Computational Phenotypes: Were the Theory of Computation Meets Evo–Devo

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This article argues that the Chomsky Hierarchy can be reinterpreted as a developmental morphospace constraining the evolution of a discrete and finite series of computational phenotypes. In doing so, the theory of Morphological Evolution as stated by Pere Alberch, a pioneering figure of Evo–Devo thinking, is adhered to.

Keywords: cognition; computational complexity; evolutionary developmental biology; faculty of language; morphological evolution

1. Introduction

This article offers an internalist explanatory model for the evolutionary origins of the computational system of the human faculty of language (FL), inspired by ideas worked out during the last decades in the field of Evolutionary Developmental Biology (Evo–Devo). In particular, we adopt the framework of 'morphological evolution' elaborated by Pere Alberch (1954–1998) in a series of papers published in the eighties and nineties of the last century (namely, Alberch 1980, 1989, 1991).

Evo–Devo aims to explain the origins and evolution of natural designs (phylogeny) by means of hereditary perturbations affecting the developmental plans of organisms (ontogeny); see in particular Hall (1999, 2002), Hall & Olson (2003a), Robert (2004), Carroll (2005), García–Azkonobieta (2005), and Laubichler & Maienschein (2007). Against this background, the essence of Alberch's proposal can be summarized by the following statements. A plan for the devel-

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opment of an organism consists of a set of morphogenetic parameters (not just genetic factors). Interactions among these parameters are complex and they relate non-linearly with phenotypic outcomes. This means that a parameter can be continuously changing without any significant consequence. However, once a certain critical value is reached, a minor change of the same parameter can be enough to introduce some radical phenotypic manifestation. These minor but far reaching perturbations on development can eventually attain evolutionary significance. Thus, evolutionary novelties can emerge without introducing new developmental factors or changing the nature of interactions. Finally, a system of morphogenetic parameters sets the limits of the forms attainable from such a developmental plan. As a consequence, the direction that development can take from a certain phenotypic state is strongly constrained by the geometry of the parametric space so defined.

The idea that evolution is strongly constrained by the very same factors that strongly constrain the development of individuals is common ground for every Evo–Devo oriented approach. Conversely, this idea is not congenial with the more classical stances of neo-Darwinian selectionism. According to the adherents of Modern Evolutionary Synthesis (MES), natural selection acts on the diversity randomly introduced into populations by point genetic mutations, totally unrestricted in scope (see the classical formulations of Morgan *et al.* 1915, Dobzhansky 1937, Mayr 1942, Huxley 1942, and Simpson 1944; see also Mayr & Provine 1980 for a general overview). Consequently, natural selection is believed to be the only creative force capable of organizing an otherwise amorphous material. Evo–Devoists, in contrast, attribute part of this creative capacity to constraints acting upon development and that limit the scope of attainable designs: They redefine natural selection as a mechanism filtering out those designs which fit environmental and populational conditions more efficiently (see Goodwin 1994: 143 or Wagensberg 2004: 125, as well as Alberch 1980: 664, Oster & Alberch 1982: 455, Alberch 1989: 46–48, and Alberch 1991: 16).

In this article we contend that the Evo–Devo theses thus far advanced can be readily extended to the evolutionary study of the nervous system and cognition (see Griffiths & Stotz 2000, Amundson 2006, Finlay 2007, and Griffiths 2007, for some programmatic attempts in this direction). Our interest will be focused on the case of language, seen as a particular aspect of human cognition and, more specifically, on the computational system in charge of generating internal linguistic expressions (Chomsky 1986). This system is thought to contain some unique features in the context of animal cognition, hence its special interest (Hauser *et al.* 2002).

The main claim of the present contribution is that the different levels of computational complexity reflected in the Chomsky Hierarchy (Chomsky 1956a, 1959) are the possible phenotypes of a cognitive parametric space defined by a restricted set of morphogenetic factors. These parameters are non-linearly related to the development of the cortical resources that supply the memory requirements of each computational model. We argue that the kind of (mildly) context-sensitive grammar which can be attributed to the computational system of FL is an emergent consequence of a minor perturbation affecting the development of a cortico-striatal circuit, once the value of a morphogenetic parameter attains a certain critical value in the course of human evolution. Thus, the adoption of this computational regime by FL can be seen as an evolutionary outcome strictly channeled by the organic conditions settled by the parameters at hand. We present this idea as an alternative view to that held by contemporary evolutionary psychology, whose practitioners defend the view that the mind is a collection of purpose-specific modules, each one an adaptively meticulous answer to environmental (or external) conditions (see Pinker 1997, Plotkin 1997, or Buss 2007, as well as the application of Pinker & Bloom 1990 and Jackendoff 2002 to the evolution of FL). The internalist proposal put forward in this article is based on the idea that the internal organization of the mind is in itself a constraining system that biases evolution in favor of certain forms of cognition and limits the power of the environment in the shaping of the organic design of minds.[1]

This is not to say that environmental and populational factors can be completely put aside by internalist-oriented theories. Actually, no evolutionary theory that ignores the external factors acting as selective criteria for the diversity independently brought into being will be complete. In this sense, we advance a proposal according to which the originally maladaptive character of this feature of the human cognitive phenotype would, in an apparently paradoxical way, have played a crucial role in its fixation as a species feature.

The article is organized as follows. Section 2 is devoted to presenting the basic tenets of Evo–Devo as well as Alberch's model of morphological evolution. Section 3 introduces an extension of this model to cognition and applies it to the evolutionary origins of the computational system of FL. We conclude with some reflections concerning the application of our ideas to explaining the origins of FL in a broader sense.

2. Evolving through Development

A somehow unexpected episode in the history of biology was the recent divorce between the study of individual development (the classical subject matter of Embryology) and that of evolution at the species level (in charge of Population Genetics for the most part of the twentieth century). This fact was directly related to the fixing by the MES of the concept of evolution as a series of changes in the patterns of allelic distribution among the members of the same population (see Amundson 2007: Part I and West–Eberhard 2003: chap. 1). The idea has been used to justify the exclusion of the path leading from the variants of genes to the adult features from evolutionary explanations. The underlying argument can be summed up as follows. If the only thing that matters in natural selection is having of those versions of features capable of increasing the reproductive rates of organisms, then evolution can safely be thought of as a continuous redistributive process of the alleles that correlate with those features within the gene pool of a population. As a consequence, (i) natural selection (i.e. the external factors challenging the organism's endurance and, above all, its reproductive

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[1] On the contrast between externalist and internalist approaches, as well as on the history of the debate, see Alberch (1991: 25–28).

success) can be conceptualized as a mechanism acting upon point mutations randomly introduced on certain genomic positions, and (ii) natural selection can be credited as a creative force working on an unrestricted source of diversity. According to Amundson's analysis, this argument is the agency ultimately responsible for having converted the processes that transform genes into features (or, more generally, the genotype into a phenotype) within MES-oriented biological thinking into a 'black box' (see Amundson 2007: 157 — especially his Figure 6 — and Reid 2007: chap. 1; see also Gould 1977 and Bonner 1982).

2.1. Evolutionary Developmental Biology (Evo–Devo): Common Background and Alternative Views

In our opinion, Amundson's statement is not completely accurate, because MES's vision of the evolutionary process does not only rely on ignoring the complexities of individual development and declaring it inert for any evolutionary concern. Underlying this vision there is also a model of organic development based on a very simple and linear conception of the phenotypic expression of genes, schematically represented in Figure 1 [A]. Such a conception is a necessary condition for upholding a view on organic evolution such as that represented in Figure 1 [B]:

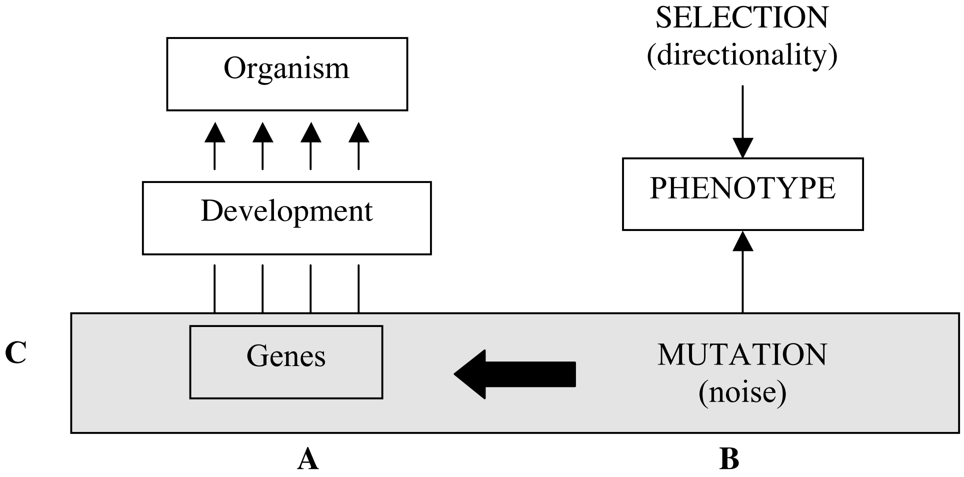

Figure 1: Modern Evolutionary Synthesis.

[**A.** Development. — The role of genes is central in the evolutionary process; they correlate with the phenotype in a simple and linear fashion. **B.** Evolution. — Natural selection acts creatively, imposing order on random point mutations, a noisy and unrestricted source of diversity. **C.** As a consequence, development (**A**) lacks any causal role in the evolutionary process (**B**).]

There are many factors that lead us to the conclusion that the omission of development from evolutionary matters cannot be sustained as straightforwardly as the argument seems to indicate. Some of these reasons are even coherent with other basic tenets of MES. For example, it should be clear to everyone that the simple fact of being capable of reaching the adult state is as important as being an adult optimally fitted to overcoming all kinds of environmental aggression. This implies that alternative routes of organic development can also reasonably be deemed targets of natural selection. As Gilbert (2003: 3) aptly puts it: "Every animal has to function as it builds itself". Consequently, a developmental path that makes the organism more robust from the start or allows an earlier emergence of certain key features, among other possibilities, is probably to be selected instead of other paths. The organism will obviously flourish and proliferate within the population. With a move like this, development can be added 'without tears' to the agenda of MES oriented approaches.[2] One only needs to conceptualize a developmental path as a specific phenotypic manifestation that, according to the Mendelian–Morganian idealization, correlates with certain genomic positions in a simple and linear fashion. Actually, this is the theoretical direction taken by a particular Evo–Devo trend, which relies on the assumption that evolution is mainly due to point mutations affecting genomic positions in charge of the regulation of the genetic activity during development. This view, accessibly introduced in Carroll (2005), can safely be judged a constructive enlargement of the strictly genocentric model of the MES.

However, this model is explicitly rejected by a number of Evo–Devo practitioners who share the belief that (i) genes are not the only causal agents in development, and that (ii) they are not the only developmental material capable of being transmitted from one generation to the next (see Figure 2 [A] below). These assumptions introduce a new and extended notion of heredity into evolutionary theory and they open an important conceptual breakdown with more orthodox forms of neo-Darwinism (see Jablonka & Lamb 2005 as a case in point). Underlying this theoretical move is the following line of reasoning:

(A) Genes are part of complex developmental processes in which other non–genetic factors are also causally involved (such as cellular products, mechanisms of cellular communication, intermediate phenotypic states, environmental factors, behavioral practices, and so on);

(B) to the extent that (i) all these factors exhibit some degree of individual variation, (ii) the variation is persistent throughout generations, and (iii) it can have repercussions on the unequal reproductive rates attained by the individuals so differentiated, it is possible to conclude that they all have a role in evolution not different from that customarily credited to genes;[3]

(C) hence, the Mendelian–Morganian idealization (establishing that the only evolutionary relevant correlation is that between genetic factors and phenotypic features) is untenable.

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[2] Waddington's (1957) concept of 'canalization' can be seen as a pioneering formulation of this stance. Waddington contended that developmental paths become stabilized and strengthened by continuous exposure to the rigors of natural selection. As a consequence, certain biases or constrictions on development could be explained as a direct consequence of standard Darwinian selection (for some comments on this matter, see Maynard Smith *et al.* 1985: 270).

[3] In Hall & Olson's (2003b: xiv) words: "Phenotypes and the processes that produce them are subject to selection; cells, embryos, and modifications of genetic and developmental processes are as much the raw material of evolution as are genes and mutations".

This is a non-trivial achievement of modern evolutionary thinking. However, it has not given place to a monolithic theoretical frame, but to a cluster of different and somehow confronted perspectives (Figure 2 [B]).[4] The main theoretical parameters underlying the diversity of approaches in this research field have to do with the number and levels of factors involved in developmental processes, the role and relative significance of each one, the nature of the interactions they sustain and the way they correlate with the phenotypic outcomes (see Robert *et al.* 2001 and especially Robert 2004). As a consequence, Evo–Devo houses theoretical stances as varied as those that maintain intact the "genetic program" metaphor (as Carroll 2005), those that extend the metaphor beyond the genetic factor and introduce the idea of a multidimensional "developmental program" (see Keller 2000 and Moore 2001), or even those that abandon the quasi-algorithmic image of development of the "program" meta-phor and endorse instead a concept of "developmental system" with complex interactions among factors of very different sorts that relate non-linearly with the successive phenotypic stages (see Griffiths & Gray 1994, Oyama 2000a, and Oyama *et al.* 2001).

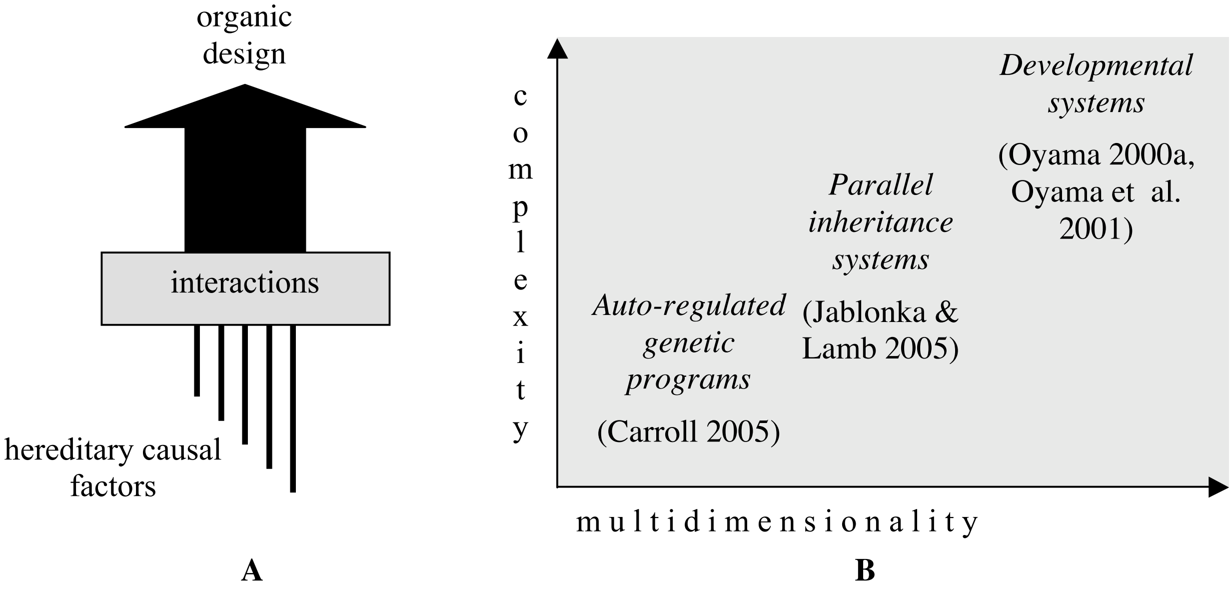

Figure 2: Evolutionary Developmental Biology (Evo–Devo)

[**A.** Organic designs are the outcome of complex developmental processes involving different types of factors, all relevant from an evolutionary point of view. **B.** The diversity of the factors (multidimensionality) and the complexity of their interactions (complexity) are the main theoretical parameters underlying the plurality of Evo–Devo thinking.]

The following contentions, even if there is not complete consensus about them, are unquestionably at the core of Evo–Devo thinking:

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[4] As Hall & Olson (2003b: xv) put it: "No unified theory of Evo–Devo exists".

(A) Neither natural designs nor the successive stages of an organism until attaining its adult steady state are preformed in genotypes;

(B) every particular stage in development is the result of complex interactions among multiple factors,[5] including the phenotypic state previously attained;

(C) genes are not the only developmental agents with a causal role in the evolutionary process; and

(D) the role of genes in development and evolution is not in a higher rank with respect to all the remaining factors.

Within this framework, the rigidity of the MES image on the evolutionary process, based on the centrality of genes and the omnipotence of natural selection in the shaping of organisms, is being left behind by Evo–Devo practitioners. In its place, a much more worked out image of development is currently allowing an understanding of ways in which the evolutionary process can be biased in favor of certain formal solutions even at the cost of losses in terms of fitness. In this regard, the following contentions are also highly representative of present-day Evo–Devo thinking:

(A) Certain developmental pathways are extremely conservative, in the sense that they are manifested, with minor modifications, across very distant taxa. The use of those very similar pathways in very different developmental contexts, resulting in a high degree of phenotypic variation, is a significant feature of evolution;[6]

(B) the above-mentioned modifications of the developmental pathways can be classified using a limited (and in itself constraining) inventory of descriptive categories: Displacements of onset and offset points, modifications of the rates of growth, alterations of the terminal state, changes in the plan of execution, and so on (see, among other sources, Gould 1977: Part II, Parker 2000, and Alba 2002);

(C) both the persistence of developmental pathways and the restrictive character of their possible routes of change must be seen as forces counteracting the pressures of the environment. As such, they must be acknowledged with a creative character similar (if not superior) to that of natural selection.

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[5] Johnston & Edwards (2002) is an especially significant model, based on fourteen different kinds of factors and almost thirty paths of interaction.

[6] This is a very old idea, probably due to Aristotle. It is also one of the defining notions of nineteenth century (pre- and post-Darwinian) embryology, especially for the defenders of the idea that ontogeny recapitulates phylogeny. See Gould (1977: Part I) for a detailed historical account. It is fair to say Evo–Devo has rescued and updated this idea. Shubin (2008) contains an interesting and accessible revision of the similarities of the genetic and developmental background across the species.

These statements do not entail that natural selection is completely neglected by Evo–Devoists, who have just opened a discussion concerning the extent of creativity of the Darwinian mechanism relative to that of the constrictions imposed by development. Actually, the different Evo–Devo approaches introduced so far maintain divergent positions on this issue, ranging from classical "genic selectionism" (Carroll 2005) to a radical redefinition of selection, understood as a filter rather than as a creative mechanism (see Goodwin 1994 and Kauffman 1995).

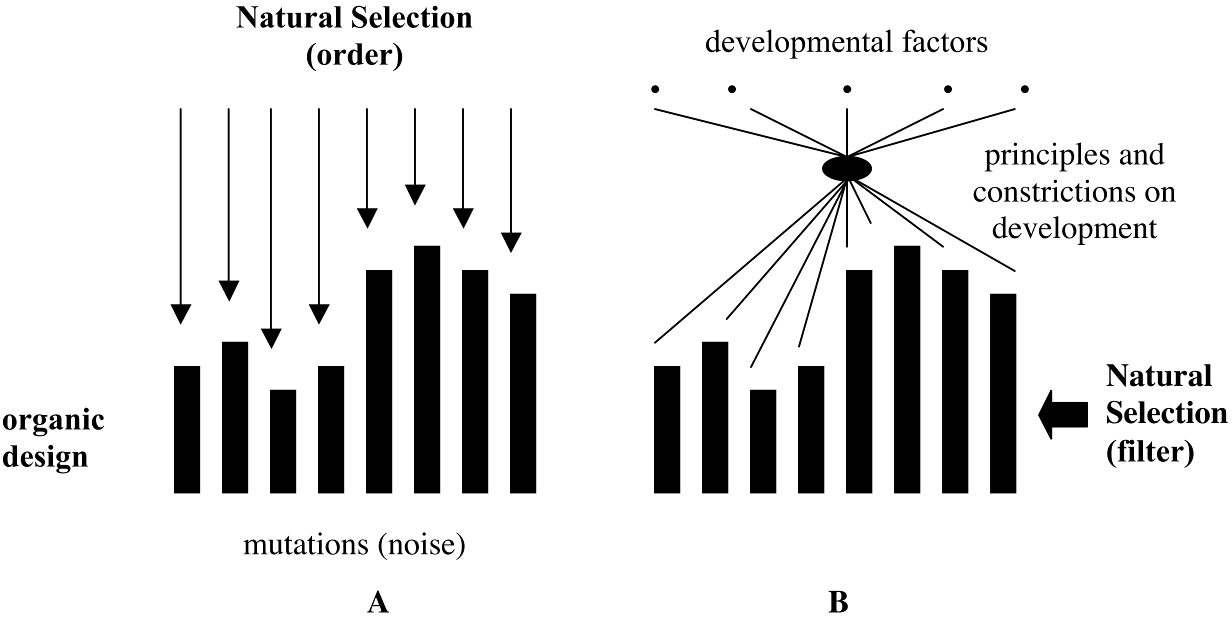

Fig. 3: Two views on Natural Selection.

[**A.** Creative selection. — The unrestricted variation introduced by random point mutations into populations is selected in favor of the variants of those individuals showing more resistance to environmental aggression and higher reproductive rates. **B.** Stabilizing selection. — Organic designs resulting from principles and constraints on development are filtered attending to their resistance to environmental aggression and their reproductive success relative to other designs also present in the population.]

2.2. *Pere Alberch's Concept of 'Morphological Evolution': Principles and Applications*

The proposals of Pere Alberch concerning the phylogeny of organic designs (or 'morphological evolution') are entirely sympathetic with the core Evo–Devo contention: The evolution of the formal patterns of organisms is due to perturbations on the parameters underlying their ontogeny. We start this section by presenting his ideas on individual development, strongly connected, in our opinion, with those of the most innovative of contemporary Evo–Devoists.

As a starting point, Alberch rejects the idea that development could be explained as a simple or direct mapping of the genotype onto the phenotype. He defends instead the idea that complex systems of genetic and embryonic factors underlie the growth of organisms and that those factors correlate non-linearly with the resultant morphologies. This amounts to saying that minor perturbations affecting any of the 'morphogenetic parameters' (genetic or non-genetic) can introduce wide-ranging consequences on development and, eventually, readdress the evolutionary course of a whole lineage of organisms. Thus, developmental paths show, according to Alberch, the properties of "complex dynamic systems" (see Kelso 1995, as well as the synthesis in Thelen & Smith 1994: chap. 3), which are summarized in the following points:

(A) A 'dynamic system of development' is composed of a high number of factors ('morphogenetic parameters') of very different characters (genetic, cytological, tissular, and so on);

(B) there is parity in their causal capacities and, thus, none of the factors acts as a 'central control parameter';

(C) they establish complex interactions and, consequently, no factor correlates directly and exclusively with any particular aspect of the resulting phenotype;

(D) the values of parameters can be subject to continuous perturbations without any significant consequence on the phenotype; however, once certain 'critical values' are attained, small perturbations can be enough to trigger a 'qualitatively new' morphology; and

(E) as a consequence of the diversity of causal agents, the complexity of their interactions and the non-linear character of their relation with the outcomes, identical results can be attained by means of perturbations of the values of different parameters of the systems.

In other words, from Alberch's point of view, neither the course nor the outcome of development is 'preformed' or 'programmed' within genotypes, the interactions among the different parameters at work being non-trivial, and both the order of the process and the heftiness of the results being emergent properties of the dynamics of the system. Figure 4 captures all these ideas:

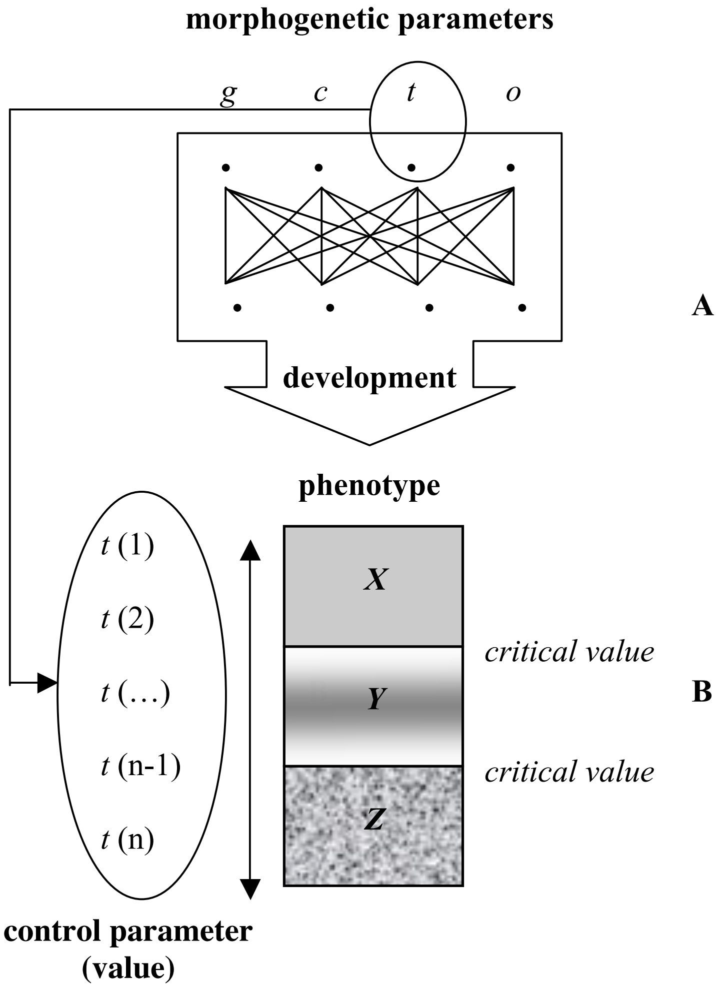

Fig. 4: Dynamism and complexity of organic development

[**A.** A system of development is characterized by the diversity and causal equality of the compounding morphogenetic parameters, the complexity of their interactions and the emergent character of the resulting morphologies. **B.** Once certain critical values have been attained, small perturbations on any of the parameters of the system (parameter t, in the figure) can result in discontinuous variety (i.e. different and qualitatively new designs: X, Y, Z).]

This set of assumptions situates Alberch's ideas not far from current Developmental Systems Theory (DST; see, among other sources, Griffiths & Gray 1994, Griffiths & Knight 1998, Oyama 2000a, Oyama *et al.* 2001, and Griffiths & Gray 2005), except for two non-negligible details. Alberch, in a strictly internalist vein, does not acknowledge the role that DST concedes to environmental factors, whereas the idea that opposing 'organism vs. environment', 'nature vs. culture' or 'internal vs. external' is completely artefactual is at the core of DST thinking (see, particularly, Oyama 2000b). Alberch's framework, on the contrary, takes only morphogenetic parameters of an internal sort into account (rates of kinetic activity of cellular diffusion, viscoelastic properties of the cellular matrix, mitotic rates, and so on; see, for example, Oster *et al.* 1988). Furthermore, Alberch points out in certain passages (e.g., Alberch 1991: 15) that morphogenetic parameters are ultimately genetically determined, which represents a (somewhat) residual genocentric stance. DST, in contrast, abolishes any version of the thesis of the centrality of genes.[7]

Another important component of Alberch's framework is the relevance of the concept of 'heterochrony' as the chief mechanism underlying morphological changes and evolutionary innovations. A 'heterochrony' is basically an alteration of the chronogram and/or the rate of growth for unit of time along the process of development leading to some significant impact on its final product,[8] something to which Alberch was very attentive throughout his career (for a very illustrative piece, see Alberch & Alberch 1981). Section 3 of our article is devoted to presenting an application of Alberch's ideas on heterochronies to the special case (not considered by him) of the evolution of the nervous system and cognition.[9]

Another very distinctive aspect of Alberch's model is the idea that systems of interactions underlying developmental processes are rather stable and that changes in these processes are mostly due to modifications in the values of one or another of the morphogenetic parameters of the system (Alberch 1989: 44). Thus, neither changes in the system of interactions nor in the nature of interactors themselves seems to be needed in order to explain certain major achievements in the course of natural evolution.[10] In the study of complex dynamic systems, the concept of 'control parameter' refers to the systemic component whose perturbations correlate with the emergence of new morphologies (a new pattern in the surface of a chemical solution, a new embryological state, a new form of behavior, and so on; see Thelen & Smith: 63–64). A control parameter is not, however, a central agent in causing phenotypic variation, in that the effects of its perturbations do not immediately reflect on morphological outputs, but on the other morphogenetic parameters instead (Kelso 1995: 7; see also Thelen & Smith: 112).[11]

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[7] There exists a connection between these two aspects of Alberch's thinking: The genetic determination of morphogenetic parameters presents itself as the only possible reason for excluding environmental factors from systems of development.

[8] 'Heterochrony' is a concept that originated with Ernst Haeckel (1834–1919), who used it as the conceptual basis of his Biogenetic Law (i.e. the initial stages of embryonic development represent the adult states of ancestral organisms). For Haeckel, the only possible heterochronic formula was the acceleration of the appearance of early stages so as to give place to the introduction of further stages. The idea that heterochronies can also consist of decelerations is due to Gavin de Beer (1899–1972). See Gould (1977: Part I) for a historical view, and Gould (1977: Part II) and Alberch *et al.* (1979) for systematic and formal descriptions of heterochronies.

[9] Alberch introduced some clarifications of the concept of 'heterochrony' in papers such as Alberch (1985) and Alberch & Blanco (1996), his intention being to liberate the concept from its strong dependency on the idea of 'time' and to connect it more directly to the internal dynamics of development (see Etxeberria & Nuño de la Rosa, in press).

[10] Alberch (1991: 17–18) speculates with the idea that this 'evolutionary mode' could be an outcome of natural macro-evolution, naturally selected by its advantageous combination of robustness and flexibility: A system of development so defined is very resistant to external aggressions, but it also allows the exploration of new designs, eventually needed in relatively or radically unstable environments.

[11] In Thelen & Smith's (1994: 112) words, a control parameter "constrain[s] the interacting elements, but [does] not prescribe the outcome in a privileged way". Or in Kelso's (1995: 7) words: "[The] control parameter does not prescribe or contain the code for the emerging

Within this model, development (even the development of novel forms) is always a function of the system as a whole. The idea of 'control parameter' basi-cally introduces the possibility of signaling a single parameter of the system as the starting point of the chain reaction leading to new morphologies.

For our own purposes, however, the most relevant aspect of Alberch's proposals is the contention that developmental systems foreshadow the scope of their attainable phenotypes, as well as the trajectories leading from a certain phenotypic state to another. It is the concept of 'parametric space' that in Alberch's framework is in charge of theoretically representing the finite and discrete set of the possible outcomes of any developmental system (Alberch 1989, 1991).[12] The main properties of parametric spaces are summed up in the following paragraphs (see Figure 5 below as a point of reference):

(A) A parametric space is a finite set of discrete phenotypes. The discontinuous character of phenotypic variation is captured in Figure 5 by the separate spaces named with capital letters;

(B) each phenotype has a characteristic probability of coming into being, represented in Figure 5 by the extension that it occupies ([D] is thus the most probable phenotype, while [B] is the most improbable one);

(C) moreover, each phenotype is also characterized by the relative probability of transforming itself into one or another of the neighboring phenotypes. In Figure 5 this aspect is represented by the extension of the line separating different phenotypes ([A] has a strong probability of turning into [D], a low probability of turning into [B], and no probability at all of turning into any of the remaining phenotypes).

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pattern. It simply leads the system through the variety of possible patterns or states".

[12] The notion 'parameter space' is related to a certain point to Waddington's (1957) concept of 'epigenetic landscape'. This concept refers to the strong 'canalization' of certain developmental paths (see fn. 1 of this article), an effect that makes them highly resistant to external perturbations. These pathways are thus firmly established and only very radical perturbations can serve to redirect development to another less canalized but also genetically available path.

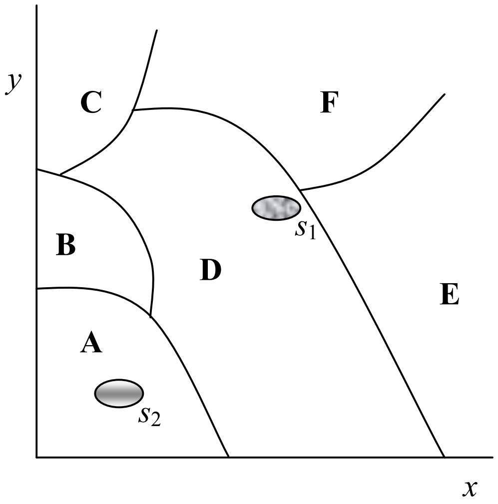

Figure 5: Parametric space

[The figure represents a parametric space ideally defined by means of two morphogenetic parameters (*x* and *y*). The space delimits a finite number of discontinuous phenotypes (**A, B, …, F**). Perturbations of the values of the parameters can transform a phenotype into another. Each phenotype has a characteristic probability of coming into existence (in the figure, the space of the relevant phenotype) and a certain propensity of transforming itself into another phenotype (in the figure, the extension of the lines limiting phenotypes). (Based on Alberch 1989: 51 and Alberch 1991: 16.)]

Moreover, species are represented in Figure 5 by means of the oval items (‘s_1’ and ‘s_2’). From a populational point of view, the model incorporates the following contentions:

(A) Every species falls within one or another phenotype (‘s_1’ belongs to phenotype [D], whereas ‘s_2’ fits in phenotype [A]);

(B) the morphological stability of a species is a function of both (i) the probability of its phenotype (‘s_1’ is, in principle, a more stable population than ‘s_2’) and (ii) its proximity to a point of bifurcation to other phenotypes (‘s_1’ is thus a rather unstable population within its phenotype, given its vicinity with the bifurcation leading to [E] and [F]);

(C) the proximity to a point of bifurcation as well as the relative propensity of its own phenotype to transform into one or another phenotype puts a certain population at the edge of undergoing a radical morphological reorganization (‘s_1’, for instance, has a high propensity of acquiring the properties of phenotype [E]).

‘Bifurcation’, a point within a parametric space in which a minimal perturbation is capable of bringing about qualitatively new morphologies, is thus another key concept in Alberch’s framework (Oster & Alberch 1982). In Figure 5, for example, species s_1 can easily shift to phenotype [E], attending to its proximity to the bifurcation between [F] and [E] from its original phenotype [D], as well as to the higher propensity of phenotype [D] for transforming into [E]. Using the jargon of dynamic systems theory, we can say that population s_2 occupies a 'well of attraction' in the situation depicted in Figure 5, whose depth guarantees a high degree of stability to its phenotype (of type [A]). On the contrary, population s_1 is at the edge of its well of attraction (i.e. of a 'phase shift') due to its continuous exposure to a certain kind of perturbing factor, a situation that makes it highly susceptible to entering into a different well of attraction. Figure 6 is thus an alternative way of symbolizing the situation previously presented in Figure 5. Figure 7 summarizes a particular application of this model to the study of an entire family of organic structures.

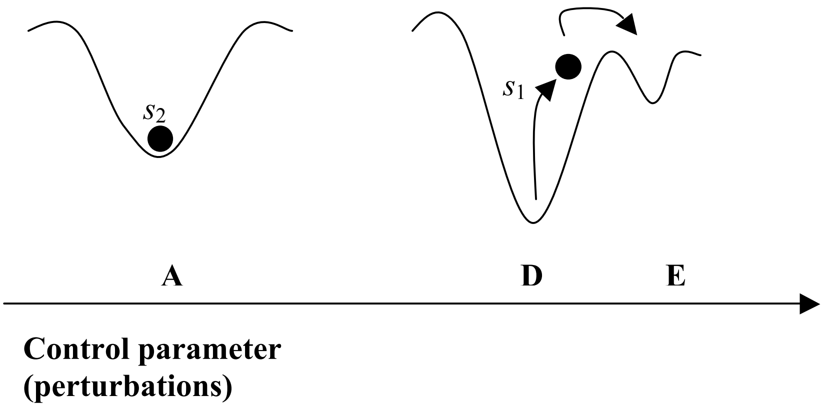

Figure 6: Wells of attraction and phase shifts

[Some morphologies are located in a region of the parametric space that guarantees them a high degree of stability in spite of the perturbations of the morphogenetic parameters. They occupy a 'well of attraction', as it is the case of population $\mathbf{s_2}$ within phenotype **A**. On the contrary, some other morphologies are in positions that render them highly unstable and exposed to radical changes with a minor perturbation of a single parameter. This is the case of population $\mathbf{s_1}$, at the edge of undergoing a 'phase shift' within phenotype **D** to phenotype **E** (based on Thelen & Smith 1994: 64).]

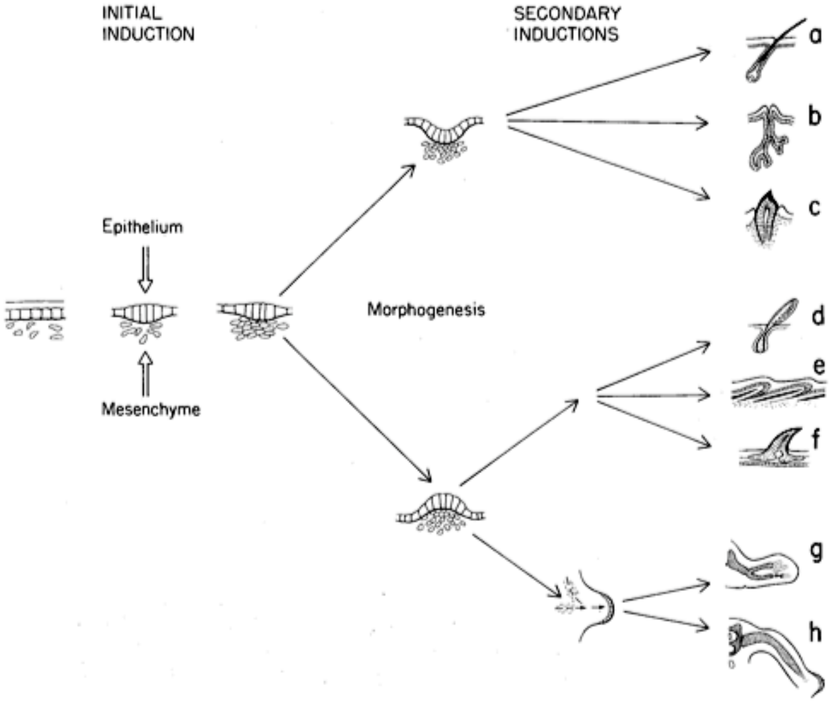

Figure 7: Morphogenesis of dermal organs

[The skin is made of structures (hair, salivary glands, teeth, feathers, scales, limbs and carapaces, among others) that are discontinuous from species to species, in the sense that no structure can be said to be a transition form between any other two structures. However, they all originate in equivalent inductive processes having to do with the thickness of the epithelium and the concentration of the mesenchymal tissue. Depending on the elasticity and the strength obtained in each case, the epithelium can (i) invaginate, giving place to hair, glands and teeth, or (ii) evaginate, giving place to feathers, scales or carapaces. Thus, each structure is only accessible through perturbations acting upon a particular phenotypic stage in the course of development (see Odell *et al.* 1981 and Oster & Alberch 1982; the figure is from Alberch 1989: 47).]

From an evolutionary point of view, an important corollary of this model is that the geometry of parametric spaces, representing forces of an internal sort acting upon individual development, works as a very strong constraining force, capable of counteracting that of natural selection. As explicitly stated by Alberch, although this stance does not discredit the role of natural selection as a filter in the evolution of organic designs, it nevertheless strongly decreases the creative character that this mechanism has to the adherents of MES-oriented frameworks (Alberch 1980: 664, Oster & Alberch 1982: 455, Alberch 1989, 46–48, Alberch 1991: 16; see also Goodwin 1994: 143 and Wagensberg 2004: 125).

In this sense, Alberch's model connects to an old pre-Darwinian tradition known as Transcendental (or Rational) Morphology, with such illustrious repesentative proponents as Johann Wolfgang von Goethe (1749–1832), Étienne Geoffroy Saint–Hilaire (1772–1844), Richard Owen (1802–1892), and Isidore Geoffroy Saint–Hilaire (1805–1861); see Russell (1916). In spite of the unequivocal empiricist aims of this historical trend, interested in the formal study of organisms, its influence on the biology of the twentieth century was truncated because of the accusations of Platonism by MES-inspired historiographers (see Amundson's 2007: Part I analysis of this episode of the history of modern biology). It is our opinion that Alberch's ideas serve as a clear demonstration that the belief in organic types fits perfectly well with a materialistic world view, as far as the different types result from natural constrictions and cannot be said to be ideal or abstract ideas that are alien to a physical order of things (Amundson 2001, Love 2003).

In connection with this, Alberch emphasized the evolutionary interest of the study of developmental monsters (or teratologies), recovering a tradition also embraced by Transcendental Morphologists (see Figure 8 below); see especially Alberch (1991).[13] In Alberch's opinion, teratologies are demonstrative of the strength of development against the pressures of natural selection, in that they are, by definition, maladaptive. However, a teratology can be the basis of organic novelties with a potentially evolutionary import.[14] Furthermore, the range of possible teratologies seems to be very strictly constrained (for example, duplication, but not triplication, of structures is common in abnormal development). This fact points to the existence of strong constraining forces on development not directly coming from natural selection (see Figure 9 below).

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[13] See Geoffroy Saint–Hilaire (1822) and Geoffroy Saint–Hilaire (1832-1837).

[14] Alberch (1989: 28) points out that the evolutionary potential of teratologies can be rather limited. Anyhow, he observes that it would be an error to discard them as a possible source of raw material for the evolutionary process. In his own words (Alberch 1980: 656):

> The argument that most developmental anomalies are harmful, commonly used to 'discredit' the relevance of these 'mutations' to evolution, is fallacious. Most genetic mutations were once thought to be deleterious (presently it is recognized the most of them appear to be selectively neutral, but that does not affect my argument), however nobody doubts that they provide the raw material for evolutionary change.

Alberch's position is thus not far from that of Richard Goldschmidt (1933, 1940: 390–393): "Mutants producing monstrosities may have played a considerable role in macroevolution. A monstrosity appearing in a single genetic step might permit the occupation of a new environmental niche and thus produce a new type in one step" (Goldschmidt 1940: 390).

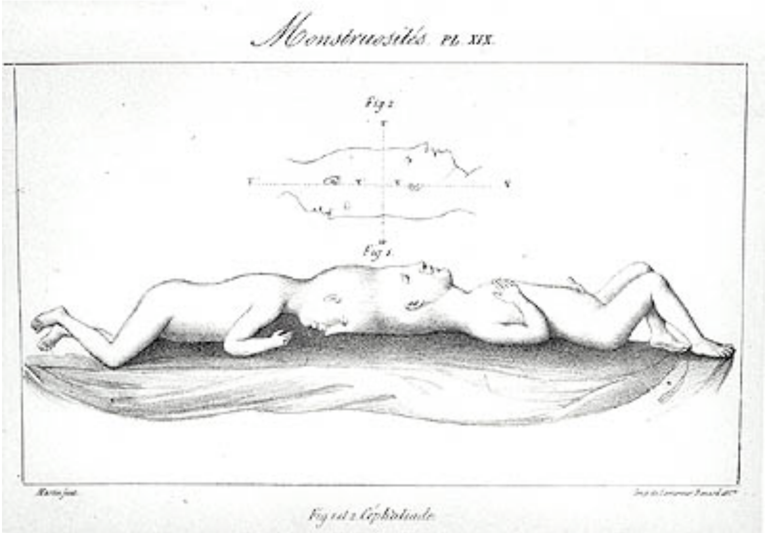

Figure 8: The logic of monsters (I)

[“After having studied anomalies in their special conditions and established the laws and general relations underlying all particular facts, I will demonstrate the way in which these laws and relations are but corollaries of even more general laws of organization; […] the way in which […] many principles established on very weak evidence find in anomalies a complete demonstration. And the way in which teratology, among its many concerns, covers every single condition of the organization of life” (Geoffroy Saint–Hilaire 1832–1837, vol. I: xi; our translation — SB & GL).]

Figure 9: The logic of monsters (II)

[“Monsters are a good system to study the internal properties of generative rules. They represent forms which lack adaptative function while preserving structural order. An analysis of monsters is a study of pure form” (Alberch 1989: 23). “These major deviations from normal development result in forms that are often lethal, and always significantly less well adapted than their progenitors. Therefore, one expects monsters to be consistently eliminated by selection. This is a useful property because if, in spite of very strong negative selection, teratologies are generated in a discrete and recurrent manner, this order has to be a reflection of the internal properties of the developmental system” (Alberch 1989: 28).]

Anyway, Alberch did not contend that natural selection was to be deprived of any creative role in evolution. Actually, he noted that natural selection biases evolution just by filtering out those designs unable to withstand populational and environmental pressures, thus having the effect of directing the process towards the morphologies accessible from the selected designs. Therefore, natural selection is continuously determining the probability of the presence of certain organic designs at future stages of evolution, an unequivocal creative intervention on the evolutionary process (Alberch 1989: 46 and Maynard Smith *et al.* 1985: 270).

3. The Evolution of Grammar through the Development of the Mind

"If the ideas that make up Evo–Devo have been so productive in opening up new lines of investigation into morphological evolution, they may be equally productive for psychological evolution". These words by Paul Griffiths (2007: 196) are particularly well suited to mark the transition of our work, so far devoted to an exposition of the theoretical underpinnings of Evolutionary Developmental Biology in the field in which it has become a mature scientific discipline — that is, in the field of the evolution of the formal patterns followed by organisms, to the study of a specific aspect of the evolution of human cognition.

Griffiths reminds us that, inasmuch as cognition is just another dimension of the organic world, there is no principled reason for not extending the core theses of Evo–Devo to this domain. Indeed, to the extent that we eschew any hint of 'mind/body' dualism, the fact is that there exists a perfectly natural path to extend and apply these ideas to the field of the evolution of mind. Taking then what in any case appears to be the most logical assumption, if what we call 'mind' — or 'cognition', as, for the purposes of this article both terms can be taken as synonymous — is nothing else than what "the brain does", to use a well-known expression by Searle (1985), it is obvious that the study of the morphological evolution of the brain is a first step towards the evolutionary study of mental functions. It is also clear therefore that the evolutionary study of the brain qua organic structure and, specifically, the evolutionary study of its formal diversity among the species endowed with complex nervous systems presents itself as a natural field of application for Evo–Devo.

It goes without saying, however, that the evolution of brain morphology is just a part of a broader Evo–Devo agenda, aiming at the investigation of the evolution of mental functions. In this sense, it may be useful to distinguish three different levels of analysis, all involved in the study of such functions, and briefly to consider in these preliminary remarks their positions within the kind of evolutionary explanations specifically devoted to the phenomena of development. The three levels are: (i) brain anatomy, (ii) brain function, and (iii) observable behavior.

As for the first level (brain anatomy), we already pointed out that, for Evo–Devo, it just is a specific area of application within its broader research program centered on the evolution of formal organic patterns. As a matter of fact, there already exists a number of very interesting findings, such as those reported in Parker *et al.* (2000), Falk & Gibson (2001), and Minugh–Purvis & McNamara (2001), for example, just to restrict ourselves to the evolution of the primate brain.

As for the second level (brain function), this is where most problems traditionally associated with the study of mind are concentrated. In this work we will assume, as already pointed out, that when talking about the mind we are talking about the functions related to brain activity. Therefore, this level adds up a new level of analysis whose phenomenology goes way beyond the mere facts of brain morphology. Nevertheless, the fact that, at this level, most theoretical approaches tackle the study of brain function abstracting away from its physical realization does not mean that it is really abstract and with irreducible properties to its material base.[15] Thus, we share point of view of Noam Chomsky, who in his works has argued that framing an explanation on a strictly physicalist language or using an abstract vocabulary to talk about these matters is just a mere question of perspective, and that decisions must be made simply on the basis of practical issues, such as the accessibility to observation of the considered domain or the significance of directly observable data (see, for example, Chomsky 1980). Also, from the Chomskyan point of view, similar considerations dictate that in the study of higher cognitive functions in humans there often prevails a computational and more abstract approach. Whatever the most convenient or just possible approach that one may take, the truth is that the exploration of the putative modifications in brain function regarding such aspects as the timing of the onset and stabilization of brain development, its maturation rhythms, the alteration of intermediate states or of the terminal state, and so on appear to us as topics which fit perfectly well within the Evo–Devo agenda.

Finally, we come to the study of observable behavior, which for a long time was the alibi of twentieth-century behaviorist psychology to attain the kind of scientific respectability imposed by the dominant positivist ideology in the philosophy of science. Curiously enough, Amundson (2006) suggests that transition of theoretical psychology towards a more cognitivist approach is, historically, comparable to the deliverance of Evo–Devo from the narrow-minded perspective imposed by the MES. In both cases, so Amundson argues, we observe a transition from an approach focused on environmental conditioning factors to a perspective where the search for internal constraints prevails. As Amundson himself suggests, such a situation may well be interpreted in the sense that both Evo–Devo and cognitive psychology are the products of the same *zeitgeist*, which should favor the convergence of both scientific approaches, along the lines of what we sketch in the previous paragraph.

All these considerations notwithstanding, we believe that the study of behavior must not be eschewed in order to favor only the study of internalist issues. As a matter of fact, the kinds of explanations based on the interaction among multiple domains which are generally favored within Evo–Devo make us believe (i) that in the application of this discipline to the realm of cognition none of the three aforementioned levels must be privileged over the others, and (ii)

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[15] But see the introduction to Fodor (1975) for an alternative point of view, and Churchland (1981) for the defense of a radically different stance from the one adopted in this paper.

that such an application may foster the formulation of complex interactions in different directions among these levels, such that these very same interactions may be seen as the *locus* of alterations in development with a potentially evolutionary significance (Figure 10). Indeed, the fact that specific environmentally induced alterations in the behavior of an organism during its development may be the basis of further modifications of the anatomic, physiologic and, eventually, genetic determining factors capable of inducing a new behavioral pattern is a non-problematic idea in the context of Evo–Devo and one that has contributed to vindicate certain models of change — such as 'organic selection' or 'genetic assimilation', which apparently stand in direct contradiction with the dominant genocentric logic of the MES, by letting in the Lamarckian ghost of the inheritance of acquired characters.[16]

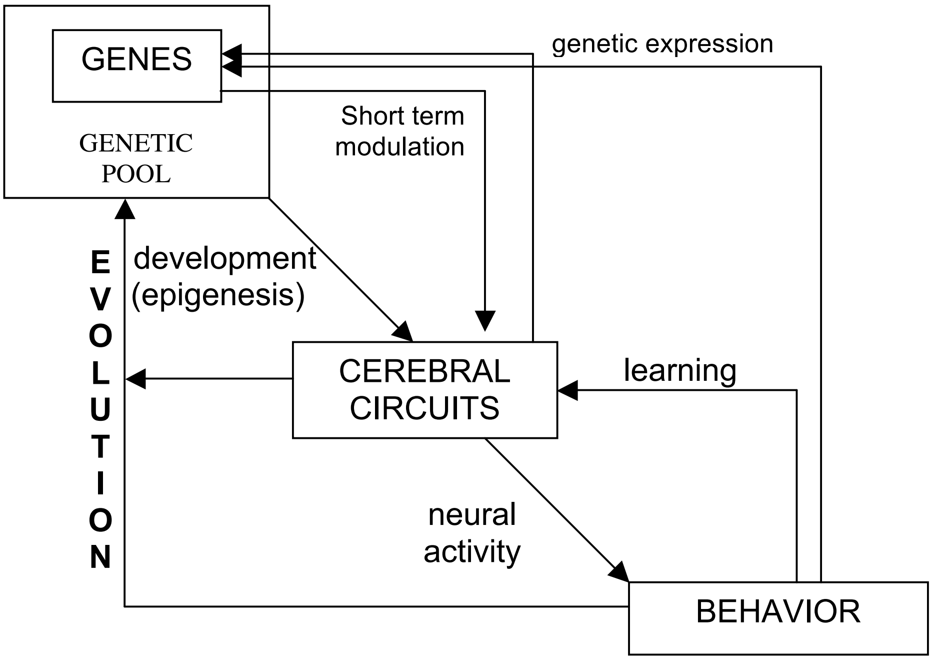

Figure 10: Evolution and behavior

[Interactive model with multiple levels of development and activity in higher organisms (based on Plotkin & Odling–Smee 1981; see also Johnston & Edwards 2002 for a still more complex model in terms of levels and interaction loops, and in terms of the specified morphogenetic parameters). In this model, the intergenerational recurrence of alterations within a specific behavioral pattern may have evolutionary repercussions, either through a novel redistribution of the dominant alleles in the genetic pool of the population ('genetic assimilation') or through the selection of new mutations that occurred in it ('organic selection').]

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[16] For a synthesis of these ideas and models, see Gottlieb (2003: 14–23). The original references for each of them are Baldwin (1896), Morgan (1896), Osborn (1897), and Waddington (1953), respectively. Longa (2006) is an interesting clarification of the ideas of these authors, often wrongly identified in certain recent applications of the so called 'Baldwin Effect' to the evolution of language. Jablonka & Lamb (1995) is a recent vindication of the 'Lamarckian dimension' in evolutionary biology.

3.1. *The Evolution of the Brain through Development*

The application of the Evo–Devo assumptions to the particular case of a species' psychological endowment in essence implies trying to find out what alterations in the development of the mind/brain of the organism might be capable of introducing into the population to which the organisms in question belong a heritable variety, eventually capable of making them fitter with respect to the rest of the population. In the light of the ideas exposed in Section 2 of this article, if we are to find any illuminating answers, this task involves taking into account the following four key points:

(A) Identify the morphogenetic parameters which make up the developmental system of a particular feature of the mind/brain;

(B) identify the control parameter or parameters whose perturbation acts as a trigger for change;

(C) specify the constraints imposed by the developmental system itself, defining parametrical spaces of possibilities; and

(D) elucidate the populational and environmental conditions capable of filtering the distribution of phenotypes within the population and favoring the resulting solution of the process of change in question.

That said, we will devote the following paragraphs to briefly discussing a number of important contributions connected to the issue of the study of the evolution of human cognition in any of its dimensions (i.e. structure, function, and behavior). As we already hinted in section 2, all share the assumption that one form or another of 'heterochrony' is the basic mechanism able, just as in the case of morphology,[17] to explain the evolution of the human nervous system and cognition, which would thus be a product of some alteration in timing and/or intensity of development of closely related species (Table 1).

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[17] As stated by Gould (1977: 4):

> Evolution occurs when ontogeny is altered in one of two ways: when new characters are introduced at any stage of development with varying effects upon subsequent stages, or when characters already present undergo changes in developmental timing. Together, these two processes exhaust the formal content of phyletic change; the second process is heterochrony.

Heterochrony. Evolution through changes in developmental timing and intensity. Types:

1. Paedomorphosis (underdevelopment or terminal truncation). Subtypes:
    - 1.a. Reduced rate of development (neoteny);
    - 1.b. Earlier offset (progenesis); and
    - 1.c. Delayed onset (postdisplacement).
2. Peramorphosis (overdevelopment or terminal extension). Subtypes:
    - 2.a. Increased rate of development (acceleration);
    - 2.b. Delayed offset (hypermorphosis); and
    - 2.c. Earlier onset (predisplacement).

Table 1: Heterochrony: Definition and types

[Based on McKinney (2000) and Parker & McKinney (1999); other sources: Gould (1977), McKinney & McNamara (1991), and Alba (2002).]

In the study of the evolution of mind, brain structure as the result of transformations that have occurred in the ontogeny of organisms is the most studied area. This is not at all surprising, as it is the domain which stands closest to the typical body of applications of Evo–Devo. As a consequence of that, one may take as an established fact, for example, that both larger brain size and connectivity rate among its components (especially, but not exclusively, at the cellular level) may result from alterations at very early stages of embryonic development. In this connection, Kaskan & Finlay (2001) point out that an increased rate of production of precursor cells or an extension of cytogenesis during embryonic development may result in significant differences in brain size. These authors, in fact, define ‘cytogenesis’ as the period spanning from a point where production of precursor cells of some structure starts to the point where a maximum of cell division obtains and the resulting cell does not divide but ‘migrates’ to the forming structure (Kaskan & Finlay 2001: 17). They note moreover that in the development of different brain structures from the neural tube of mammals one observes clear displacements once the highest point of such asymmetric terminal divisions is reached. Finally, they also contend that in each case the resulting neural population grows exponentially with respect to the displacement of this peak (Figure 11).

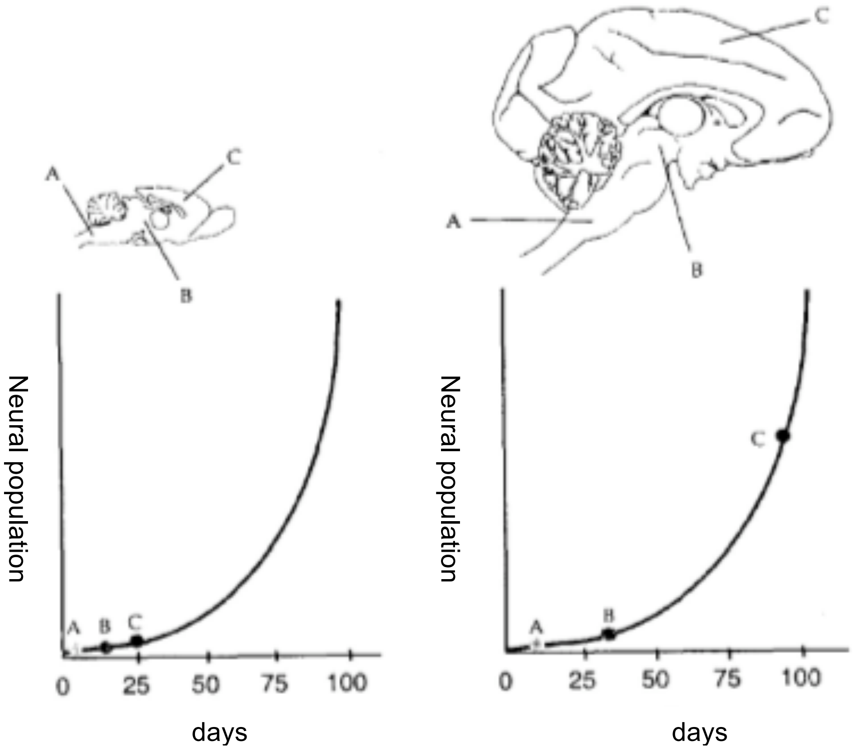

Figure 11: Extension of cytogenesis and exponential growth of brain structures

[The temporal extension of this 'summit' of asymmetric cellular divisions causes an exponential increment in the population of resulting neurons. The charts above show how such displacement is generalized in the cytogenesis of different brain structures in primates (right) compared to the homologous structures in rodents (left). They show moreover that a greater displacement in the formation of the cortex (**C**) results in an increased neural population for this structure, much larger than that for other structures, such as the spinal chord (**A**) or the basal anterior brain (**B**); this increment has an exponential character. (Taken from Kaskan & Finlay 2001: 20.)]

Rakic & Kornack (2000), for their part, offer some interesting quantifications. They point out that the phase of asymmetric cell division yielding to neural cells (that is, the phase to which peak Kaskan & Finlay refer to) starts in monkeys some four weeks later than in mice, which entails an extension of the period of symmetric cell division, where the majority of neural precursors are produced. According to the data presented by these authors, as a result of this displacement on the onset of a characteristic phase of embryonic development, the population of neurons in monkeys doubles that of mice. Moreover, as Rakic & Kornack (2001: 45–46) point out, in the case of humans the onset of asymmetric cell division is displaced only a few days later than that of monkeys, but, given the exponential effect of such displacement on the production of neural precursors, the population of neurons in humans is estimated to be between some eight or sixteen times larger than that of monkeys. In the light of these data, the authors conclude that the mutation of some regulatory gene (or a collection thereof) may have been responsible for the reorganization of the neo-cortex and of the cognitive and behavioral novelties associated with it (Rakic & Kornack

2001: 46).[18]

It must be taken into account, however, that this is not the only known difference in the developmental pattern of the human brain as compared to that of monkeys. Parker & McKinney (1999) and McKinney (2000), for example, contend that (i) fetal growth of the human brain is 25 days longer than that of monkeys, (ii) myelinization of the neo-cortex (and, especially that of the frontal cortex) is extended in humans until the age of 12, whereas in rhesus monkeys it lasts only 3.5 years, or (iii) dendritic growth is extended in humans until the age of 20, well beyond that of any other of its close kindred species. All these cases have to do with factors affecting the neural interconnectivity rate and their combined effect must no doubt have some far reaching consequences, as explicitly argued for by Parker & McKinney (1999) in their comprehensive comparative study of cognitive development in monkeys, apes and humans.

It is also relevant to point out, however, that the alterations of developmental phases with direct repercussions on the proliferation of neural precursors or on the interconnection of the resulting neural populations cannot bring about a totally unconstrained type of growth or of brain reorganization. Metabolic and energetic limitations aside — which are in any case an important factor in limiting brain capacity — Hofman (2001) reasons that certain aspects of the *Bauplan* followed by the primate brain impose limiting constraints on its evolutionary potential. He points out, for example, that the exponential character of the increment of the cortical mass with respect to cerebral mass as a whole is not observed in other brain structures (all playing a relevant role in regulating cortical connectivity, such as the cerebellum, the basal ganglia, etc.), where growth follows a linear pattern. As a consequence of that, the more the brain grows, the more disproportionate is the relation between cortical mass and these structures, which will eventually be inadequate for processing the same kind of complex information the cortex would be able to process (Hofman 2001: 115–119). Besides, Hofman contends that there are limitations on axon length which may cancel out the effects of an increased cortical mass, for the simple and practical reason that it could not be supplied with the appropriate wiring to ensure the connection between areas distant from each other in the cortex. Hofman points out that this may be the underlying cause for the compartmentalization of the cortex into specialized areas or modules within which highly interconnected neurons are concentrated.[19] A disproportionate growth of the brain would, in any case, bring the issue back to the level of inter-modular wiring which is necessary to support the characteristic flexibility of human-like cognition (Hofman 2001: 119–124).

Findings such as these provide additional support to the idea that alterations in brain development may be at the basis of the evolution of human cognition, and that factors such as the significance of genetic regulation as a

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[18] In this connection, we find promising some recent findings pointing at genes which regulate certain phases of brain growth (see Dorus *et al.* 2004). In connection with some of them, like *Microcephalin*, relatively recent mutations specific to modern humans have also been identified (see Evans *et al.* 2004 and Evans *et al.* 2005); for a comprehensive overview of the genes implied in brain development and growth, see Benítez Burraco (2009: chap. 3).

[19] See Griffiths (2007) for a defense of the concept of 'modularity' in the application of Evo–Devo to the study of mind.

particularly relevant control parameter, or the role of allometry as a constraint on possible phenotypic spaces constitute a serious hypothesis and are of major importance in this research. Unfortunately, they are rather uninformative at the time of concocting an explanation at the level of the resulting mental functions and their reflection on specific behavioral patterns. This point is not only relevant for the definition of parametric spaces of brain functionality, but also because, as we already pointed out, the identification of some specific population within one space or another may in turn have repercussions on the evolution of the morphogenetic parameters delimiting these spaces.

In this connection, and deserving of special attention, there already exists an important line of research focusing on the study of mental function as a result of alterations in developmental systems which adopts a comparative perspective similar to that of the works cited above.[20] Thus, for example, Langer (2000) compares physical and logico-mathematical intelligence in humans, chimpanzees and monkeys, whence he derives a series of conclusions about the onset and culmination of the development of such cognitive abilities in these species and, additionally, about the relative intensity of its progress in each case. The most fundamental conclusion derived from this comparison is that, evolutionarily speaking, there appears to have occurred an early onset and an acceleration in the development of these cognitive dimensions (particularly pronounced in the case of logico-mathematical intelligence), as well as a synchronization of the processes involved, favoring a mutual inter-penetrability with clear repercussions on how the surrounding world is conceived and explained. Langer specifically points out that the emergence of physical intelligence takes place early in all cases, but logico-mathematical intelligence in monkeys appears only after maturation of the former has been completed; this happens only a bit earlier in chimpanzees, while in humans both processes are entirely synchronized. Langer moreover contends that certain particularly complex aspects of human cognition, such as the ability to perform specific mental operations in an integrated and simultaneous way (e.g., deal with two sets of objects, compare them and redistribute their elements to make them identical) are an effect of this pattern of premature, accelerated and synchronized development of the aforementioned abilities. Lastly, Langer observes that the development of these abilities in humans goes well beyond that of the species taken as a point of comparison, which takes him to speak about a model of cognitive evolution through "overdevelopment" or "terminal extension" (Langer 2000: 229). As he himself emphasizes, this conclusion is particularly interesting, since it is consistent with the hypothesis of a parallel process of overdevelopment at the level of brain structure, with an equal involvement of different aspects of brain anatomy (extended growth of glial cells, axon myelinization, synaptogenesis, and dendritic growth in the cortex) (Langer 2000: 227). As a whole, this is clearly an important step in the establishment of bridges between the neural and the mental levels.[21]

The next section of this article may be seen as an attempt to put forth some

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[20] See also the work by Parker & McKinney (1999) cited above, as a key reference in this direction.

[21] See Gibson (1990, 2004) as additional representative references in this direction.

concrete proposals within this same line of thought regarding human cognition as an effect of the evolutionary history of its developmental pattern. We try to bridge the gap as much as possible between the physical and functional levels of analysis. We will be concerned with a particular aspect of the human mind, namely the computational system associated with the FL. We will more concretely explore the kinds of morphogenetic perturbations that may be the cause of its origin; also, and from a representational and abstract perspective, we will suggest a localization for such a system within a parametric space of possibilities, and the network of bifurcations leading to the position that it occupies today. Finally, we will also suggest some ideas about the environmental and populational conditions that may have made this system possible, while filtering out other alternatives within the same parametric space.

3.2. A Model of the Evolution of the Nervous System and Cognition: Parametric Space and Computational Phenotypes

As was mentioned at the end of the preceding section, there are not very many proposals where an explicit connection is established between the development of new neural structures and novel cognitive abilities. In this section, we will try to tackle this problem by sketching a proposal built on the principles of Evo–Devo, where we apply Alberch's notion of parametric space to different possible phenotypes of the nervous system and where we associate each possible phenotype with specific computational properties.

To the extent that "development of form cannot be straightforwardly related to genetic change, because the relation of function to new morphologic structures is not simple or direct" (Edelman 1988: 156), any proposal along these lines should, on the one hand, seek to determine what morphogenetic parameters make up the developmental system and, on the other hand, define the space of possible phenotypes on the basis of each and every parameter of the system. For expository reasons we will, however, limit ourselves to representing parametric spaces on a bi-dimensional plane, adopting Alberch's convention of considering only two 'abstract' parameters — x and y — from which one should be able to define the phenotypes in question. Additionally, and despite the considerable progress in the study of the different factors involved in embryonic development in general and in the development of the nervous system in particular, it would at present be practically impossible for us to precisely pinpoint all these factors: The fact is that many important aspects of the process still remain a mystery. We can nevertheless assert that these factors are not only and exclusively of a genetic nature and, as is made explicitly clear in the proposed models (see, for example, Edelman 1988, for development in general, and Edelman 1987 and Ebesson 1980 for the development of the nervous system), such factors cover a wide spectrum of elements. For example, in Edelman's topobiologic model, the main developmental processes are cell division, cell movement, and cell death, the driving forces of the whole process, with cell adhesion and differentiation acting as regulatory processes. It is important to point out, however, that these processes, which are responsible for building and giving form to an organism, are the result of a complex balance between genetics and epigenetics. Indeed, as emphasized by Edelman (1987: chap. 4), the development of the brain is one of those cases where special attention must be paid to epigenetic mechanisms, since, although the anatomical structures in specific brain areas in individuals belonging to a particular species are very similar and therefore their development must obey some specific genetic constraints, it is also true that an extremely high degree of variation is observed at the levels of neuronal morphology and neural patterning, especially at the level of axonal and dendritic branching. It goes without saying that such a degree of variation can only be the result of epigenetic factors acting during development on what Edelman calls the "primary repertoire" with a genetic basis (but also variable). As the process moves forward, new elements of variation are introduced, particularly at the synaptic level, in the form of changes in the biochemical structure and the appearance of an increasing number of different neurotransmitters. It is obvious, then, that a process of this kind possesses enormous potential for the introduction of morphological novelties, and even more so if we factor in the possibility that it be affected by some kind of heterochrony altering developmental timing and rate of growth.[22]

A developmental system of this kind, with a high creative potential, is not, however, totally unconstrained. Remember, in this respect, Hofman's (2001) considerations about the structural and connectivity restrictions that constrain the space of possible phenotypes for the nervous system of an organism, and which are, moreover, the kinds of constraints over form alluded to by several scholars since the beginning of the nineteenth century as the basic ingredient to explain the phenomenon of form.[23] In accordance with this stance, we understand that it is perfectly licit to assume that the developmental system of the nervous system defines a finite set of possible phenotypes, in such a way that a specific organism might have access to any of them, should the necessary perturbations to remodel it or relocate it in a new position occur. In addition, and coming back to our discussion concerning the different levels of analysis in the study of cognition, we propose to extend such distinctions to the realm of parametric spaces, such that, in parallel to the morphological parametric space, another parametric space would exist with what we may call a collection of 'cognitive phenotypes', where to every phenotype in the space of forms there corresponds a unique cognitive phenotype.[24]

Even though an exhaustive and detailed characterization of all the defining properties of a specific morphological phenotype is impossible, at least we have

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[22] See Edelman (1987: chap. 6) for a concrete proposal along these lines.

[23] The most significant — and radical — representative of this line of thought is, without doubt, D'Arcy Thompson (1860–1948), who presented his ideas in his monumental *On Growth and Form* (D'Arcy Thompson 1917). It is possible, however, to identify similar ideas in the thought of earlier authors, such as Richard Owen (see Owen 1848: 102–106) and, in particular, William Bateson (1861–1926) (see Bateson 1894). Webster & Goodwin (1996) is perhaps the most comprehensive an detailed exposition of the theoretical and empirical underpinnings of contemporary 'Generative Biology'; see also Goodwin (1994).

[24] Note that it is not strictly necessary that the number of morphological phenotypes be equal to the number of cognitive phenotypes. In fact, we deem it perfectly reasonable to assume that this is not the case and that a single cognitive phenotype may be associated with more than one morphological phenotype or, in other words, that different morphologies may be susceptible of an identical abstract characterization.

at our disposal a powerful theoretical tool that makes it possible to identify its main features at the computational level, and to elaborate concrete proposals about what structures and neural organizations could be associated with these properties. In concrete terms, we will assume that the parametric space of cognitive phenotypes contains a minimum of four phenotypes, in direct correspondence with the four levels of computational complexity of the Chomsky Hierarchy (Figure 12). We speak of a minimum of four phenotypes, because we will for the moment stick to the original version of the Hierarchy (Chomsky 1959). We are perfectly aware, however, that at a later date new levels were added to it. For example, Chomsky himself argued soon after for the necessity of distinguishing between strict context-sensitive systems and systems capable of generating any recursive system (Chomsky 1963); Aho (1968) described indexed systems within the complexity space originally reserved to type 1 systems (see also Hopcroft & Ullman 1979: chap. 14), whereas Aravind Joshi and collaborators (see Joshi 1985, Joshi *et al.* 1991, and Vijay–Shanker & Weir 1994) added new compartments to this space with the extended context-free systems or, alternatively, mild context-sensitive systems. What follows, however, does not particularly hinge on the exact number of phenotypes (although we will come back to these new developments) and, for ease of exposition, we will stick to a parametric space with four phenotypes, without forgetting that human language would be somewhere within the 'lower' area of type 1 systems.

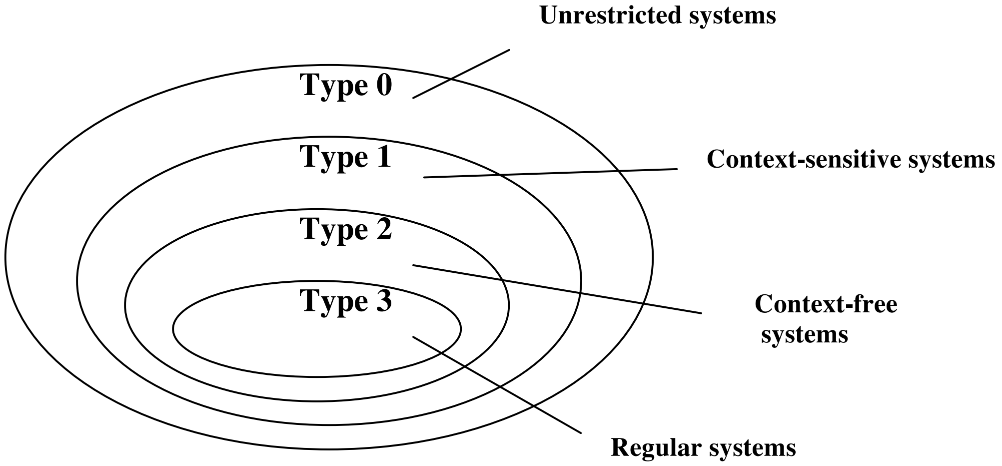

Figure 12: The Chomsky Hierarchy (Chomsky 1959)

[The Chomsky Hierarchy defines a scale of systems with an increasing generative power, and capable of generating different types of recursive sets whose elements show increasing levels of complexity (type 3 to type 1), and, eventually, any type of recursively enumerable set (type 0).]

In Figure 13 we sketch our proposed parametric space of cognitive — or, better perhaps, computational — phenotypes. In the figure, we label the phenotypes as FC_3, FC_2, FC_1, and FC_0 in correspondence with the four levels of the

Chomsky Hierarchy; with arrows we indicate the possible transitions between one space and another.

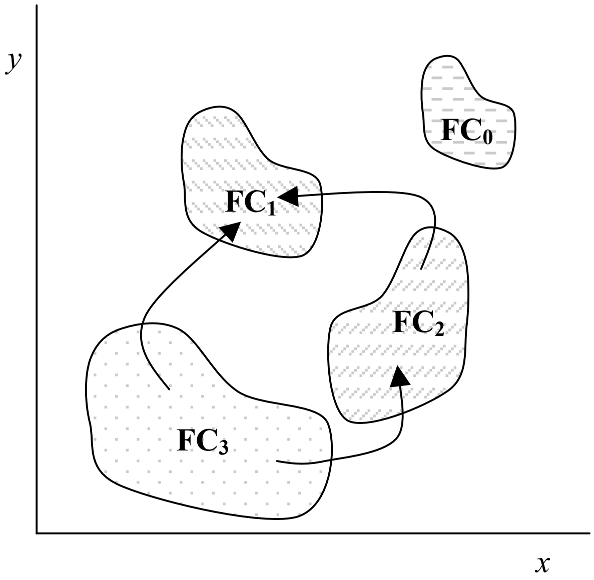

Figure 13: The parametric space of Chomskyan computational phenotypes

[Each computational phenotype occupies a specific area within the space brought about by the interaction of the morphogenetic parameters involved in cognitive development (here just two idealized parameters *x* and *y*). Once one or more parameters — the control parameter(s) — attain some critical value, the conditions are met for a 'jump' (arrows) within the space of possibilities. This kind of figure (which Alberch also used in his writings) differs slightly from the one we used before for representing parametric spaces (Figure 5), because it remains silent as to the relative probability of a jump from one phenotype to another. The larger or smaller surface of a phenotype still represents, however, its greater or smaller relative stability and, consequently, the probability of its occurrence. Finally, as for the absence of arrows pointing toward the FC$_0$ phenotype, this is our way to capture the idea that there may not exist any possible developmental path leading to it. Contrary to what it may seem at first blush, this is not at all problematic. As pointed out by Rasskin–Gutman (2005: 214–215), we must distinguish between (i) a 'theoretical morphospace', including possible (both actual and potential) and impossible phenotypes, and (ii) an 'empirical morphospace', excluding the latter. Its exclusion is justified by natural limitations on the parametric factors involved.]

Note, then, that, despite the fact of not having a precise characterization of phenotypes at the morphological level (but see section 3.3 below for some proposals in this direction), we do have a precise computational characterization of our computational phenotypes. In fact, whatever the specific morphological properties of a phenotype, we know that, if it is associated with phenotype FC$_3$, its computational power will be equivalent to a finite-state automaton; if it is associated with FC$_2$, it will be equivalent to a push-down automaton; if it is associated with FC$_1$, it will be equivalent to a linear-bounded automaton; and, finally, if it is associated with FC$_0$, it will be equivalent to a Turing machine.

Observe, moreover, that the parametric space of cognitive computational phenotypes possesses the very same properties as the morphospaces proposed by Alberch in his works. That is, it shows a non-continuous distribution of phenotypic variation, with discrete and easily identifiable states. Thus, the transition from one state to another is, in fact, a 'jump' that is only made possible once a specific critical point is attained (possibly as a result of the accumulation of small gradual changes). As a consequence, just as in Alberch's model there is no sense to be made of the phrase "being between phenotype A and phenotype B", in ours one cannot describe a system whose computational regime is somewhere in between, say, a finite-state system (FC_3) and a context-free system (FC_2). It is nevertheless important to take into account that, as already pointed out by Bateson (1894), the fact that there is discontinuity in *variation* is not in contradiction with the idea of gradual change at the level of *processes*; this is, in fact, a fundamental feature of the concept of 'critical-point emergence' to which we shall appeal here (see Reid 2007: chap. 8, for details). According to our proposal, then, the evolution of what we call 'the computational mind' would have consisted in a historical process where complex interactions among genetic and epigenetic factors during the individual developmental process of the nervous system would have given rise to qualitatively differentiated phenotypes via a sequence of 'critical-point' emergent processes. Such phenotypes would have been able to act as the material support for richer computational regimes, and one of these 'jumps', the one leading to a computational regime of type 1 (FC_1), would have been the one that made possible the emergence of human language.

Before sketching our proposal for an evolutionary scenario, to which we turn presently, we would like to devote some space to describe some of the most important properties of the different systems and of the different computational regimes capable of generating them. We shall begin with the less relevant ones (type 0 systems), which will additionally serve as a justification for our having relegated them to the realm of impossible phenotypes within theoretical morphospace. Next, we turn to the remaining cognitive phenotypes, much more relevant for our purposes.

Chomsky (1959: 126–127) has already pointed out that we could not learn much about language if its elements are specified in the form of "such 'unstructured' devices as general Turing machines". In order to grasp the essence of this assertion, it may be relevant to recall some basic aspects of the mathematical theory of recursive functions, to which the theory of computation is intimately related.[25]

Remember, first, that, as stated in the caption of Figure 12, a Turing machine has the power of generating *any* recursively enumerable set, that is, any finite or infinite set that may be put in a one-to-one relation with the set N of natural numbers. This implies that, if some set A is enumerable, then a bijective function *f* exists assigning to every element of A an element of the set N, and, consequently, that the cardinal of A is, at most, $\aleph_0$, that is, equal to the cardinal of

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[25] To be precise, we should have written 'μ-recursive functions'. The thesis that μ-recursive functions and Turing machines are equivalent is traditionally known as Church's Thesis or the Church–Turing Thesis; on this topic and for a large part of what is discussed in the text, see Lewis & Papadimitriou (1981).

the set of natural numbers. The property of being recursively enumerable implies, therefore, the theoretical possibility of counting the elements in the set, such that all finite sets plus all infinite sets (or also the finite ones) sharing with N the (crucial) property of being *recursive* are recursively enumerable. This point is crucial, because, from the enumerability of a set one may not necessarily deduce its recursivity (although the reverse is always true: Any recursive set is enumerable). In this case, one must resort to a different class of recursive functions, namely those which, given an arbitrary element x, are capable of returning a result of 1 or 0 (or True or False), such that, if the result is 1, then $x \in$ A, and, if the result is 0, then $x \notin$ A. Note that, now, it is not a matter of *counting* the elements of a set, but of *deciding* (or *generating*) what are the elements of that set and, indirectly, those of its complement.[26] From this it follows that the set N of natural numbers is an ideal model to deal with these issues, since we know that it is enumerable (we can put it in a relation to itself to count it) and that there is a finitely definable procedure capable of generating it (for example, Peano's axioms).[27] The notion of a finitely definable procedure brings us to the point at which we can add a third fundamental element to Church's Thesis, which asserts that any μ-recursive function may be imitated by a Turing machine (and vice-versa). This third element asserts that a Turing machine may be imitated by a rewriting system or *grammar*, understood as a system of rules the recursive application of which allows us to put a string of symbols in a relation with another string of symbols.[28]

And thus we come to the point where Chomsky's words quoted above can be clearly interpreted. The family of rewriting systems equivalent to a Turing machine is the family of unrestricted rewriting systems, that is, those systems whose rules can put strings of an arbitrary length into a relationship with strings of an arbitrary length. With no constraints on the nature of rules, any rewriting system may be able to generate any set of strings of symbols, such that, for example, the set of all strings made up by the iteration of any instance of the symbol *a*, which we can abbreviate as a^* (any sequence of zero or more *a*s), might be generated by a system of rules like $S \rightarrow \varepsilon$, $S \rightarrow a$, $S \rightarrow aa$, $S \rightarrow aaa$, and so forth, where ε represents the empty string. Clearly, *this is not a finitely definable procedure* to generate the set a^*. This is perfectly natural for a computational device like a Turing machine, since it has, after all, an unlimited amount of time and space available to carry out its work; but it is not so for us, because what we want is a finite device for generating the elements of a set (such as, for example, the set of sentences of a natural language), and the simple fact that a set is recursively enumerable is not a guarantee of the existence of such a procedure. The only family of sets for which we know for certain that such a procedure exists is recursive

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[26] Which moreover implies that, if set A is recursive, both A and its complement are recursively enumerable, but not, of course, that the complement is also recursive.

[27] Or, to be precise, Peano's ninth axiom of his *Arithmetices principia* (1889) or Principle of Induction, which defines the successor function σ, such that $\sigma(n) = n+1$ for all $n \in N$, and which is one of the primitive recursive functions from which it is possible to define all other recursive functions, including the μ-recursive functions.

[28] What Church's Thesis states, therefore, is that the three ways of understanding the idea of computation — recursive functions, automata, and grammars — are strictly equivalent.

sets. This is not, however, the only problem posed by unrestricted rewriting systems, as — and returning to the case of the set a^* — we see that what we have just demonstrated is that a Turing machine is able to give an extensional definition of the set, that is, that it is able to enumerate each and every element of the set, but nothing else. This is what Chomsky refers to when he says that these systems are 'unstructured': A mere list of its elements tells us nothing about the properties of the elements of the set, when, in the case of natural language, for example, we are not only interested in knowing whether some sequence of words belongs to the language or not, but also, and above all, we want to know its internal structure. Again, the only systems capable of providing us with this information are those capable of generating recursive sets, to which we turn below.

The simplest computational devices are type 3 or regular systems, whose equivalent in the theory of abstract machines is the finite-state automaton. These systems have the power of generating sets of structurally very simple strings (or languages).[29] Thus, for example, the language a^*, which we encountered above, is regular, as are languages like a^*b^* (a possibly null sequence of *a*s followed by a possibly null sequence of *b*s), a^nb^m (a non-null sequence of *a*s followed by a non-null sequence of *b*s), and the language $\{a, b\}^*$ (that is, the one constituted by sequences of *a*s and *b*s of any length and in any order). A quick glance at these languages is sufficient to see that linear order is not a problem for this kind of system, as is perfectly possible to build grammars (or automata) capable of generating sequences where symbols follow a strict order; but this is not a sufficient guarantee of adequacy and for regular grammars to capture the complexities of natural languages. In fact, Chomsky, in a brief note (Chomsky 1956b), has already demonstrated that a language like a^nb^n (a sequence of *a*s followed by a sequence with the *same* number of *b*s) is beyond the generative power of a finite-state system. The datum to which we need to pay attention here is that the complexity of this new language has nothing to do with the relative order of both substrings, but rather with the fact that both substrings must be of the same length, which is equivalent to saying that there exists a dependency relation between both substructures. In other words, in order to be sure that both substrings will be of the same length, we need some device to keep track of the number of symbols used during the process of construction of the first substring, such that we can access this information while we are building the second one. In a nutshell, we need *memory*, a resource which is not available in a finite-state automaton. As Chomsky points out in the reference cited above, natural languages have plenty of this kind of dependency relation,[30] which automatically invali-

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[29] It is important not to confuse the term 'language' as we use it here in the context of formal language and automata theory, with the way we use it in the rest of this paper, which corresponds to its traditional meaning in the field of generative linguistics. In the former case, 'language' refers to a set of strings generated by a grammar; in the latter case, to the capacity of humans to produce and comprehend sentences. The equivalence is not precise, but assuming there is one, the 'grammar' of a mathematician is like the 'language' of a linguist, who pays little or no attention at all to lists of sentences and is more interested in the construction of grammars.

[30] Such as, for example, constructions of the *if… then*-type, or relative clauses, to name just two

dates the ability of finite-state systems to capture some of the most basic properties of human language.

In the light of these results — well known, as we have seen, since the 1950s — research in the field of the formal complexity of natural language turned its attention to type 2 and type 1 systems. This research was motivated, on the one hand, by what for some linguists was a premature quantum leap towards the development of transformational models, after Chomsky's rejection of context-free systems as adequate models for natural language grammars (see Chomsky 1957: chap. 5) and, on the other hand, because of some formal results that appeared to indicate that transformational models were equivalent to unrestricted rewriting systems (Peters & Ritchie 1973). Thus, around the mid-1980s, an important body of data was available, justifying, on the one hand, Chomsky's dismissal of type 2 grammars (see, in particular, Bresnan *et al.* 1982 and Shieber 1985) but, on the other hand, showing that the necessary expressive power was only slightly above type 2 systems, within a complexity space not identified by Chomsky when he defined his Hierarchy, and which Joshi (1985) named mild context-sensitivity.[31] Whatever the definitive position of natural language within the complexity scale, however, our main concern here is to characterize the differences between the different systems within the space between type 3 grammars and type 0 grammars. For this purpose, formal languages are a useful tool, since they help us to focus on specific structural properties and on the necessary computational resources to deal with them. Let's go back, then, to the language a^nb^n, which, as we saw, is not a type 3 language, but a type 2 language. Depending on the kind of structural description we want for, say, the string *aaabbb*, a context-free grammar offers us a number of alternatives, of which we only contemplate the following,

(1) $[a_i\ [a_j\ [a_k\ b_k]\ b_j]\ b_i]$,

where sub-indices indicate the presence of some dependency between the elements sharing the same sub-index. As we will see presently, the source of complexity is not in the number of dependencies, but in the relations among them. Note that in (1) dependencies are strictly nested, and a type 2 system is perfectly capable of dealing with constructions with multiple nested dependencies (or, for that matter, with sets of independent nested dependencies, that is, $a^nb^nc^md^m$, $n \neq m$, is also a type 2 language). As we pointed out earlier, the key is

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of them. Note, by the way, that what is important is not that both strings be of the same length, but that some dependency relation holds between two elements separated by an arbitrary long sequence of symbols. As we will see presently, the number and nature of these dependencies are critical factors at the time of assessing the degree of complexity of a language.

[31] Which, moreover, means that such expressive power would sit below that of indexed grammars. So far, only one objection with respect to these results has been presented in connection with the sub-system of Mandarin names for cardinal numbers, whose properties appear to be beyond the power of mild context-sensitive grammars (Radzinski 1991). It is significant, however, that this result is connected to number names, which, for some authors, may be indicative of some extra-linguistic factor not directly related to the real complexity of natural language; see Pullum (1986).

in memory, a resource that is available to a push-down automaton (our FC_2), but not to a finite-state machine (our FC_3). The push-down stack in a push-down automaton supplies the additional workspace where we can store those symbols we have generated (for example, three *a*s) and which we pop out as we add *b*s to the string: For each *b* we add to the string, we pop an *a* out of the stack, such that, when the stack is empty, the process is over. Given the structure of the stack, which follows a first-in/last-out regime, we can see that nested dependencies fall within the power of type 2 grammars since, when we write the first *b*, we pop out the last *a* that went into the stack, and so on, until the point at which we write the last *b* and pop out the first *a* we stored in memory. Suppose now that dependencies are organized as in (2):[32]

(2) $a_i a_j a_k b_i b_j b_k$

Note that in this case the dependencies are crossed, such that the first *a* is related to the first *b*, the second *a* with the second *b*, and so on. This kind of structure is beyond the processing power of a push-down automaton, as are more complex languages like $a^n b^n c^n$. Without for the moment going into great detail (but see Weir 1994 and Joshi & Schabes 1997: sect. 7), what we need here is a more powerful automaton, one we can get by just improving the capabilities of the memory system, extending and restructuring it such that it will be able to create additional stacks to store data any time that this is required by the computation.[33]

Thus, and on the basis of the preceding discussion, it is clear that the progression up the scale of complexity is a function of the changes introduced in the memory system, *with no other modification of any fundamental property of the computational system being necessary*. This observation puts us in a position not only of being able to characterize the phenotypes represented in Figure 13 in computational terms, but also of being able to determine the kinds of alterations of the developmental system which are necessary to 'jump' from one phenotype to the other. Therefore, assuming that we have a simple (but recursive)

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[32] This is the case of the cross-serial dependencies found in Dutch and in some varieties of Southern German, where the English construction *…that John saw Peter help Mary swim* may be expressed in Dutch as *…dat Jan Piet Marie zag helpen zwemmen*.

[33] This is an extremely intuitive characterization of the embedded push-down automaton, which is equivalent to a mild context-sensitive system. We are using this example here, instead of that of the linear bounded automaton, because as Weir (1992, 1994) has shown, push-down automata constitute a general model of automata, of which the classical push-down automaton (with one stack) and the embedded push-down automaton are only two particular cases, the simplest ones within a scale of increasing complexity definable exclusively in terms of improvements introduced in the storage system.

Weir's results in fact go well beyond that, since they can be generalized to the whole family of languages made up by type 2 and type 1 languages in the Chomsky Hierarchy and which constitute a natural class within the Hierarchy, sharing a number of interesting computational properties (e.g., recognition in polynomial time and decidability, among others). Weir's work defines a sub-hierarchy within the old hierarchy, in which we observe a progression towards higher degrees of complexity definable just in terms of the levels of embedding of the memory stacks (i.e. stacks of stacks, stacks of stacks of stacks, and so on), a particularly relevant mathematical result for the proposals we develop in this article.

computational system, we only need first to add some memory, and thereafter progressively to sophisticate this system of memory, in order to make the transition from one phenotype to the other possible ones, going up the scale of complexity and concomitantly acquiring the ability to execute computational operations of an increasing complexity (Uriagereka 2008). This is, in essence, the sketch of our proposal for the origins of the FL, which would be the product of an evolutionary process with the effect of increasing and ameliorating the system of memory available to an original computational system, until the point at which sufficient capacity was reached to give way to what today we know as language.[34]

3.3. *Steps towards the Identification of the Control Parameter and the Reconstruction of the Evolutionary Process*

The steps, certainly rather tentative, towards the definition of the control parameter identifiable as the main trigger of the developmental changes capable of causing the evolutionary process described in the previous section force us to picture a minimally realistic image of the computational system underlying language. With a precision number we will introduce below, we will assume a proposal quite similar to Lieberman's (2006) model of the 'basal ganglia grammar' (BGG).

Philip Lieberman's model is based on a fundamental distinction between:

(A) a *cognitive pattern generator*, whose inhibition/excitation mechanism is localized in the basal ganglia; and

(B) a *working memory space*, which is located in Broca's area.

(Lieberman 2006: 207–209)

These are, respectively, the sub-cortical (A) and cortical (B) components of a circuit which Lieberman defines in functional terms as an *iterative sequencing machine*, which is at work when we walk, talk or understand a sentence (Lieberman 2006). Assuming this global picture, we wish, however, to introduce a couple a qualifications about the adoption of this neuro-anatomical structure as the basis of our model for the computational system underlying language.

Firstly, basal ganglia comprise a complex anatomical structure which

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[34] As the reader may have already guessed, our hypothesis rests on two basic premises: (i) that Church's Thesis is true and (2) that the set of sentences of a natural language is recursive. Of course, there is no shortage of proposals denying either (or both) of the two premises above. For example, Penrose (1994) rejects (i) in favor of what he calls 'quantum computation' which, according to him, sits beyond classical computational models. As for (ii), Langendoen & Postal (1984) argue that the set of sentences in a natural language is not recursively enumerable (and, therefore, neither recursive nor enumerable), and that its cardinal is a transfinite number, that is, greater or equal to the cardinal of the set R of real numbers. In this case, any attempt to provide a computational characterization of the FL is doomed, because a non-enumerable set is, by definition, non-computable. Indeed, then, should any of these proposals turn out to be true, we would be out of the game — as would a large part of those who strive to unveil the mysteries of human cognition.

appears to participate in several cortico–subcortico–cortical circuits associated with the regulation of different aspects of mobility, cognition, and emotivity (Figure 14). Following Cummings (1993), Lieberman (2006: 163–167) estimates that the so-called 'prefrontal dorsolateral circuit' is the one involved in the programming of the motor control of speech, in sentence comprehension, and in other aspects of cognition. This circuit projects from this cortical area towards the dorso-lateral area of the caudate nucleus, the lateral dorso-medial area of the globus pallidus, and the thalamus which, in turn, projects back to the prefrontal cortex (Figure 15). We will assume, with Lieberman, that this is in effect the circuit that language uses as a computational system.

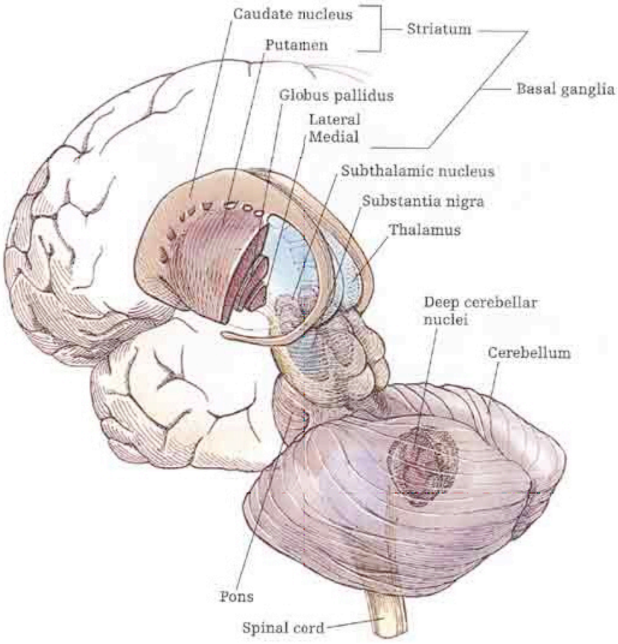
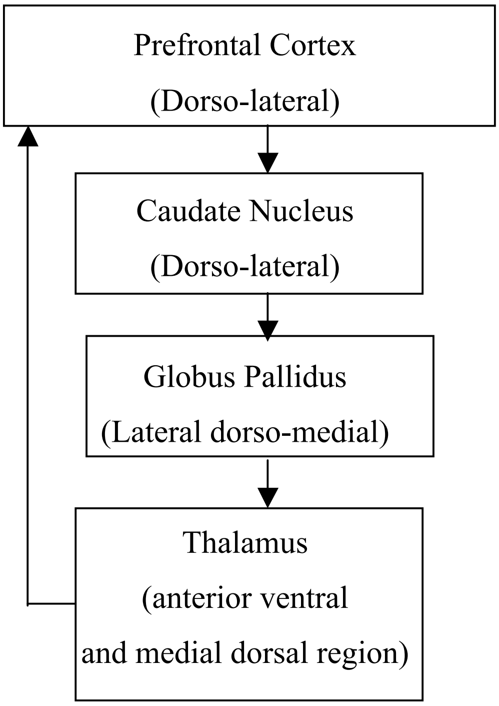


Figure 14: The basal ganglia

[The basal ganglia comprise a complex anatomical structure located in the inner brain, with numerous afferent and efferent projections among their own components and including the frontal cortex and the thalamus.]



Figue 15: Prefrontal dorso-lateral circuit
[The prefrontal dorso-lateral circuit is involved in the motor programming of speech, in sentence comprehension, and in other aspects of cognition. Other similar, and partially overlapping, cortico-subcortico-cortical circuits participate in other aspects of cognition and behavior. For example, a circuit projecting from (1) the prefrontal cortex towards (2) the striatum (caudate nucleus + putamen), (3) the globus pallidus and the substantia nigra, and (4) the thalamus which, in turn, projects back to (1) the prefrontal cortex, appears to be involved in affective modulation. (Based on Cummings 1993.)]

Now, and this constitutes our second qualification of the BGG model, we contend that limiting to Broca's area the localization of the working memory space is an assumption that oversimplifies. The involvement of Broca's area in the system of computations of the FL is unquestionable.[35] However, it is quite plausible that this structure is part of a larger cortical circuit with bidirectional projections between the frontal and parieto-temporal areas, within a system of working memory networks such as the one postulated by Aboitiz *et al.* (2006).[36] The matter is not entirely clear. However, for the purposes of this article, it is important for us to localize the working memory of the computational system within the cortical component, more or less large, of the anatomical structure making up such a system.[37]

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[35] See, among others, Embick *et al.* (2000), Grodzinsky (2000), Moro *et al.* (2001), and Musso *et al.* (2003).

[36] See also Aboitiz & García (1997). On the role of the frontal lobes in language processing, see the review by Friederici (2002), as well as the studies by Shtyrov *et al.* (2003) and Pulvermüller & Assadollahi (2007).

[37] For a partially divergent model, see Ullman (2004), where the assumption is made that the computational aspect of language utilizes a system of 'procedural memory' distributed

Our main thesis in this section is, as we already put forward at the end of section 3.2, that those perturbations which motivated the bifurcation of the computational system in the direction of context-sensitivity (FC_1) during human evolution have a direct connection with the development of the cortical structure supporting working memory. This idea is entirely justified if we take into account that the different levels of computational complexity making up morphogenetic space as defined in Figure 13 correlate with the capacity and the organization of the system of memory associated with the pattern generator. In purely formal terms, one goes up the hierarchy as memory gains capacity and, in terms of our evolutionary scenario, bifurcations occur within the morphogenetic space as a more developed cortical structure is available to support this. Within the framework of our proposal, however, no greater inter-specific differences are expected at the level of the system's pattern-generation procedure nor in the subcortical structure acting as its material support. As a matter of fact, from an evolutionary perspective the basal ganglia, as opposed to the cortex, have been described as highly conservative structures among amniotes (reptiles, birds, and mammals) (see Reiner *et al.* 1984).[38]

This thesis has a number of interesting consequences, to which we would like to devote some space. Firstly, it is our contention that the developmental event giving rise to the cortical structure serving as the physical support for the working memory space of the computational system is not an evolutionary event directly related to language. As we already noted above, the kind of brain growth which characterizes human evolution appears to be connected with the overproduction of precursor cells during cytogenesis, meaning that it is not a process oriented towards the production of one or another specific type of cell. Kaskan & Finlay (2201: 27) point out that, from the point of view of development, the brain is one of the few organs whose the development appears to follow a set rules affecting the organ as a whole. This observation is, in our opinion, particularly interesting, since it supports the idea that the perturbations giving rise to the higher level of complexity of the computational system subserving language do not seem to be, in any sense of the term, *adaptations* for this linguistic function, but rather that such a level of complexity is a mere side-effect of a more general process of brain reorganization which took place without specific motivation.[39]

That said, and along the lines of Rakic & Kornack (2001: 46), we are persuaded that the control parameter whose perturbations gave rise to the level of complexity necessary for language may well have been a regulatory gene (or a

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across the frontal and parietal cortical areas, the basal ganglia, and the cerebellum. In Ullman's model, however, no computational specializations between a sequencer and a working memory are assumed, and the basal ganglia are seen as responsible for the stimulation and inhibition of the memorized patterns across the whole brain circuit.

[38] Our proposal, therefore, has an important difference from that of Hauser *et al.* (2002) in the sense that, for us, the evolutionary novelty that made possible the emergence of language would not be, strictly speaking, recursion, but rather the ability to deal with recursive patterns via a higher level of complexity.

[39] For some considerations about this point, see Chomsky (1968: 124), Chomsky (1975: 74), or, more recently, Hauser *et al.* (2002: 1578).

collection thereof) responsible for the proliferation of neuronal precursors. A mutation in this gene (or genes) in humans would have had an effect of 'peramorphosis' or 'terminal extension' (or 'hypermorphosis') in cortical development which, even if minimal in terms of chronological timing, may have had far-reaching anatomical repercussions, given the exponential relation between the extension of cytogenesis and the development of brain structure (Figure 11).[40] With respect to this idea, however, it is important to make a couple of points clearer:

First, by pointing to a regulatory gene as the control parameter responsible for the evolutionary transformation we have just suggested, we are not denying that other morphogenetic parameters involved in the very same developmental system remained unchanged. On the contrary, the perturbation of the control parameter in question may well have triggered a whole chain of perturbations affecting other parameters, with obvious repercussions on the structure and function of the resulting phenotype. In this particular case, we can plausibly speak of a chain-effect affecting such factors as cortex myelinization or dendritic growth, for which also late termination effects have been observed (Gibson 1991). As was made clear in section 2.2, a control parameter is not a unique causal agent, but just the initial trigger in the chain of reactions giving rise to a new morphology.

Second, although a direct consequence of the late termination of the development of cortical structure, the mere gross increment in the population of neurons cannot be taken as an indication that the complexity level attained by the system is a direct function of the said increment. In this connection, it is important to take into account the general thesis of dynamic systems according to which there is no linear and simple relation between the morphogenetic parameters and the properties of the phenotype. Quite to the contrary, then, the most direct effect of a perturbation (in our case, the gross increment in the population of neurons) may trigger novel phenotypic effects which nevertheless need not imply the incorporation into the developmental system of new morphogenetic parameters. Particularly relevant for the case in point is Terrence Deacon's observation that larger brains will necessarily possess more laminated, more highly nucleated, more parcellated structures, and so on, just as a side-effect of the growth of the neuronal population with respect to brain size (Deacon 2000: 61). We understand that very plausibly these are factors capable of having a great impact on the kind and complexity of the operations the brain is able to execute.

There is another important question deserving further comment. According to our proposal, the level of complexity of the computational system of language would be explained in evolutionary terms as a particular aspect of a global perturbation in the developmental system of the brain, and not, therefore, as an episode in brain development directly selected for its advantages related to linguistic function. This is not to deny that, next to the global reorganization of the brain, other developmental events may have taken place directly related to the functionality of resulting structures of this global process of reorganization.

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[40] Along similar lines, see Edelman (1987), Finlay & Darlington (1995), and Deacon (2000).

As pointed out by Hofman (2001: 122–123), in fact, brain sub-structuring into anatomically and functionally specialized modular units is one of the effects derivable from the expansion pattern typical of its evolution, and, as Rakic & Kornack (2001: 49) add, this causes the introduction of novel organizational units and interaction pathways among these units which may later be targeted by natural selection.

In this regard, the human mutations of the *FOXP2* gene,[41] which have been the focus of various studies and interpretations in the last few years, may well find its way into our proposals. The function of this gene in the regulation and functioning of the brain structures which, following the BGG model, we identified with the computational system of language is a well established fact.[42] Remember, however, that our proposal singles out as the event responsible for the evolutionary change of this system the increment in the capacity of its working memory, which, in turn, we identified with the cortical component of the BGG. Thus, our suggestion puts special emphasis on the overdevelopment of the cortex, but less so — in evolutionary terms — on the basal ganglia. The idea is, therefore, compatible with our observations above concerning the fact that in brain growth a disproportion is observed between the growth of the cortical component and that of sub-cortical structures, the basal ganglia among them (Hofman 2001: 117–118). Now, this is not incompatible with the fact that in this context some specific mutations capable of adding robustness to development and of modulating the global activity of this system may have been selected. This is in fact what, as we see it, appears to be the more realistic interpretation for the positive selection of the human variety of *FOXP2*, which would thus not be responsible for the evolution of the computational system of language per se, but rather a response to the kind of functionality independently attained by this system during its recent evolutionary history.[43]

One must not forget that language is not only a system with specific computational properties. It is also a symbolic system which, precisely because it possesses such computational properties, also possesses the property of discrete infinity.[44] This is important because, as pointed out by Lorenzo (2006), it is perfectly plausible to assume that in the animal kingdom certain behaviors are

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[41] See Lai *et al.* (2001). The exact dating of said mutations is still a much debated issue: Enard *et al.* (2002) originally attributed to them an antiquity of some 125,000 years, but Krause *et al.* (2007), after the identification of some fossil DNA from Neanderthal individuals found in the cave of Sidrón (Asturias), extend this date to 300,000 years and argue for the existence of the human variety of the gene already in Archaic sapiens. Coop *et al.* (2008) argue, however, that the application of their statistical method for phylogenetic dating yields a result below 50,000 years; for a critical overview of the Neanderthal *FOXP2* and its possible implications for the linguistic capacities of these hominids, see Benítez Burraco *et al.* (2008) and Balari *et al.* (2008).

[42] See Ferland *et al.* (2003), Lai *et al.* (2003), Liégeois *et al.* (2003), Takahashi *et al.* (2003), and Benítez Burraco (2009) for a comprehensive state of the art.

[43] In this connection, it is interesting to note the recent identification of a gene (*CNTNAP2*) involved in cortical development and which integrates the *FOXP2* regulatory chain. Some varieties of this gene may be the source of diseases more or less selectively affecting language; see Vernes *et al.* (2008).

[44] For a characterization of this property, see, for example, Hauser *et al.* (2002: 1571).

observed which suggest the presence of a symbolic system (or the rudiments thereof) — as is perhaps the case of the systems of calls and gestures of some primates (see Cheney & Seyfarth 1990, 2005; also Tomasello & Call 1997: chap. 8), or the use of very complex recursive patterns, as may be the case with some birds (Marler 1998), *without this implying the simultaneous presence of both complex recursion and symbolism*. To extend and to perfect the working memory space is, therefore, a necessary condition for the emergence of language, but not a sufficient one. This dissolves a potential objection to our notion of computational phenotype, namely that it may not necessarily be the case that this phenotype (and its corresponding morphological phenotype) correlates with the presence of FL. In fact, this observation is correct and our FC_1 might well correspond to non-linguistic 'minds' which would nevertheless be capable of producing complex recursive patterns within other areas of cognition, such as, for example, motor sequences or melodic sequences in birdsong. Remember that, according to Lieberman's (2006) model, the basal ganglia comprise a sequencer of cognitive patterns, but cognitive patterns may be of many different sorts and the sequencer, just because of connectivity and working space limitations, might have access to only a single type of pattern or to a limited collection of them (motor patterns and melodic patterns, for instance), but not to others (symbolic patterns, assuming these are even available). In the wake of this line of reasoning, a whole mosaic of evolutionary possibilities opens itself, where symbolic capacities and complex recursion may have appeared independently from each other or even coexist without meeting, with the single exception, perhaps, of human language.[45] Thus, for example, and focusing on birds and primates — which are, perhaps, the most interesting species in this connection, apart from also being the most studied ones — we see that complex recursion may have evolved associated with some abilities observed in birds, specifically with bird-song and nest building (Figure 16), whereas evidence for symbolic behavior is meager and, in any case, with no hint of complex recursion.[46] As for primates, hardly any evidence exists suggesting the possession of abilities with a subjacent complex recursion apart from, perhaps, motor control,[47] whereas some observations suggest the presence of vestigial symbolic or proto-symbolic capacities.[48]

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[45] For example, Balari (2005, 2006) argues for such a scenario of the casual 'meeting' between a symbolic capacity grounded on social cognition and complex recursion through a heterochronic process in the development of the nervous system as the basis for the origins of human linguistic capacities; see also Lorenzo (2008).

[46] Griesser (2008) notes, for example, that the Siberian jay (*Perisoreus infaustus*) makes use of a series of alarm calls whereby it discriminates whether a hawk, its main predator, is (1) inactive sitting on a tree branch, (2) looking for prey, or (3) in attack attitude. These signals nevertheless lack the structured and discrete character of other forms of birdsong with which, without any hint of symbolic content, many birds attract the attention of potential sexual partners.

[47] See Tomasello & Call (1997: chap. 3) for an overview of manual dexterity and use of tools in different species of monkeys and primates.

[48] The presence of alarm call systems in inferior primates has been known for years, usually based on specific associations with one or another type of predator. See the pioneering work by Struhsaker (1967) on the alarm calls of vervet monkeys, as well as Hauser (2000) and Cheney & Seyfarth (2005) for up-to-date overviews of this issue. Recently, Arnold &

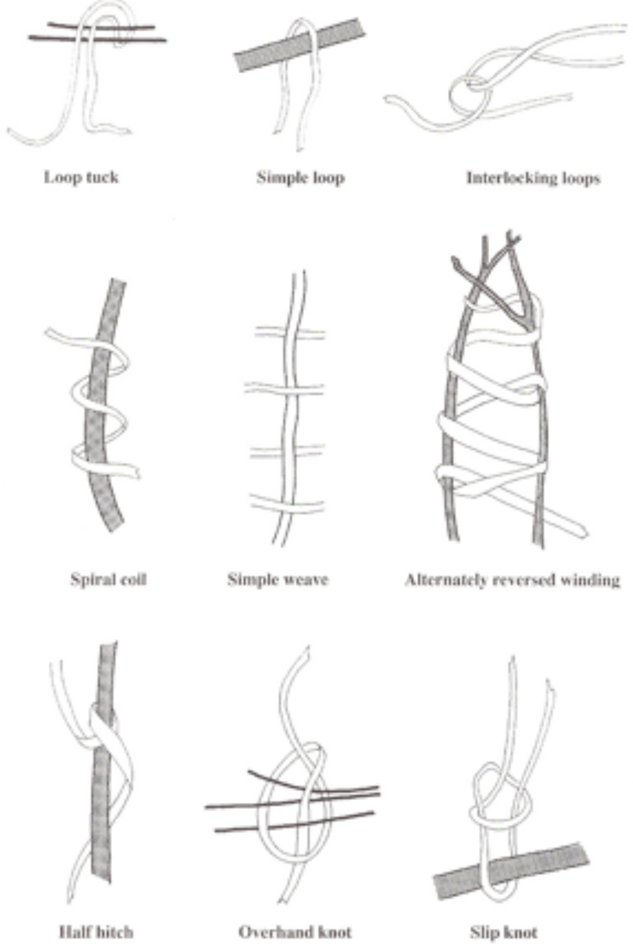

Figure 16: Computational complexity without symbolic representation & communication

[Making a knot requires the application of an operation over a part of the constructed figure, and keeping it in active memory until the moment at which the operation completing the figure is executed. It requires, therefore, the participation of a working memory capable of an active bookkeeping of the operations executed. Thus one must not exclude the fact that the level of computational complexity required for building a hanging nest, such as those constructed by many species of weaver birds, occupies a relatively high position within the Chomsky Hierarchy, even perhaps within our FC_1. For the building behavior of birds and other animals, see Hansell (2000 and 2005). On the relevance for knots to infer complex computations, see Camps & Uriagereka (2006). In the image, some knotting and weaving techniques used by weaver birds. (Taken from Hansell 2000: 85.)]

Zuberbühler (2006a, 2006b) have argued that some Old World monkeys (specifically *Cercopithecus nictitans* or white nose monkeys) can combine two different kinds of calls they also emit independently. The truth is that this type of capacity does not seem to require more than our FC_3; it will then be very far from the computational complexity of the phenotype corresponding to human linguistic capacities. The 'parametric distance' between one phenotype and the other foreseen in this work automatically invalidates Arnold & Zuberbühler's thesis that human language syntax may be derived from the kinds of combinatorial capacities observed in these monkeys through a simple process of gradual and continuous evolutions. This issue is discussed further in Lorenzo (2008) and in Longa (2008).

We believe that these considerations have important methodological implications, especially with respect to the application of the comparative method when seeking precursors of the FL or of some of its constituent properties like complex recursion. Indeed, one of the most direct consequences of what we have said so far is that formal grammar and automata theory may prove to be an extremely useful tool at the time of assessing the abilities and capabilities shown by other animal species, a point also argued for by, for example, O'Donnel *et al.* (2005). However, one must also be careful when using these theoretical tools in experimental design, for example, in order to avoid an excessive trivialization of the results. There already exist, as a matter of fact, some works along these lines which have been the target of very strong criticisms. For example, Gentner *et al.* (2006) have experimentally tested the abilities of some specimens of European starling (*Sturnus vulgaris*) to learn to discriminate songs with different degrees of complexity, correlating with different types of formal grammars. The birds in this study were instructed, using reinforced conditioning, to identify sequences following a pattern of *n* repetitions of a succession of two characteristic sounds (ab^n) of the species' birdsong, formally characterizable in terms of a regular grammar (type 3 in the Chomsky Hierarchy). These birds were moreover instructed using the same method to identify songs following a pattern of *n* repetitions of a sound followed by an identical number of repetitions of other characteristic sounds of the species (the language a^nb^n, we have already come across before in this article; see the end of section 3.2). Unlike the former case, the grammar associated with this pattern is a type 2 context-free grammar, with a principle of recursive embedding of each new pair (*[ab]*) within another identical pair (*[a[a[...]b]b]*). Not without difficulties, but with a level of success above chance (nine in every ten individuals), starlings were capable of identifying the songs following this complex pattern. Similar experiments carried out by Fitch & Hauser (2004) with tamarin monkeys (*Saguinus aedipus*, a species of New World monkey) offered quite different results. According to the authors, these monkeys find almost no difficulties in discriminating sequences of several repetitions of an ab^n pattern, made up by a syllable picked from an initial inventory of eight syllables (*a*), followed by another syllable picked from a second inventory with eight different syllables (*b*), from other sequences not following this pattern. They find, however, insurmountable difficulties when it comes to discriminating sequences made up by some specific number of syllables from the first inventory followed by the same number of syllables from the second inventory (again, a^nb^n) from deviant sequences that do not follow this pattern. These monkeys, then, appear to be able to classify sequences unproblematically within the range of a regular grammar, but appear to be incapable of doing so with only slightly more complex sequences but which are already within the context-free space. One interpretation of these works is, then, that tamarin monkeys possess a computational regime located within our FC_3 phenotype, whereas starlings would have reached at least our FC_2 phenotype. In their reply to Fitch & Hauser (2004), however, Perruchet & Rey (2005) question the validity of these results on the basis of the fact, so they argue, that humans probably do not process patterns like a^nb^n making use of a center-embedding context-free grammar, which might be an indication that other species, like starlings, also process them by means of a different strategy.[49] Besides, and as pointed out by Pullum & Rogers (2006) and Rogers & Pullum (forthcoming), another problem with the Fitch & Hauser (2004) experiments is that these focus their attention essentially on the auditory processsing capabilities of tamarins and, along the lines of the preceding discussion, there is no guarantee that animal species different from ours show the very same abilities within the very same areas of cognition. In fact, let us suppose that, say, tamarins (unlike starlings, for example) might not be able to auditorely discriminate very complex sequences, but might possess abilities in other areas which could effectively be formally characterized by means of more complex systems. Despite this slightly skeptical note, we still believe that research aimed at the identification of the computational phenotypes instantiated by different species may play a crucial role at the time of validating the hypotheses presented above.

Returning then to the case of humans, in short, it is clear that the evolutionary process that gave rise to the FL, and which we characterized as an extension of the working space in the cortical area, would also have allowed the general sequencer access to cognitive types of several modalities, essentially of the symbolic type. This need not, however, be taken as an inevitable consequence of the growth of the cortex,[50] which may eventually explain the observed differences among other hominid species regarding their symbolic capacities.

Also in this connection, and without going into extensive detail, our opinion is that the evolutionary change that took place in connection with the emergence of the FL occurred only recently, after the branching point eventually leading to *Homo neanderthalensis*, meaning that this species never benefited from these changes. In the archaeological record associated with Neanderthals, no evidence is found that suggests the presence of a computational endowment either equivalent or even similar to what is needed for processing human language. For example, Camps & Uriagereka (2006) observed that the absence of objects implying the elaboration of knots — like necklace beads, fishing implements, small projectiles, and so on, all common enough in the sapiens record since some 80,000 years ago — may be illustrative of this fact (see also Piattelli–Palmarini & Uriagereka 2005).[51] As before, we must be careful and not forget the methodological cautions mentioned above and be prepared to discover that Neanderthals might have possessed such computational capacities in other

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[49] It is a well known fact that center-embedding structures are not easily processed by humans — at least since the observations made by Noam Chomsky and George Miller in the early 1960s (Chomsky & Miller 1963 and Miller & Chomsky 1963) — and this must be taken into account at the time of assessing some complexity results. Center-embedding structures are, in some sense, simple, since they fall within the computational capabilities of a type 2 system, but, at the same time — for humans, at least — they are complex, since center-embedding appears not to be one of the structural options selected by our species for the construction of linguistic objects. We use, however, other, formally more complex structures in addition to showing a clear preference for right-recursive objects. Note, however, that these considerations apply only to constituent structure, since, as pointed out in section 3.2, other kinds of dependency relations do follow a center-embedding pattern. Of course, as we already underline in the text, this may not necessarily be the case with other species.

[50] For some considerations about the functions of a hyper-developed cortex in humans, see Gibson (1993), Calvin (1993, 1996), and McKinney (2000).

[51] See, again, what was pointed out in the caption to Figure 16.

domains.[52] Whatever that ability may have been, we are pretty sure that it was not symbolic communication, in the light of the otherwise symbolic poverty of Neanderthals and of the strong asymmetry between their archaeological record and that of anatomically modern humans (see Balari *et al.* 2008 for an in-depth and recent analysis of these matters).[53]

4. Final Considerations

A complete fulfillment of the research agenda sketched in section 2 of this article and made explicit at the beginning of section 3.1 would require a detailed clarification of the environmental and populational conditions which were capable of filtering the distribution of computational phenotypes among the first humans in order to favor the result whose evolutionary model we developed throughout the preceding sections. However, we are not in a position to tackle this issues rigorously for reasons we hope will not be taken as the mere justification of patently visible gaps in our explanation (which we openly assume), but simply as the compromise that we will devote special attention to these topics in the very near future in what must be taken as the second part of this article.

Here we specifically focused on the evolutionary explanation of the computational system underlying the human faculty of language (or, following Hauser *et al.* 2002, the Faculty of Language in the Narrow sense, FLN). This means we only dealt with a particular aspect of language and, therefore, that we

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[52] That said, it may be convenient to recall that Frederick Coolidge and Thomas Wynn have long defended the idea that the deep asymmetry between the fossil records associated with Neanderthals and anatomically modern humans might be due to the lack on the part of the former of the kind of 'extended' working memory which the latter eventually accessed. According to these authors, the singularity of the Neanderthal behavior would not really be a matter of lack of connections between a complex computational system and the kinds of abilities subjacent to the material culture associated with this species, but rather directly to the lack of a computational system as complex as the one evolved by the modern mind. See Wynn & Coolidge (2004) and Coolidge & Wynn (2005, 2007) for their analysis of technical intelligence, and Wynn & Coolidge (2008a) for their analysis of collective activity; for an overview, see Wynn & Coolidge (2008b).

A word of caution is advisable here. Both Coolidge and Wynn and the present authors appeal to evolutionary changes affecting the working memory space as an explanation of modern 'mentality'. However, it is important to see that in our case the term 'memory' is used from a computational perspective only, with no compromise in regard to some specific psychological model of memory. This is not the case of Coolidge and Wynn, who assume the model developed by the British psychologist Alan Baddeley since the mid-1980s (see Baddeley 1986, for a classical formulation, and Baddeley 2000 for the most recent version of the model). Of course, our proposal and that of Coolidge and Wynn are compatible, but we still want to emphasize the fact that, so far, ours does not commit us to any specific psychological model.

[53] For additional evidence supporting this view, the analysis of the patterns of dentition in Neanderthals appear to indicate that their developmental program proceeded much faster than that of humans (see Smith *et al.* 2007), which may be taken as an additional clue in favor of the fact that the alteration in the developmental pattern that gave rise to the reorganization of the human brain may not have occurred before the speciation event leading to modern sapiens.

have so far only provided a partial explanation of this uniquely human capacity. True, this is a particularly crucial aspect of the evolution of the FL, especially if we accept the thesis of Hauser *et al.* (2002) that this aspect might concentrate the most distinctive (even exclusive) aspects of language within the broader context of animal cognition. We only slightly qualified this assertion, pointing at evidence which may indicate the presence of computational systems with degrees of complexity similar to the FL but associated with cognitive capacities that give rise to such disparate behavior as nest building.[54] In our opinion, the most distinctive element of language, seen from an evolutionary perspective, is the kind of associations this computational system has been able to establish through the recent evolutionary history of the human species via other capacities (sensory, motor, conceptual and intentional ones), bringing about a unified cognitive system dedicated to the internal representation and external transmission of complex contents. Our ongoing work is already oriented towards an attempt at explaining the evolutionary convergence of all these 'precursors' in a unified mental system as a result of alterations in the developmental pattern of the human brain. To the extent that no clear answer to this matter is available to us, we will also not be able to provide a rigorous answer to the questions posed at the beginning of this last section. The reason is simple: We believe that the populational processes which made possible the proliferation and generalization of the FC_1 associated with the FL had little to do with the emergence of this particular cognitive phenotype, but they are instead related to the association of FL with the kind of mental capacities which made it a system apt for the computation of externalizable mental representations (or, again following Hauser *et al.* 2002, the Faculty of Language in the Broad sense or FLB).

We can, however, offer a brief preliminary sketch of our ideas in this respect. We believe that the first humans who showed the capacity to externalize the complex expressions which their computational phenotype was able to process did not obtain great benefits from it. On the contrary, in the context of an evolutionary scenario dominated by forms of expressivity completely alien to the degree of sophistication of the sequences emitted by the members of this mutant population, it may well have been the case that it was taken as an element of stigmatization and exclusion for these individuals, who would have effectively been seen by the rest of the population as true "social monsters".[55] From a wider

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[54] Hauser *et al.* (2002) also contemplate this possibility when they note that the most formally complex features of language may also characterize other species' representational systems like social intelligence or spatial orientation. The thesis they present as the "most probable option" is, however, that those systems are exclusively present in the linguistic computational system.

[55] And here we can only borrow Lewontin's (1998: 113) words:

> Thus a species that possesses linguistic competence may indeed take over the earth as a consequence of the technological and managerial capabilities that are the result of language, but in a species lacking linguistic competence, the rudimentary ability to form linguistic elements by a few individuals may be taken as a sign of difference that causes them to be expelled or even killed.

We want to make clear, however, that this notion of "social monster" is not the same notion of 'monster' as it was used in classical teratology nor, more concretely, the same as the perspective, then, they would be 'misfits' to the social conditions in which their emergence took place. We believe, however, that social stigmatization against these individuals is the key factor that eventually favored the conditions for isolations (not necessarily allopatric) which made possible the preservation of the phenotype within the population (originally restricted to this stigmatized group), first, and eventually their proliferation and generalization within the whole population at some critical point in the early history of the human species. We tend to believe that such a critical point may coincide with the demographical crisis which, according to some authors like Behar *et al.* (2008), took place immediately before the intercontinental dispersion of modern humans. This situation, described as very close to extinction in a context of extreme environmental adversity, could effectively have fostered populational replacement in favor of a cognitive phenotype which may have been extremely advantageous for its possessors. According to this idea, then, the special cognitive endowment of this 'founding' population (Mayr 1963) would not have originally been an adaptation, given the dominant social conditions at the moment of its emergence, but it would have possessed from the very beginning some adaptive potential (or 'adaptability' in the sense of Reid 2007) which openly manifested itself at a critical point of human evolution.

What we have just sketched is prone to further elaboration and sophistication and, to this end, we need first a concrete model of the evolution of the FLB through development. In this article we have taken a first step in that direction, proposing a model for the evolution of its core component or FLN, based on the alteration of the developmental pattern of the cortical component serving as working memory for the computational system with a sequence machine located in the basal ganglia. The increment in memory capacity thus attained would have permitted the human brain to 'jump' towards a cognitive phenotype with qualitatively different computational capabilities compared with other existing phenotypes within a discontinuous space of computational regimes. To this end, we have followed rather closely some recent proposals within Evolutionary Developmental Biology and, in particular, those of Pere Alberch, a number of whose key ideas originally inspired this work. We are convinced that this inspiration will also take the lead in our future attempt to explain how the developmental pattern of the first humans may have been altered in order for this computational phenotype to give rise eventually to the linguistic phenotype that at present singles us out as a species.

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"logical monsters" of Alberch (see Figures 8 and 9). It is true, however, that underlying the "social monster" which we allude to in the text is a "biological monstrosity", which is not in any way the case, of course, in all cases of social stigmatization.

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