomsky 2007: 3 himself cites Carroll 2005, a leading practitioner of Evo-Devo_{GEN}, as a representative instance of Evo-Devo).

4. The Evo-Devo Approach Chosen by Chomsky

As pointed out, Chomsky's analogies between Evo-Devo and the BA are based on Evo-Devo_{GEN}. Although, as Gould (2002: chap. 10) discusses, Evo-Devo_{GEN} has changed relevant assumptions of orthodox Neo-Darwinism (which assumed that genes of different animals were different as well), in another respects Evo-Devo_{GEN} still accepts core Neo-Darwinian premises; for instance, the prominent role attributed to genes (and the notion of genetic program). However, it is our opinion that this primacy of the genes is in conflict with the reduction of the genetic endowment that MP has brought to the fore (see Chomsky 2005 for more discussion as well as sections 5 and 6 below).

The genetic primacy is clearly perceived in Carroll (2005). In fact, Carroll's (2005: 8) initial claim that "genes must be at the center of the mysteries of both development and evolution" advances the content of the whole book. Carroll (2005: 9) reduces Evo-Devo to "the comparison of developmental genes between species", an assumption which is denied by other Evo-Devo theories. More concretely, Carroll's book is built around the notion of 'genetic tool kit', which is common to complex organisms. Therefore, the diversity of animal forms is not to do with different genes, but with how the same genes are used differently. According to Carroll (2005: 11), the development of form "depends upon the turning on and off of genes at different times and places in the course of development". That is, Carroll's framework is entirely based on genes.

For that reason, Carroll's recurrent references to the genome as the source of form (which point to the prominence of the notion of genetic program), do not come as a surprise. Carrol's (2005) own words illustrate:

⁵ See Walsh (2007) and Pigliucci (2007) as interesting attempts to widen the Modern Synthesis in the light of the findings raised by developmental biology.

Evo-Devo_{GEN} derives from developmental genetics which emerged in the eighties (Raff 2000: 75; Gilbert 2003: 473, Griffiths & Gray 2005: 421; see Gould 2002: chap. 10). For that reason, Goodman & Coughlin (2000) or Baguñá & García-Fernández (2003) conflate Evo-Devo with developmental genetics.

[...] the species-specific instructions for building an animal are encoded in its DNA [...] (p. 11)

Evolutionary changes within this regulatory DNA lead to the diversity of form (p. 12)

This regulatory DNA contains the instructions for building anatomy (p. 12)

Where do we look these rules and instructions [for generating animal form]? In DNA. In the entire complement of DNA of a species (the genome), there exists the information for building that animal. The instructions for making five fingers, or two eyespots, or six legs, or black and white stripes are somehow encoded in the genomes of the species that bear these traits (p. 35).

Therefore, according to Carroll (2005: 35), "[e]volution of form is ultimately then a question of genetics." Balari & Lorenzo (2009: 6) argue that this understanding of Evo-Devo_{GEN} "can safely be judged a constructive enlargement of the strictly genocentric model of the MES [Modern Evolutionary Synthesis — ABB & VML]". That is, as the quotes above make clear, Evo-Devo_{GEN} clearly assumes the Neo-Darwinian genocentrism (or dictatorship of the genes, following Goodwin 1994), which means, in words of Oyama (2001: 177–178), to attribute a special directive power (both formative and informative) to the genes.

To make this point clearer, we should notice the great resemblance between Carroll's assumptions and those of Neo-Darwinian scholars, like Dawkins (1976) or Maynard-Smith & Szathmáry (1999), who also argue for the existence of master plans within the genes:

[...] the genes are not only the Andromedans [i.e. the devices — ABB & VML] who sent the coded instructions; they are also the instructions themselves (Dawkins 1976: 54).⁷

[...] each egg contains, in its genes, a set of instructions for making the appropriate adult. [...] it is the information contained in the genes that specifies the adult form (Maynard-Smith & Szathmáry 1999: 2).

The basic picture, then, is that the development of complex organisms depends on the existence of genetic information, which can be copied by template reproduction. Evolution depends on random changes in that genetic information, and the natural selection of those sets of instructions that specify the most successful organisms (Maynard-Smith & Szathmáry 1999: 2).

To sum up, we believe that Robert *et al.* (2001: 959) accurately contend that Evo-Devo "continues to show a tendency toward reductionism and genecentrism; developmental mechanisms are ultimately genetic".⁸ Therefore, Evo-Devo_{GEN} does not run the risk of being gene-centric, as argued by Robert (2003a: 479); indeed, Evo-Devo_{GEN} is clearly gene-centric.

⁷ See Dawkins (1976: chap. 3) for a wide exposition presenting genes as a collection of instructions for building the body.

⁸ For instance, Raff (2000: 74) writes that "[d]evelopment is genetically programmed". Such a claim is strongly rejected by those who 'take development seriously', quoting Robert (2004) (see Blumberg 2005, Moore 2001, and Oyama *et al.* 2001a for wide discussion).

5. Is Evo-Devo_{GEN} a Good Analogy for the Minimalist BA?

The take-home message of the above discussion is the following: $Evo-Devo_{GEN}$ may be a fine analogy for the BA derived from the PPT. However, it is not an accurate analogy as regards the minimalist BA. We develop both claims in turn.

As pointed out in Section 2, Evo-Devo_{GEN} shows clear parallelisms with PPT. Besides from those raised by Chomsky, we would like to add another one: PPT shared the strong geneticism held by Evo-Devo_{GEN}. PPT, and the remainder of the generative models previous to MP, took for granted the need to postulate the notion of 'genetic program for language' (Chomsky 1980: 234) or equivalent notions for characterizing UG.⁹ Lightfoot (1982: 22) illustrates that position:

The genotypical principles responsible for language acquisition can be viewed as a theory of grammar, sometimes called Universal Grammar. This represents the genetic equipment that makes language growth possible.

That is, (non-minimalist) Generative Grammar considered the genes to be the primary or central cause, in the same way as in $Evo-Devo_{GEN}$. The linguistic plan of the organism would lie in the genome, and this assumption has a clear parallelism in $Evo-Devo_{GEN}$: The source of the form or body plan would lie in the genome, as Carroll's previous statements made it clear (see Longa 2006, 2008, and Lorenzo & Longa 2009 on the generative gene-centrism).

For those reasons, we have argued before that $Evo-Devo_{GEN}$ could be an interesting analogy for PPT and for the BA arising from it. However, we do not share Chomsky's (2010: 45) statement that "the analogies have been suggestive in the past, and might prove to be more than that in the years ahead". Those analogies are not valid for characterizing the BA arising from the minimalist agenda. That is because the minimalist BA abandons core assumptions of the previous models, like gene-centrism itself, and the notion of UG, which is reduced to a minimum. Thus, we do not really expect $Evo-Devo_{GEN}$ to inspire the minimalist research.¹⁰ We will justify the reasons (see Longa & Lorenzo 2008 for an extensive analysis of differences between PPT and MP).

As specified above, all the models previous to MP, and PPT paradigmatically, assumed the need for postulating a "genetically determined initial state" (Chomsky 1980: 233) for explaining language growth in the individual. Such a

⁹ Some of these notions being 'linguistic genotype' (Chomsky 1980: 65, Lightfoot 1982: 21, 1999: 52, 2006: 45–46), 'blueprint' (Hyams 2002: 229), 'genetic endowment' (Anderson & Lightfoot 2002: 22, Guasti 2002: 271, Lightfoot 1982: 56), 'genetic equipment' (Guasti 2002: 18, Lightfoot 1982: 22), or 'genetic make-up' (Thornton & Wexler 1999: 1). Given that framework, Jenkins (1979: 106) characterized Generative Grammar as belonging to the "traditional study of the genetics of organisms".

¹⁰ This means we consider that MP is not a mere extension of PPT nor does it presuppose its validity, as opposed to the 'consensus view' held by Boeckx (2006), Hornstein (2009), or Hornstein *et al.* (2005). The 'consensus view' contends that when agreement is reached about PPT as an optimal format to characterize Plato's Problem, "an opening is created for simplicity, elegance, and naturalness to emerge from the long shadow cast by Plato's problem" (Hornstein *et al.* 2005: 5). MP would be "the concrete application of such criteria to the analysis of UG" (Hornstein *et al.* 2005: 6). Thus, Hornstein (2009: 116) considers that MP does not replace the previous theory, but presupposes its validity, MP being a mere extension of PPT/GB. It seems to us that this analysis is based on a methodological minimalism instead of a really ontological one, following Martin & Uriagereka's (2000) divide.

state, or UG, was conceived of as a body of specifically linguistic knowledge, that is, principles which "do not arise in other cognitive domains" (Tracy 2002: 656). According to that perspective, it is safe to say that "a strong background of genetic instructions is supposed to govern the acquisition of grammars" (Lorenzo & Longa 2009: 1302).

MP, though, has sustained a great reduction of the role given to genetic endowment (such a reduction fitting in well with the analysis of alleged 'genes of language'; see the wider discussion in Benítez Burraco 2009). Minimalism has therefore originated a new way of understanding the Faculty of Language (henceforth, FL), which is specially connected to the issue of language specificity: How specific or unspecific is language? The minimalist answer to that question is the opposite of the one suggested by the previous models.

Pre-minimalist models assumed as a basic statement that "the functioning of the language faculty is guided by special principles specific to this domain" (Chomsky 1980: 44), that is, principles of a purely grammatical nature, and "encoded in the genes of the children" (Smith 1999: 173). According to those models, FL was endowed with a high specificity. However, MP rejects that format, and assumes a language architecture which is characterized by its opposing statement, unspecificity in FL. Minimalism considers that the mind does not require a specific grammatical system. From the view of the strongest minimalist thesis (Chomsky 2000), the best minimalist version is the version postulating the most direct connection (i.e. optimal) between the two external modules. That amounts to saying that the best minimalist version is the version containing a minimum of specific grammatical machinery (Lorenzo & Longa 2003), because that machinery would 'disturb' the direct nature of the relationship.

From that perspective, the structure of FL would be minimal, with no hints of specific principles; its mechanisms would have to do (i) with requirements imposed by the external modules, or (ii) with principles derived from conceptual necessity, which 'come for free', that is, the simplest solutions amongst all conceivable ones, for which there is no need to postulate special stipulations in the form of grammatical principles arising from genetic instructions. For instance, movements of constituents are as short as possible not because that condition is stipulated by an autonomous grammatical module, as in GB, but because it is the most economical and efficient way for a computational system to operate. To summarize, from the viewpoint of MP, FL is the simplest way to productively link sounds and meanings. Thus, the specificity thesis argued for by the previous generative models and the unspecificity thesis sustained by MP are conceptually in conflict (for a wider analysis, see Longa & Lorenzo 2008).¹¹

The unspecificity thesis has been made especially clear in Chomsky's recent papers (Chomsky 2004 *et seq.*), which consider that the abandonment of grammatical machinery will let us go "beyond explanatory adequacy" (Chomsky 2004), thus reaching a true principled explanation of language design. Chomsky (2005: 6) proposes three factors in language growth: genetic endowment, external data

¹¹ In fact, Chomsky (2000: 113) clearly contends, as regards GB, that "a basic assumption of the work in [PPT], with its impressive achievements, is that everything just suggested [by MP; ABB & VML] is false: That language is 'highly imperfect' in these respects." MP assumes quite the opposite: The optimal or perfect design of language.

(experience), and "principles not specific to the faculty of language" — those principles comprising, amongst others, principles of structural architecture, efficient computation, etc. The point in order is that MP's unspecificity thesis leads to the primacy of the third factor; as Chomsky (2005: 9) points out, "we need no longer assume that the means of generating expressions are highly articulated and specific to language. We can seriously entertain the possibility that they might be reducible to language-independent principles".

This way, the minimalist proposal of reducing the role of genes in language growth leads to reducing the UG to a minimum. That means, as clearly stated by Chomsky (2005: 9), that MP crucially implies "shifting the burden of explanation from the first factor, the genetic endowment, to the third factor, language-independent principles of data processing, structural architecture, and computational efficiency". It is in this sense that the notion of (a rich) genetic program for language seems to be ill-suited from a minimalist perspective.¹² To sum up, we claim that, if the minimalist unspecificity thesis is seriously considered, the assumption of a highly detailed structure of purely linguistic knowledge, as sustained by GB, should be replaced by another according to which the initial state should be freed from any grammatical residue (Lorenzo & Longa 2003). This means the abandonment of gene-centrism by MP.

To summarize the discussion, if the differences opposing $\text{Evo-Devo}_{\text{GEN}}$ (based on the notion of genetic program), and the minimalist BA (which avoids that notion), are considered, $\text{Evo-Devo}_{\text{GEN}}$ does not seem an accurate analogy for the minimalist BA.

6. Are There Analogies between the Third Factor and Evo-Devo_{GEN} Constraints?

As pointed out above, Chomsky's second analogy between Evo-Devo and the BA refers to the third factor conditions. According to Chomsky (2007: 3), "some of the third factor principles have the flavor of the constraints that enter into all facets of growth and evolution, and that are now being explored intensively in the evo-devo revolution", because evo-devo discoveries point to "architectural constraints that limit adaptive scope and channel evolutionary patterns" (Chomsky 2010: 51). However, to our mind, this analogy is not accurate either, if referred to Evo-Devo_{GEN}.

It is safe to argue that $Evo-Devo_{GEN}$ has shown that not every organic design is feasible. This topic is emphasized by Gould's (2002: chap. 10) discussion of Evo-Devo. This author claims that Neo-Darwinism attributed an excessive power to natural selection. If this mechanism had the power it is usually endowed with, more than 500 million years of independent evolution should suffice to erase any trace of genetic homology, that is, adaptive evolution should have reconstructed every locus over and over again to face the changing requirements of changing environments (see Goodwin 1994: 116–121 for a similar argument related to the

¹² As Lorenzo & Longa (2009: 1306) point out, even if a minimal version of UG were found to be necessary for explaining language growth, its residual character would prevent to consider it as an articulated blueprint of language.

models of phylotaxis). Therefore, Gould considers natural selection to have a restricted scope, as opposed to Neo-Darwinist expectations.

That said, we believe that the minimalist third factor conditions and the architectural constraints brought to the fore by Evo-Devo_{GEN} cannot be conflated or compared: Practitioners of Evo-Devo_{GEN} attribute those constraints to purely genetic factors. For instance, Carroll (2005: 64) claims that "these Hox genes were so important that their sequences have been preserved throughout this enormous span of animal evolution [since the Cambrian to the present — ABB & VML]". A quite similar statement is made by Raff (2000: 76): Those architectural constraints are due to "deeply conserved gene expression patterns", which in turn are motivated by the fact that "the same regulatory genes have conserved roles in development" (Raff 2000: 75). As we can appreciate, the explanation raised by Evo-Devo_{GEN} to account for those architectural constraints is merely genetic, the evolutionary novelties arising because "conserved genes and gene pathways can be and are co–opted to new functions" (Raff 2000: 76). (This issue is widely analyzed in Carroll (2005) by means of the genetic switches of the genes, which can augment in number but where switches already existing are preserved.)

We think that Evo-Devo_{GEN}'s geneticist view of constraints on animal form is very different from what third factor effects actually mean: Third factor principles are based on the opposite premise, conditions which spontaneously arise, with no role for genetic specifications. Furthermore, it should be noted that these principles do not depend on the environment, but derive from the dynamics of the system itself (in this case, language). However, Evo-Devo_{GEN}'s opinion on that matter is different. For instance, Carroll (2005: 165) states that genes from the toolkit represent possibilities, but the actual fulfillment of potential is ecologically guided. More specifically, "the realization of this power is shaped, of course, by natural selection" (Carroll 2005: 287). Sincerely, we do not find many differences from the Neo-Darwinian view on natural selection. According to Carroll, gene stability and gene expression patterns are due to their functionality.¹³

That is, again, the opposite of the meaning of the third factor effects argued for by the minimalist BA. Therefore, Chomsky's analogy does not seem to be valid. It could well be valid if Chomsky referred to an Evo-Devo approach different from the geneticist one. If this were the case, though, Chomsky should explicitly point that out. In fact, one of the research programs that Müller (2007: 943) recognizes in Evo-Devo points to "properties of development that are not directly genetically determined, such as self-organization or geometric and physical factors." This view would agree with Chomsky's position; however, such a view seems absent from Evo-Devo_{GEN}.

7. Therefore: Which Evo-Devo — If Any?

We have argued that Chomsky's election (i.e. Evo-Devo_{GEN}) in order to draw an-

¹³ This seems to cast doubt on Fodor & Piattelli-Palmarini's (2010: 32) claim that Evo-Devo findings on gene conservation imply internal filters in the phenotypes on which exogenous selection operates.

alogies between Evo-Devo and the BA does not fit in at all with MP. Does this mean that we should avoid any kind of analogy between the minimalist BA and Evo-Devo? Not really. We should keep in mind that the Evo-Devo perspective can be implemented through several theories; any theory reliably linking evo-lution and development will undoubtedly be an Evo-Devo theory, even although it does not share Evo-Devo_{GEN}'s strongly geneticist assumptions.

If the reduction of the role of genetic endowment raised by MP is considered, in order to draw analogies between Evo-Devo and the minimalist BA an Evo-Devo theory rejecting gene-centrism and the notion of genetic program should be chosen. Such an Evo-Devo theory could well be Developmental Systems Theory (henceforth, DST; see Oyama 1985, 2000, Oyama *et al.* 2001b; see also Longa 2008 and Lorenzo & Longa 2009 for a implementation of the minimalist framework from the DST view).

DST is a general theoretical perspective on development, heredity, and evolution, according to which the need exists to reduce the importance that genes were traditionally given. According to DST, development does not entail any kind of pre–existing genetic program; genes are not the source of the form. Quite the opposite: Genes are just one of many developmental resources. Therefore, DST rejects the idea that genes are endowed with any special directive power.¹⁴ The main notion of DST is that of 'developmental system', which is to be understood as the overall collection of heterogeneous influences on development.

DST's key idea is represented by the so-called 'parity thesis': "Parity is the idea that genes and other material causes are on a par" (Griffiths & Gray 1998: 254), this thesis having its source in Oyama's (1985: 201) 'parity of reasoning'. According to DST, development arises from interaction between a wide number of heterogeneous resources and factors, all of them necessary (not only genetic ones) for development to take place.¹⁵ Accordingly, it is not possible to provide genes with any special formative power, nor is it possible to consider that genes contain the master plan of the organism either (on DST features, see Oyama *et al.* 2001a, Robert *et al.* 2001, Robert 2003b, or Longa 2006, 2008). DST contends that phylogeny is simply the derivational history of developmental systems (Oyama 1985: 179), and is explainable through a progressive modification of those systems.

We think that DST seems more promising than Evo-Devo_{GEN} for drawing analogies with the minimalist BA. Anyway, DST is not the only Evo-Devo theory suitable for approaching such an objective. Other Evo-Devo theories could be suitable for such a task; for instance, the view represented by West-Eberhard (2003), which relies on the concept of phenotypic plasticity. According to Walsh (2007: 193), such an approach "reverses the causal priority of genotype over phenotype in evolution that is the cornerstone of sub–organismal, replicator interpretation of the modern synthesis. Phenotypic novelties are initiated in development and not by mutation."

¹⁴ As Oyama (2000: 118) puts it, "a gene is a resource among others rather than a directing intelligence that uses resources for its own ends".

¹⁵ In this sense, the third factor deserves careful consideration because it widens the 'conventional interactionism', to put it in Oyama's (2000) term, between genes and environment which traditionally characterized Generative Grammar; see Lorenzo & Longa (2009).

8. Conclusion

This paper has aimed to show that the analogies between the minimalist BA and the Evo-Devo version adopted by Chomsky (Evo-Devo_{GEN}) do not seem applicable to the minimalist BA. Evo-devo_{GEN} is a gene-centric theory, and its essence does not agree at all with the reduction of the power attributed to genes that MP has placed on the agenda. In order to establish more productive analogies, it would be necessary to adopt another Evo-Devo version that, at least, assumes the parity thesis. This is not made by the approach represented by Sean Carroll. If the minimalist BA is to be seriously considered, our conclusion is clear: Evo-Devo, of course, but not Evo-Devo_{GEN}.

To put it in other words, Boeckx (2006: 10) wrote that minimalism "may well turn out to provide remarkable support for a silent revolution in biology (often called the Evo Devo revolution)". We strongly agree, but we believe that minimalism will not provide any kind of support for Evo-Devo_{GEN}.

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