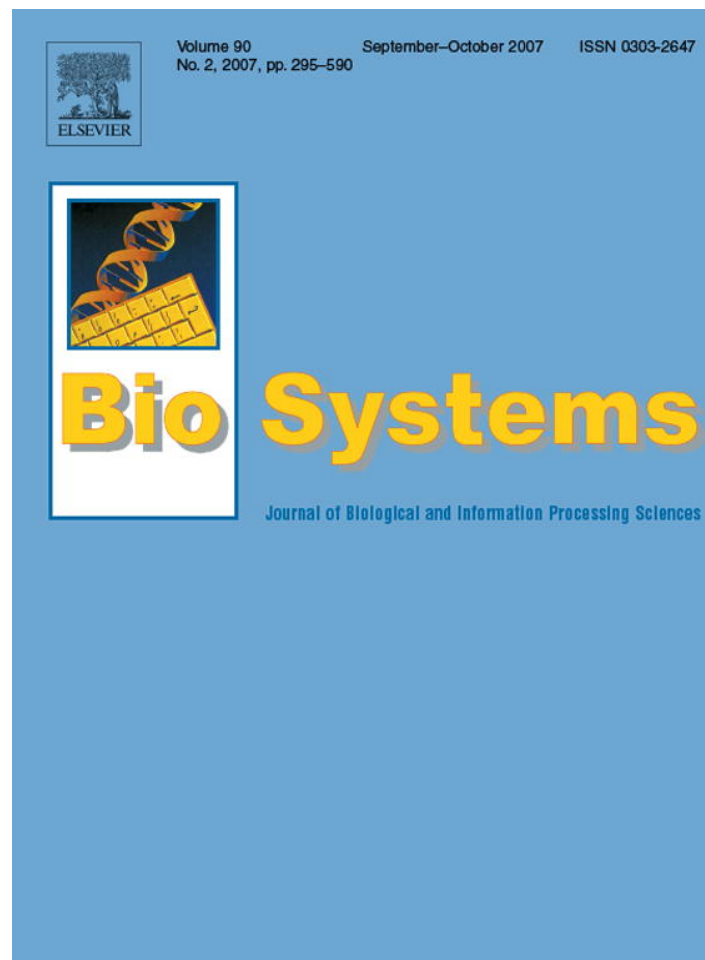


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A semiotic framework for evolutionary and developmental biology

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Abstract

This work aims at constructing a semiotic framework for an expanded evolutionary synthesis grounded on Peirce's universal categories and the six space/time/function relations [Taborsky, E., 2004. The nature of the sign as a WFF—a well-formed formula, SEED J. (Semiosis Evol. Energy Dev.) 4 (4), 5–14] that integrate the Lamarckian (internal/external) and Darwinian (individual/population) cuts. According to these guide lines, it is proposed an attempt to formalize developmental systems theory by using the notion of evolving developing agents (EDA) that provides an internalist model of a general transformative tendency driven by organism's need to cope with environmental uncertainty. Development and evolution are conceived as non-programmed open-ended processes of information increase where EDA reach a functional compromise between: (a) increments of phenotype's uniqueness (stability and specificity) and (b) anticipation to environmental changes. Accordingly, changes in mutual information content between the phenotype/environment drag subsequent changes in mutual information content between genotype/phenotype and genotype/environment at two interwoven scales: individual life cycle (ontogeny) and species time (phylogeny), respectively. Developmental terminal additions along with increment minimization of developmental steps must be positively selected.

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1. Introduction

Mayr (1997), one of the most authorized voices of mainstream biology stated that “the term selection is unfortunate because it suggests that there is some agent in nature who deliberately selects”. The point, however, is to naturalize the notion of agency that goes against the dualistic mechanical and Darwinian view through which scientists interpret nature. I consider agency to manifest whenever entities behave as internal observers that process information in order to capture free energy for their own sake. These actions are elections among

several alternatives through gambling with incomplete and partial information about their surroundings, but nonetheless oriented towards the minimization of risk. In order to naturalize the idea of agency it is needed to construct a semiotic framework for biological discourse. I will show how the foundations for a semiotic approach lie buried within the major evolutionary theories, which are interpreted as steps towards an expanded synthesis.

In Section 2, I will summarize for these theories, (Lamarckism, Neo-Lamarckism, Darwinism, Neo-Darwinism and Epigenetic), their basic assumptions and the aspects that contribute to the construction of a semiotic model. In Section 3, the model will be applied to the current Evo–Devo debate, by advancing the notion of evolving development agents.

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2. The construction of a semiotic integrative framework

2.1. Basic assumptions, contributions and limitations of existing theories

2.1.1. Lamarckism

Lamarckism is based on the ontological distinction between “internal” and “external” zones or the confinement of life to an internal space separated by a boundary from the external inorganic one. Organisms’ “inner drive” pushes them to develop according to the plan of nature that tends to produce an increasing differentiation of the body parts and higher complexity, while the coherence of the organism as a whole is always preserved (Lamarck, 1803). Thence, the historical transformations of living forms were likened to embryological processes dependent on intrinsic and extrinsic factors. Intrinsic factors play the primary role and correspond to the *vital force* (heat and electricity) that tends to make organization more complex (Burkhardt, 1995). The vague concept of *vital force* aimed at providing a physical explanation of the transformation, though with the advent of the mechanical theory of heat, it turned out to be wrong. Extrinsic factors correspond to the conditions of life (environment) that act on the structure and heredity (Jacob, 1982), so producing an accidental detour from the plan of nature (Burkhardt, 1995). Lamarck distinguished between organism’s inner impulses that produce the basic pattern of the form and the environment that shapes the external secondary features. At this point Lamarck (1803) postulated the transformation of form by the influence of circumstances upon the habits of the organisms and the inheritance of such acquired modifications. Individual time appeared as a shift from potentialities to actualities, whereas the idea of a global universal time was absent because Lamarck did not envision a unique life history arising from a common ancestor but envisaged instead, a series of identical transformations arising from several events of spontaneous generation.

The contributions of Lamarckism for an expanded synthesis are: (1) the search for a physical law of transformation; (2) the distinction between internal/external zones that expressed the specificity of individualized living beings; (3) the need to explain increases of complexity; (4) to posit the role of organisms’ habit in evolution; (5) the search for an explanation of how the environment influence the heredity of the organisms.

The pitfalls that have been and are to be overcome are: (1) the grounding of physical explanations on a mistaken view of fluids; (2) the idea of the plan of nature

that associates teleological with deterministic explanations; (3) to minimize chance and restrict it to exclusive external environmental factors; (4) the absence of the notion of common ancestry; (5) the lack of agency since organisms follow internalized deterministic tendencies.

2.1.2. Neo-Lamarckism

Neo-Lamarckism posited more explicitly a relation between ontogeny to phylogeny and asserted that from birth onwards a series of structural modifications are incorporated into the germ when organization is still flexible (that is, in childhood), and then became fixed as if this structural modifications had been added on to old individuals during thousands of centuries, (Darwin, 1838; Richards, 1992). The entailment between ontogeny and phylogeny is expressed in the theory of recapitulation. Quoting Haeckel (1879) (Raff and Kauffman, 1983):

“These two divisions, Ontogeny, (embryonic development of the individual) or the history of the germ, Phylogeny, or the history of the tribe, are intimately connected, and the one cannot be understood without the other . . . Ontogeny is a recapitulation of Phylogeny; . . . the series of forms through which the individual organism passes during its progress from egg cell to its fully developed state, is a brief, compressed reproduction of the long series of forms through which the animal ancestors of that organism . . . have passed from the earliest periods of so called organic creation down to present time”.

Accordingly, the same laws ruled both the evolution of species and the development of embryos (Richards, 1992). Haeckel justified recapitulation by asserting that evolution proceeds by continuous additions of new steps to growth (Bowler, 1992). The inheritance of acquired characteristics requires the speeding up of individual growth; the ancestral adult shape becomes a state through which organisms must pass towards a new mature state, so that the features of ancient adults appear earlier in their descendants. As the characteristics are compressed and pushed back to earlier ontogenetic stages they get incorporated into the *Bauplan*. Following Richards (1992), Darwin (1836–1844a,b) argued that embryological development evolved by terminal additions produced as a response to the external conditions of life, that is that evolutionary variations are dependent on organism’ need to cope with the environment (Richards, 1992).

The contributions of Neo-Lamarckism for an expanded synthesis are: (1) the search for an explanation of how the interactions between organisms and environment induce evolutionary variations and influ-

ence heredity; (2) to admit the close relation between ontogeny and phylogeny; (3) to view variations as arising from modifications of embryological and behavioral processes; (4) to naturalize the existence of organism's *Bauplan*.

The limitations that have been and are to be overcome are: (1) the idea of directed evolution; (2) to consider organisms' reactions to the environment as a source of directed variations without any explicit initiative on the side of the organisms; (3) the neglect of chance.

2.1.3. Darwinism

Darwin differentiated between individuals and populations, while considered development and evolution as open-ended processes. For him, evolution was no longer a pre-established line of increasing complexity but a diverging branching tree rooted on a common ancestor. Non-directed variations play a major role so making evolution an unpredictable non-directed process and doing away the notion of the plan of nature. Natural selection was introduced as a non-physical explanation in terms of survival of the fittest that accounts for increasing adaptation in local environments, so that specific variations were retained for their adaptive advantages. Evolution was perceived as a series of steps in which only one was favored among different possible options. The structuralism of developmentalist views were replaced by the functionalism of the selectionists as natural selection became the accepted cause of transformation.

Nature brings forth novelty since it is permanently coming into being. Natural selection conceived, as the result of competition for scant resources became an external force that is permanently shaping the natural world. The idea of evolution as a process in which some steps lead to choices among real options was difficult to accept in the nineteenth century, and that was the reason why Darwinians tried to assimilate it to a physical law, though it was more adequate to conceptualize it as an analog of intentional systems. Darwin expressed his rejection to consider natural selection as an analogous of a conscious intentional action in the following paragraph:

“Others have objected that the term selection implies conscious choice in the animals which become modified; and it has even been urged that as plants have no volition, natural selection is not applicable to them. In the literal sense of the word, no doubt, natural selection is a false term. . . It has been said that I speak of natural selection as an active power or Deity; but who objects to an author speaking of the attraction of gravity as ruling the movements of the planets? Everyone

knows what is meant and implied by such metaphorical expressions; and they are almost necessary for brevity. So again it is difficult to avoid personifying the word Nature” (Darwin, 1859: 91–92).

Regardless of the status that should be given to natural selection, Darwin's theory was condensed in the triad: variations, heredity and natural selection. According to Darwin variations were thought to be random since they occurred independently of the organisms' needs and conditions of life; heredity was not understood then, but was associated with development, and natural selection was seen as survival of the fittest.

The contributions of Darwinism for an expanded synthesis are: (1) the explanation in terms of natural selection and its continuous action; (2) the distinction between individuals (development) and populations (evolution); (3) the introduction of a global evolutionary time from a single origin of life; (4) to open up evolution into branching lineages that stem off from common ancestors; (5) to admit the existence of non-directed variations, while discussing the possibility of modifications in embryological development and habit as a response to the conditions of life.

The limitations that have been and are to be overcome are: (1) the assimilation of natural selection to an external (Newtonian) force; (2) the view of evolution as necessarily adaptive; (3) to admit chance more as the ignorance of the causes of variations than as an ontological fact; (4) the rejection of agency in living beings; (5) to undermine the role of structural restrictions imposed by developmental paths.

2.1.4. Neo-Darwinism

According to Weismann, the phenotype is determined by the genotype so that phenotypic modifications by the environment cannot affect the genetic content of the egg. This reasoning inspired the Neo-Darwinist approaches to evolution and the central dogma of molecular biology. The formal incorporation of the individual/population distinction was credited to Fisher who made use of Boltzmann statistical analysis in populations' genetics. In turn, statistical analysis fostered the idea that individual properties were deviations from statistical averages and evolution became the change in the genetic composition of populations by the action of natural selection. Organisms are studied as populations of genes that tend to disperse randomly in populations; every individual gene acts independently and contributes additively to the fitness of the organism, consequently, natural selection provokes statistical changes in the genetic composition of populations. In this view, adaptations lead to an equi-

librium state in constant environments in which fitness reaches its highest values at the expense of genetic variability.

This approach furnished evolutionary theory with a mathematical formalism. Nonetheless, it led to the understanding of organisms as non-autonomous entities determined by two opposing causes, genes and environment. Neo-Darwinians consider that environment poses challenges that are to be solved by the organisms, in a process of adaptation in which it is assumed *a priori* that among the random variants, the very few that possess an adequate fit give abundant offspring and increase their frequency in the next generation.

Accordingly, organisms vary and react randomly without processing information from the environment, so rendering their problem solving activity in adaptation a mere metaphor! Insofar as organisms are not understood as agents, random and deterministic factors are confined exclusively to either or genes and environment, without weighting the specific contribution of each and what is worse neglecting organisms' active mediation. The eradication of teleological explanations led, in turn, to the elimination of individuals' intentionality. With the rise of genetic determinism it was thought that the embryo was genetically preprogrammed, closed and oriented to a specific goal (the adult stage), so that it did not contribute to the production of evolutionary novelties. Then, embryology became a secondary consideration. The modern synthesis shared the assumptions of Fisher, though Wright postulated epistatic interactions between genes and evolution in a multip peaked adaptive landscape where more than one adaptive solution is accessible to the evolving local interbreeding subpopulation that shifts from one equilibrium state to another by going through periods of drift. In this view shared by Dobzhansky and Ayala natural selection favors genetic variability that confers adaptability to the populations.

The contribution of Neo-Darwinism for an expanded synthesis are: (1) the employ of statistical analysis in population evolutionary research; (2) to formalize the distinction between individuals and populations; (3) to acknowledge the role of genes in evolution; (4) to integrate short-term drift and adaptation with long-range tendencies of increasing fitness.

The limitations that have been and are to be overcome are: (1) the view of evolution as necessarily adaptive; (2) to admit chance only at the micro level due to the assumption of an statistical global regularity; (3) the rejection of agency in living beings; (4) to overemphasize the role of genes while not considering a real processing of information.

2.1.5. Epigenetic theories

For Waddington (1957, 1961) development is an evolutionary canalized process, illustrated as a ball running down through the valleys of an epigenetic landscape whose features are shaped by both the genetic network and the environment. In this view, early developmental pathways are fixed while the late ones are susceptible to modification by a permanent interaction of organism's populations with the environment. Genotype and environment do not cause phenotypic traits directly; instead, as development goes on the epigenetic landscape opens up new routes and deepens some others. The epigenetic landscape is a dynamic interface between the genetic endowment of the egg and the environment and is permanently tuned by the developing organisms. Waddington (1957) coined the term "genetic assimilation" in order to account for the fixation of genes that reinforce the effect produced by external stimuli on individuals. In early stages of development, the epigenetic processes are influenced by external morphogenetic factors that act on cellular aggregates (Goodwin, 1994; Ho and Saunders, 1979; Jablonka and Lamb, 1995, 1998; Newman and Müller, 2000; Salazar-La Ciudad et al., 2003). Here, external determinant morphogenetic factors are reinforced by genes that supply structural proteins but do not exert a direct influence on the resultant architecture. Genetic assimilation (Waddington, 1957, 1961) connects morphogenesis to a genetic network that eases the generation of informative records for producing constitutive materials. In other words, genes came late to consolidate and stabilize existing epigenetic processes (Newman and Müller, 2000). Along these lines developmental systems theory (DST) searches the laws of phenotype construction, within the context of epigenetic and environmental interactions. Phenotype is the developing organisms' analog record that cannot be decomposed into separate genetic and environmental contributions, or the structure that determines moment by moment (Salazar-La Ciudad et al., 2003) its way of interactions with the environment in the course of its ontogeny.

The contributions of epigenetic theories for an expanded synthesis are: (1) to contextualize the role of genes in development and evolution; (2) to merge development and evolution; (3) to view chance both at the macro level (organisms' interaction with the environment) and at the micro level (random genetic mutations and recombination); (4) to place deterministic factors both in the stabilizing effect of genes and in the regularities of the environment; (5) to view the success of evolution more in adaptability than in adaptation.

The limitations that are to be overcome are: (1) the lack of a more explicit notion of agency and (2) the lack

of a mathematical formalism that may help to build up models. This approach needs an alternative framework in which it might be embedded and further developed. I will pass to show how this framework might be constructed.

2.2. The semiotic framework for evolutionary and developmental biology

The above quick review evokes a scheme of reality that surpasses classical mechanical ontology in breath and depth. Peirce semiosis as understood by Taborsky (2002, 2004, 2005) and Salthe (1993, 1999), describes the more general framework of reality in which mind and matter are not substances but only encoding modes of a complex reality that exhibits a continuous behavior that goes from sheer randomness to law-like behavior, from mindfulness to inert matter, from bursts of dissipated energy to passive matter. Reality does not exist as discrete particles, or as abstract bits of information, but rather as a complex network of continuous morphogenesis, dissipation and transformation.

Reality is continuously coming into being, from energy into matter and as different configurations of material forms are produced, energy is dissipated. Semiosis is not only the framework that we can use in order to interpret the living world but mostly it is the recognition that living systems themselves are informational processes that measure energy–matter within defined parameters. In order to clarify matters let's go back to Darwin's triad, variation, heredity and selection. Peirce regarded Darwinism as a specific case in which his three universal categories (*Firstness*, *Secondness*, and *Thirdness*) were found (Peirce, 1931–1958, 1965; C.P. 1.398–1.399). *Firstness* corresponds to spontaneity, inner drives, chance, randomness, pure potentiality and is associated with the production of evolutionary variations; *Secondness* corresponds to reaction, discreteness, definiteness, actuality, and is associated with the heredity of fixed characteristics; *Thirdness* corresponds to mediation, agency, habit, continuity and processes that generate regularity and symmetry, or the manifestation of an evolutionary law considered as a generalizing tendency to take habits. Natural selection is understood as a specific form of *Thirdness*. *Thirdness* is the equilibrating tendency that is produced as a consequence of open systems' dissipating tendency to attain far from equilibrium states. However, in order to explain mind Peirce also includes the readiness to take and lay aside habits in terms of states of unstable equilibrium in which minute causes may produce startlingly large effects (Peirce, 1931–1958, 1965; C.P. 6.101, C.P. 6.613, C.P. 6.264).

“If the laws of nature are results of evolution, this evolution must proceed according to some principle, and this principle will itself be of the nature of a law. But it must be such a law that it can evolve or develop itself. (. . .) Evidently it must be a tendency toward generalization, - a generalizing tendency. But any fundamental universal tendency ought to manifest itself in nature. Where shall we look for it? (. . .) But we must search for this generalizing tendency rather in such departments of nature where we find plasticity and evolution still at work. The most plastic of all things is the human mind, and next after that comes the organic world, the world of protoplasm. Now the generalizing tendency is the great law of mind, the law of association, the law of habit taking. We also find in all active protoplasm a tendency to take habits. Hence I was led to the hypothesis that the laws of the universe have been formed under a universal tendency of all things toward generalization and habit taking”. (Peirce, 1931–1958, 1965; C.P. 7.515).

Entities like signs, organisms, atoms, etc., are spatial–temporal configurations of an energy–matter, mind–body continuum that comes into being through interactions. These interactions or relations are captured like a snapshot of a measurement of energy–matter in space, time and mode. Space can be considered to be internal or external according to the ontological cut introduced by Lamarck. However, this can be subdivided into local and global domains according to the Darwinian cut that severed the individual from the population phenomena. The local/global cut is equivalent to an *epistemic* cut in the sense that knowledge requires instances of increasing generalization and symbolic representation that can only be provided at the global level. Thus, taking both cuts together we define four spatial zones: internal-local, internal-global, external-local and external-global. Time is not taken as an absolute Newtonian time but rather as a truly constitutive aspect of reality that can be subjectively experienced in the sense of whether it is present, perfect or progressive. Mode refers to processes in the sense of being possible, actual or necessary. These relations or measurements are codified as dyadic combinations of the three universal categories and so, there are six (Taborsky, 2002, 2004):

(1) *Firstness as Firstness* [1-1], defines the local internal field at a present time. It corresponds to impulses, drives, unbound information, chance, spontaneity and potentiality existent at the present time. It is an internal analog code represented in Fig. 1 by quadrant II. (2) *Secondness as Secondness* [2-2], defines the external local

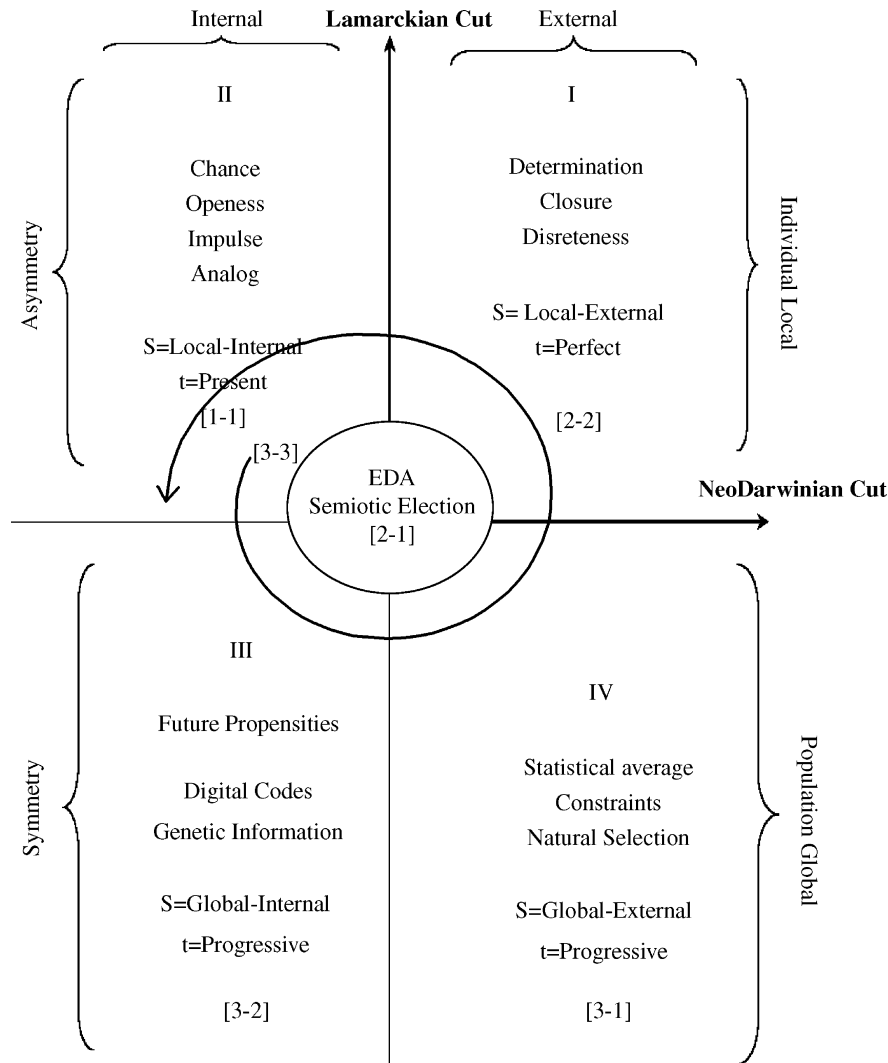


Fig. 1. The Lamarckian/Neodarwinian quadrant (modified after Taborsky, 2004). The Y-axis divides the internal (left) from the external (right) zones. The X-axis demarcates the local (upper) global (lower) zones, so creating four spatial zones local-external (Q I), local-internal (Q II), global-internal (Q III) and global-external (Q IV). Individual development corresponds to a morphology built by three relations: [1-1] as input, [2-2] as output, and [3-2] as mediator, these three relations are connected by the [2-1] relation and it is visualized as a transition from quadrant II (internal-individual potentiality) to I (external-individual completion). Evolution corresponds to a morphology built by three relations: [2-2] as input, [3-2] as output, and [3-1] as mediator, these three relations are connected by the [2-1] relation and it is visualized as a movement from quadrant IV (external-global reality or population) to III (internal-global codes or updated genetic information). In both cases, we find the presence of a law-like relation, which is genetic information for development and natural selection for evolution. However, the relation [2-1] is crucial in both situations for it represents agent's choices that lead to the establishment of connections.

field in a perfect time. It corresponds to what is definite, discrete, closed, the actually given as manifested in individual differentiated forms. That is reality as described in the perfect time. It is an external analog code represented in Fig. 1 by quadrant I. (3) *Secondness as Firstness* [2-1] defines the border or interface between internal/external, individual/population, present/past/progressive time. It is a relation that performs the analog/digital code conversion and the establishment of couplings, so creating a network of connections. It is represented by the intersection of X–Y axes. (4) *Thirdness as Firstness* [3-1],

defines the external global field in a progressive time. It corresponds to a law of aggregation and environmental constraint that in biology are seen as fitness and population statistical regularities introduced by natural selection. This relation is represented by quadrant IV. (5) *Thirdness as Secondness* [3-2], defines the internal global field in a present progressive time, the inner digital codes shared by the population. The processing of genetic information by DNA mutation, recombination, duplication, etc., result in the production of new genetic texts some of which define future propensities and con-

fer new possibilities It is represented by quadrant III. (6) *Thirdness as Thirdness* [3-3] corresponds to an unbound aspatial and atemporal relation that is a property of every informational system. It is a principle of regularity that operates by the establishment of habits or the state of unstable equilibrium that gives continuity to the evolutionary process that is represented by the spiral in Fig. 1.

Following Taborsky (2004) morphological units like organisms are functionally selected signs composed by three of the six relations, as input (raw sense data), mediation (memory and analysis) and output (interpretation of data). Since mediation requires a more general stance of memory it must be in a relation that involves *Thirdness*. A morphogenetic analysis must go beyond the dichotomy that conceives determinism as dependent on either genetic (internal) or environmental (external) factors; and randomness as originating either from within (DNA mutation) or from without (environmental fluctuations). Although, the internal/external and local/global boundaries are so thoroughly implicated as to be almost indistinguishable, the analytic dissection of these spatial–temporal–functional zones would permit to examine the relationships between ontogeny and phylogeny. Consequently, the morphology or biological organism will make use of at least three of these relations at any one time. Biology becomes a specific case founded on empirical evidence that not only corroborates this evolutionary ontology, but contributes to its development and contextualization in different research programs. In what follows I will restrict myself to depict the most general framework of discourse of biology, but my purpose is to show how relevant Peirce's cartography is to today's "Evo–Devo" or "nature–nurture" debate and to show how this debate requires a semiotic approach for its comprehension and interpretation of empirical data.

Following Darwin, it is tempting to see evolution as a semiotic process in which the population plays the role of a non-local information processor. However, Neo-Darwinians while highlighting the population-global external domain neglected the internal zone, (see quadrants I and IV in Fig. 1), and by restricting themselves to natural selection, ran contrary to the internalist viewpoint of Darwin—who stood close to recapitulation (Richards, 1992). The "internalist" Darwin (1836–1844a,b) attempted an embryological account of evolutionary variations, discussed the possibility of directed variations by means of use and disuse, wondered whether instincts were learnt, and also postulated the influence of organisms' actions on heredity in his theory of pan-genes (Darwin, 1868).

3. Developmental systems theory and evolving developing agents

3.1. The Evo–Devo debate

There has been a long debate about the relations between ontogeny and phylogeny, since each one has been hypothesized as the efficient cause of the other. The theory of evolution by natural selection assumes the randomness of pre-existing individual variations, so neglecting the environmental influence on development and behavior in the production of variations. Mainstream biologists affirm that embryos develop according to a genetic program encoded in Hox genes, a standpoint that undermines the search for developmental factors other than genes. Far from neglecting the decisive influence of Hox genes in the determination of body segments, semiosis asks why is it that development came to be determined to large extent by genes and how far goes this determination? That is, to what extent is ontogeny influenced by factors other than genes? and to what extent does ontogeny shed light on the origin of evolutionary variations? The understanding of development as a succession of stages that go towards higher differentiation, rekindles the specter of recapitulation because of the fear that evolution might be interpreted as teleologically directed. But semiosis regards ontogeny as a non-programmed open-ended process that frees recapitulation from natural philosophy.

The traditional preformists versus epigenetists dispute reappears today as the "Evo–Devo" debate over the roles that must be assigned to genetic information and epigenesis. Oyama asserts that genetics is preformism in a new guise inasmuch as development is thought to be a genetically programmed process in which the formative factors preexist in an encoded or encrypted way (Oyama, 2001). On the other hand, epigenetists affirm that development is self-constructed in the organisms–environment interactions. The resolution of this debate would clarify whether evolutionary variations are influenced by "nature" (genome) or by "nurture" (environment). Likewise, it would bridge micro and macroevolution.

Ontogeny depends on analog information (Hoffmeyer and Emmeche, 1991; Hoffmeyer, 1996), that according to Fig. 1 can be divided into external and internal zones encoded in the [2-2] and [1-1] modes, respectively (Fig. 1, quadrants I and II). However, the potentiality of ontogeny is linked to a relation in the mode [3-2] that impresses a law like behavior; otherwise, the transition from [1-1] to [2-2] would represent individual processes of self-organization. Analog information

refers to the recognition of patterns by structural motifs of the agent within a continuous threshold of variability. Analog means that agents recognize through structural complementarity and establish non-random reversible interactions (Root-Bernstein and Dillon, 1997). These interactions among inner constitutive components preserve coherence of the individual as it interacts with the environment. Analog recognition of external factors guides the internalization of information by interactions and measurements. The internal and external analog zones are connected through the epigenetic inheritance system (EIS) (Jablonka et al., 1992; Jablonka and Lamb, 1998; Smith and Szathmary, 2001), since an adjustment to an external factor implies a readjustment of inner states. The dynamics of EIS is expressed by [2-1] that enables external/internal connections.

On the other hand, digital information is encoded information in the form of a text composed of basic symbols (DNA) that can be modified by discontinuous variations such as mutation and recombination. Digitally recorded information appears when any structure becomes a symbol that can be permuted giving rise to potentially different functional content. In Fig. 1, digital information is encoded in the [3-2] mode, which is associated with the definition of future propensities. Genes as bits of genetic information belong to the relation [2-2], but considering that they overlap, are physically discontinuous, found within other coding sequences, and their continuity is observed only at the RNA level, one is led to conclude that their discreteness is a Mendelian approximation that does not hold at the DNA level. Instead, genes make up part of a functional informational network under the command of the epigenetic system and so belong to the [3-2] mode. Natural selection configures the digital genetic record of the population, the fittest are the carriers of a more faithful (though outdated) inner representation of environment, that is the survival of the best encoders of environmental information.

These two dualities (internal/external) and (individual/population) are currently, the source of endless “either/or” debates. However, semiosis favors a coherent integration that is congruent with DST, one that asserts the existence of a fundamental symmetry between genes and other developmental resources (Griffiths and Gray, 1994; Oyama, 2001). Semiosis is based on the acceptance of a real interpretation of all informative resources by the developing organisms.

3.2. Evolving developing agents

I propose the notion of evolving and developing agents (EDA) as a way to formalize a theory of organisms

as interpretants embedded in a system of interpretance (Salthe, 2001) that fluctuate between alternative states and cope with external factors. The term merges development and evolution to the extent that both processes are mediated by the agency of the organisms themselves. This notion agrees with Baldwin's idea of organisms as participants in the production of their own adaptations by means of organic selection.

“Organic Selection. – The process of ontogenetic adaptation considered as keeping single organisms alive and so securing determinate lines of variation in subsequent generations. Organic Selection is, therefore, a general principle of development which is a direct substitute for the Lamarckian factor in most, if not in all instances. . . . The use of the word “Organic” in the phrase was suggested from the fact that the organism itself cooperates in the formation of the adaptations which are effected, and also from the fact that, in the results, the organism is itself selected; since those organisms which do not secure the adaptations fall by the principle of natural selection. And the word “Selection” used in the phrase is appropriate for just the same two reasons”. (Baldwin, 1896).

The upper quadrants in Fig. 1 correspond to asymmetric relations while the lower ones account for symmetry or regularities that are properties of *Thirdness*. Considering the potentiality derived from digital information (quadrant III), ontogeny would be the transformation from genotype to phenotype at individual scale, or from the potentialities given in the present to an already manifested determination (perfect time) that is from [1-1] to [2-2]. However, this transformation requires an interpretation of the DNA by the egg (Hoffmeyer, 1996). Likewise evolution is understood as a transformation from phenotype to genotype by means of an interpretation of the ecological niche by the population or lineage (Hoffmeyer, 1996). The entailment of these two processes is seen in the fact that every single phenotype that makes up part of the evolving population proceeds from an individual developmental process, and that individual DNA sequences that are interpreted along development come from a previously selected population (genetic pool). To grasp the complexity of these processes requires the specification of the internal/external and individual/population interface encoded in the [2-1] mode. I name this interface as evolving developing agents (EDA). Agents explore, starting randomly with measurements of the possibilities of environment, and as information is gathered measurements get more oriented. In this sense measurement makes possible to go from local asymmetry to global symmetry as expressed

in the relation [2-1]. EDA pick up input information in order to enhance adaptability and capacity to promote individual diversity, so opening up future possibilities. Nonetheless, there will never be enough information that assures the best choice, so that EDA bets to minimize risk. The notion of EDA assumes that organisms are inner observers that partially know their immediate environment, and are the products and the instruments of mind operations, as long as they are connected to the modes [3-1], [3-2] and [3-3]. Agency refers to the fact that there is interpretation of both genetic and environmental resources that leads to the availability of many options. Digital information in the mode [3-2] enables the realization of some among the multiple options. Organisms are processes that tend to individuation at the interface [2-1]; to the extent that they tend to closure and get localized make part of the material world in the mode [2-2], and to the extent that they open up, connect to *Thirdness*. By capturing free energy, they connect to the relation [1-1]. The interface [2-1] interacts for network construction, while the relations [2-2] are mechanical and do not contribute to information exchanges. The interface [2-1] is always being trespassed in either direction: (1) Uncertainty about the environment decreases by means of measurements and (2) uncertainty about the environment increases with record erasure and environmental change.

EDA are embedded in a system of interpretance and mediate between internal/external and individual/population domains so paving the way to the comprehension of the ontogeny/phylogeny common characteristics like, self-reference, information increase, open-endedness, lack of a prior program and irreversibility. Therefore, EDA must be studied simultaneously in two time-frames (ontogenetic and evolutionary). The ontogenetic (analog) record or phenotype has two measurable parameters: (1) specificity (how specific is its relation with a particular environmental factor) and (2) stability (how constrained is the span of possible conformations). These two parameters point to the uniqueness or individuality of every single phenotype. The phylogenetic (digital) record is the DNA.

However, EDAs activities in ontogeny define and canalize tendencies that can be verified in evolutionary time. Global long-range evolutionary tendencies are the result of local short-range processes that occur at the individual level within the ontogenetic context. The key concept of recapitulation theory is that young adults of ancestral life forms determined tendencies of change influenced by the environment through change of behavior and habit, and some of these modifications as they were pushed back to earlier ontogenetic steps became

part of a descendant species *Bauplan* (Wagner and Misof, 1993), (Wimsatt, 2001).

In a universe composed of EDA, ontological chance (observer-independent) is the agents' epistemic uncertainty (observer-dependent). Chance as a property of *Firstness* refuels evolutionary potential and nature creative impulse; however, its renewal is a manifestation of a continuous atemporal and aspatial dynamics encoded in the relation [3-3].

“Continuity, as generality, is inherent potentiality, which is essentially general. (...) The original potentiality is essentially continuous or general”. C.P. 6.204-205.

The central dogma of molecular biology states the impossibility of modifying the genotype by the action of phenotype during individual life cycle, but it does not preclude the change of genotypic composition of the populations (or the updating of the genetic record) through selection of the fittest phenotype. Besides, the increment of information during individual lifetime expressed as modification of epigenetic inheritance systems (EIS) does not violate the central dogma. Organisms as EDAs are information encoders and niche constructors. The genome and the environment open up possibilities but do not specify the ontogeny of their offspring, in other words, as development goes on, the phenotype in permanent interaction with the environment modulates the epigenetic landscape and regulates gene expression.

This internalist approach highlights the inseparability between subjective and objective reality as EDA permanently shape the environment while are being imprinted by it, in other words they encode information from an environment that is being modified by the impact of their activities. Organisms through niche construction and interactions among them actively participate in the formation of their own inner experienced environmental representations, so accounting for an unavoidable non-formalizable self-referential loop in the relation organism/environment.

An entity that can only be defined by making reference to the context or system it belongs, and a system that can only be defined by specifying the entity we want to define to start with, cannot be mathematically computable (Rosen, 2000). EDA cannot have a mathematical formalization unless the logical loop is open up. Circular thought was eliminated by asserting that development depends on a preexisting genetic program or by affirming that the information flux goes only in one way departing from DNA; however, the attempt to solve the questions about the origin of genetic information high-

lights the need to consider the influences of environment (E) on the phenotype (P) and of the latter on the genotype (G) or of downward causality $E \rightarrow P \rightarrow G$. Likewise, the origins of body patterns, adaptations, evolutionary variations and in general the major evolutionary transitions are undeniably influenced by the environment in two senses, as a direct contributor to the form by means of physical forces, and indirectly through organisms' needs to cope with uncertainty. The Neo-Darwinian approach and the central dogma of molecular biology disregard the entailment evolution/development by doing away with closed causal loops in favor of a linear reasoning.

3.3. EDAs measure in order to cope with environmental uncertainty

I aim to substantiate the following propositions: (1) ontogeny and phylogeny are aspects of the same general transformative tendency that is driven by EDA interactions with environmental factors. (2) This general transformative tendency results in a functional compromise between: (a) increments of the phenotype's uniqueness (stability and specificity) and (b) Anticipation of environmental changes. (3) The elimination of redundancy and the increment minimization of developmental steps must be positively selected.

Let us represent this general transformative tendency as a vector that increases the mutual information content between phenotype (P) and environment (E). This vector can be decomposed into two: developmental vector represented by X-axis that describes increases in G/P mutual information content, and evolutionary vector represented by Y that describes increases in G/E mutual information content (see Fig. 2), as long as the environment remains stable. Due to the instability of the environment, it is expected evolution by drift.

EDA interact (measure) in order to acquire the information that is needed to optimize free energy extraction. Measurement is any kind of interaction between an observer system and an observed one that generates a simplified functional description of the latter (environment) by the former (EDA), (Pattee, 1995). By means of measurement, EDA filters and picks up the relevant information from the environment. An event of measurement requires: (1) recognition and (2) structural adjustments. Recognition is achieved by structural complementarity that uses a structure as a yardstick to gauge a variety of external factors. Structural adjustments narrow the set of accessible conformations, so that the number of different individual conformers for the uncoupled state is higher than for coupled states. Interactions reduce phenotypic

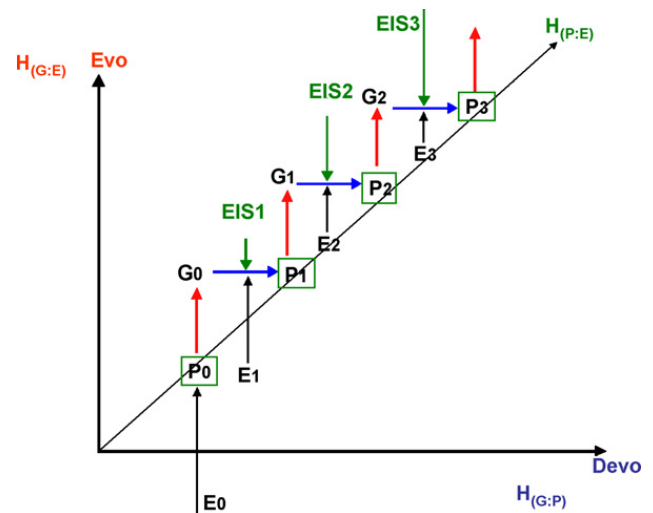


Fig. 2. The dashed diagonal shows increment in mutual information content between phenotype (P) and environment (E) in a stable environment. P_i stand for phenotypes that go from low to high uniqueness. This vector can be decomposed into two: the vertical axis shows increments of mutual information content between genotype (G) and E along evolutionary time and the horizontal axis shows increments of mutual information content between G and P along the evolution of development. E_i stand for environmental physical influence on shape that decreases with evolutionary time: $E_0 > E_1 > E_2 > E_3$. EIS_i stand for epigenetic inheritance systems that show a growing tendency along time: $EIS_0 < EIS_1 < EIS_2 < EIS_3$. Horizontal arrows from G to P stand for development at the level of individual, while vertical arrows from P to G stand for evolution at the level of the population.

plasticity producing unique and individualized states. Then, phenotype adjustments register a simplified functional description of the environment that corresponds to the set of configurations for the coupled state.

Encoding efficiency is a function of the ability to “model” the experienced world in terms of regularities. Phenotypes lack evolutionary memory and are sensitive to external influences that threaten their stability; hence genetic information buffers and stabilizes phenotypes. EDA strive to cope with the environment, and by means of reciprocal adjustments create a network, in which mutual information content between phenotype and environment tends to increase while allowing a wide span of fluctuations and flexibility. Although the adjustment phase is reversible (in the sense that the character can still disappear when the external stimulus is removed), the adjustment phase becomes a prior condition for the selection of genomic variants that fix the record irreversibly. In other words, analog records create the context in which genetic variations may arise and get fixed.

Developmental processes are subject to two forces: (1) *Firstness* is the expansive force that is responsible

for: (a) tendency to add new developmental steps and (b) combinatorial randomization of developmental steps. (2) *Thirdness* is a compressing force that is responsible for: (a) condensation (tendency of characters to appear earlier than they appear first in their ancestors) and (b) removal of late stages. The joint actions of these two forces manifest in the incremental minimization of developmental steps. This model agrees with a loose interpretation of recapitulation while accounting for neoteny and other departures from recapitulation. Agreeing with Arthur (1997, 2002) and Ekstig (1994), recapitulation is fulfilled and observed in the establishment of organization patterns of growing complexity, thus, embryos correspond to primitive life forms.

“... metazoan development reflects a legacy of past interactions between variant cell lineages arising within the ontogeny of ancestral forms. ... The fact that metazoans develop via a complex of epigenetic interactions between cell lineages is *prima facie* evidence that the principal modes of metazoan development arose as variants in the course of ontogeny ... Ontogeny must re-enact the interactions which gave rise to it”. (Buss, 1987).

Today's embryos are structurally closed or buffered to environmental influences while primitive life forms were open to them. Structural closure of today's embryos resulted from the digital symbolic internalization of environmental information. To say that primitive life forms were more open than today's embryos, means that they were flexible enough to adopt a number of alternative conformations with varying affinities for environmental elements. The phenotypic plasticity that acted as an evolutionary potential in primitive life forms, was not necessarily high because the environment was more homogeneous and less complex than present day's environment. However, for a developing egg its internal environment is still more homogeneous and less complex than the environment of primitive life forms. Thompson (1942) argued that the basic living forms can be obtained by the action of physical forces from the environment and not by the action of natural selection or even less by the exclusive action of formative inherited factors (genes). Thompson's physical shaping of living forms represents the emergence of body patterns at an early stage of evolution of multicelled organisms, and in consequence the Neo-Darwinian and Mendelian modes of shaping life had to wait for the appearance of encoded information (Newman and Müller, 2000), agreeing with the tenet that organization patterns must be inferred prior to natural selection (Denton et al., 2003; Goodwin, 1994; Kauffman, 1993).

Although Richardson et al. (1997) have shown that at very early stage in ontogeny the major classes of vertebrata have accumulated enough variations so much as to refute the existence of the *phylotypic* phase, the constancy, stability and convergence characteristic of ontogenetic early stages within classes is due to two factors: (a) the re-edition of previous environmental conditions that act on the epigenetic inheritance systems and (b) genetic information.

Following Von Baer, development is a modification from general to specific. The number of states that can be accessed diminishes under stabilizing surroundings conditions, given that measurements increment the uniqueness of the phenotype. The smoothing of the epigenetic landscape speeds up ontogeny and shortens developmental steps by interacting with external factors. Internalization of these external factors constitutes a symbolic representation that stabilizes a state of structural uniqueness while the number of neighboring conformations dynamically connected in a morpho-space may change. The reduction of redundancy is generated by the acquisition of new functions by repeated structures; in this way, new tasks can be accessed without having to lengthen the developmental trajectory excessively.

As the organism “rolls down” the epigenetic landscape, its phenotype becomes more restricted, canalized, while new ever shallower routes branch down the road, so producing individual intra-specific variations. Consequently *chreods* run deeper; a fact that makes ever more difficult further shortening of development. In other words, the epigenetic landscape is shaped as some phenotypes are functionally retained, so creating deep *chreods* that canalize ontogeny. EDA themselves demarcates the path and constantly shape the epigenetic landscape. Deeper *chreods* correspond to compressed descriptions (Kauffman, 2000) high structural uniqueness and entrenchment (Wagner and Misof, 1993; Wimsatt, 2001), while the shallow valleys correspond to redundant descriptions (i.e., low uniqueness and high plasticity).

Molecular processes like protein (Balbin and Andrade, 2002) and RNA folding (Fontana and Schuster, 1998a,b) are sensible to contextual influences given by the modification of free energy landscapes. Proteins fine-tune their free energy landscape as they interact with other molecules found in the intra cellular milieu. Evolved RNA and proteins reach higher degrees of stability with narrower spans of structural variability, represented as deep free energy valleys, whereas evolutionary potential is a function of structural plasticity, depicted as shallow bottomed landscapes. In this case,

the genetic variants that are most likely to get fixed are those that streamline folding pathways by minimizing the number of intermediary steps (Balbin and Andrade, 2002). The understanding of embryological development will benefit from the extrapolation of knowledge about protein and RNA folding because organisms modify their epigenetic landscape as they interact with their immediate environment, so reaching ever narrower spans of variations or structural plasticity. Under stabilizing conditions, it is expected that factors that reinforce this loss of plasticity tend to become fixed. Constancy in ontogeny is achieved by the influence of different factors, such as stabilization of gene networks, guidance of early ontogeny by ovule factors, presence of cytoplasmatic factors, etc. The reconstruction of the bridges between ontogeny and phylogeny will contribute to an expanded evolutionary synthesis that aims at explaining divergent evolution in terms of development without disregarding the role of genes and natural selection.

To summarize, EDA identify environmental regularities that get encoded in condensed records: (1) analog condensation is inferred by incremental minimization of developmental steps needed to obtain the phenotype and (2) the condensation of the digital record is observed in the evolution of Hox genes that has proceeded from dispersion to clustering while increasing in number. The co-linearity found in most vertebrata expresses the tendency to optimize encoding.

3.4. Development and evolution are processes of information increase

3.4.1. The phenotype/environment relation

The precursor of an EDA must have been a phenotypic life without genome of the type Fox's micro spheres, or Kauffman's autocatalytic networks (Kauffman, 1993). These precursors must have been extremely unstable and susceptible to environmental influences, since they depended on self-organization for continuity, a fact that compelled the creation of a digital re-description that made evolution possible. Following Wagensberg (2000), EDA tend to free themselves from the uncertainty of the rest of the world and in so doing respond to environmental fluctuations. The ability to anticipate environmental fluctuations is related to increasing degrees of internal coordination and plasticity. EDA strive to cope with the environment and so originate an increase of mutual information content between phenotype and environment. If this information gets incorporated into the genome, higher mutual information content between the genome and the phenotype and between the genome and the environment would be detected. While the phenotype

adjusts to the environment at the level of the individual, the increases in mutual information content between the genome and the phenotype, and between the genome and the environment are detected *a posteriori* in the population. The relations between phenotype and environment correspond to an ever-going functional interaction that produces structural adjustments or analog encoding.

Let us consider the phenotype (P) and environment (E) as informative sources. According to Shannon one obtains the following equation (Wagensberg, 2000):

$$(1)H_{(P)} - (2)H_{(P|E)} = (3)H_{(E)} - (4)H_{(E|P)} = (5)H_{(P:E)}$$

Let $H_{(P)}$ (1) stands for diversity of phenotypic states accessible to the organism independently of E that is represented by a relation in the mode [1-1]. $H_{(P|E)}$ (2) stands for conditional information or the variability of P when E is fixed. It refers to phenotypic plasticity or anticipatory capacity to E changes. It is the condition for evolvability that is represented by a relation in the mode [3-2]. $H_{(E)}$ (3) stands for the diversity of states accessible to E , that corresponds to a relation in the mode [1-1]. $H_{(E|P)}$ (4) stands for environment sensitivity, impact, or capacity of being changed by P . It corresponds to variability of E when the P is fixed, that is represented by the relation [3-1]. $H_{(P:E)}$ (5) stands for structural complementarity between P/E or the information that circulates between organism and environment. It is the condition of existence for living entities and could be represented as a relation in the mode [2-2]. Noteworthy that the variability of these values through measurement is a property of the relations [2-1] and [3-3].

The higher $H_{(P|E)}$, the higher the independence to environmental uncertainty. In a fixed environment (low $H_{(E)}$), individual independence is obtained without any need to increase $H_{(P|E)}$ and specialization becomes an advantage. By contrast in a changing environment (high $H_{(E)}$), $H_{(P:E)}$ lowers and the systems may either go extinct or conversely be compelled to make a semi-otic election that opens up a new developmental and evolutionary path. Phenotypes achieve independence by investing energy every instant, thus allowing information exchanges with the surroundings in order to maintain the constraints that delimit the interface internal/external. Phenotypes' independence is paid by exporting to the outside the effects of its inner activity, so that the ensuing increases of environmental uncertainty manifest as selective pressures that forces it to change the constraining values at the interface. Furthermore, organisms produce unforeseen environmental perturbations as they try to cope with it, and their ability to deal with them depends on their flexibility (conditional information). As environ-

mental uncertainty increases, phenotype will be selected for plasticity or ability to choose and so produce further unpredictable environmental change.

Evolution and development went from primitive phenotypes with low uniqueness to present day highly individualized phenotypes, by means of the internalization of environmental information. Primitive life forms were shaped by the environment, but as evolution went on their plasticity was buffered by genetic encoding of some phenotypic features that were originally produced by organisms' response to environmental challenges. The discrimination of surrounding's factors is brought about by coupling of structural modules with environment, thus, its diversification brings forth selection for structural differentiation and consequently for discriminating ability (incrementing $H_{(P)}$ and $H_{(P|E)}$ values simultaneously). In other words, the need to cope with the environment's uncertainty promotes growing differentiation because individual differentiation and population variability enable recognition of more features from the environment, thus making it more predictable. Therefore, individual differentiation correlates with phenotype uniqueness (stability and specificity). Remarkably, organisms increase their uniqueness by means of creating conditions for the incorporation of variations that are congruent with these tendencies.

To summarize: (1) EDA cope with the environment by increasing phenotype uniqueness, the relation in the mode [2-2]; (2) the potentiality to anticipate challenges is given by the ability of EDA to propose new behaviors or manners to relate with the environment, the relation in the modes [2-1] and [3-2]; (3) development and evolution depend mostly on independence from a changing environment by maintaining the organisms' ability to make choices, the relation [2-1]; (4) along the evolution of ontogeny, information increases are detected as modifications in developmental pathways mostly by the addition of terminal steps, the relation [1-1]; (5) in evolution, there is selection [3-1], for phenotypic or developmental plasticity.

3.4.2. *The genotype/phenotype and genotype/environment relations*

Every EDA acts within a network of agents that all together are part of the environment. Increases in mutual information content between phenotype and environment are the prior condition for further increments in both mutual information content between genotype and phenotype, and between genotype and environment. Specifically, the tendency to increase the content of mutual information between the digital record and

the analog record, $H_{(G:P)}$, is the means to enhance the autonomy of EDA in stable environment. Structural uniqueness rises at the interface that permits the genetic assimilation of evolutionary innovations by the conversion of analog into digital information (Andrade, 2000, 2002, 2004). Gathered information enhances evolutionary potential after being copied into a digital format (genetic record). The problem is how information about environment gets recorded in a digital format; a phenomenon that is partially explained by genetic assimilation (Waddington, 1957, 1961). Only the digital is inherited in the standard Mendelian way, other kinds of variation can be transmitted by means of epigenetic inheritance systems (EIS) whose lasting contribution to evolution depends on its incorporation into the genetic record. Information can be incorporated into the digital record only if its corresponding analog version has been produced and stabilized by the action of the external stimulus. Analog records are reversible and unstable; nonetheless they favor the fixation of mutants that produce the same feature that organisms develop in presence of the external stimulus. Once incorporated, the organism develops the feature even if the stimulus is removed. It all boils down to saying that the evolutionary contribution of individual storage of analog information is the creation of the context in which genetic variants arise and may get fixed.

The digitalization of information manifests as increases in $H_{(G:P)}$ and $H_{(G:E)}$ that lags behind $H_{(P:E)}$ increases. In short, phenotype uniqueness is evolutionary achieved by internalization of information from the environment in the form of modifications of developmental routes. The modifications that are more likely to arise, affect terminal steps (like additions, deletions and substitutions) because they are less likely to affect inner coordination, although duplication of intermediary steps, and permutation may also be retained for their congruence with environmental changes. These processes, in as much as they contribute to streamline ontogeny, exert a pressure to minimize the increment of genetic record (digital) as well. Thence, EDA become more dependent on their genetic and structural constraints and less dependent on the environment.

To summarize, the evolution of ontogeny is a process of information gain expressed as increases of mutual information content between genotype and phenotype, though the phenotype never reaches a state of full determination by the genetic record. Likewise, phylogeny is a process of information gain expressed as increases of mutual information content between genotype and environment, though external information is only partially incorporated into the genome.

4. Conclusions

In reference to EDA, the differentiation between *ontic* and *epistemic* descriptions is problematic (Atmanspacher, 2002). Environmental uncertainty can be interpreted as *ontic* description of intrinsic structural probabilities that can be attained by EDA. However, at the same time, it can be regarded as *epistemic* for it refers to environmental uncertainty from the viewpoint of EDA, the very fact that uncertainty diminishes with measurements means that it is *epistemic*. In the same way, encoded digital information is necessarily *epistemic* because it refers to what was incorporated as knowledge by the EDA; however, this knowledge becomes *ontic* as long as it can be identified objectively as an analog (phenotype) and/or digital record (genetic).

The study of the interrelations between genotype, phenotype and environment explains how evolution cannot depend on random variations, but on the joint action of internal/external and individual/population factors that give a “more or less” directed response based on semiotic choices that minimize risks. To assert that all variations are random is to reject the very possibility of evolution; on the other hand, to say that all variations are directed means that evolution is preprogrammed leaving no room for original innovations, freedom and creativity. Variations are the very products of semiotic choices neither directed, nor random but canalized. Chance occurs within the more or less flexible thresholds that canalization allows. This is a model that cuts down chance without falling into the opposite mistake, a goal directed evolution. Choices are made within a somewhat restricted span of possibilities but specific choices that will be selected depend on evaluations made by EDA. But these choices bring forth new possibilities that were unforeseen before they were made, so that potentiality, [1-1], is always renewed. *Firstness* brings in the freshness of an evolutionary impetus within an evolutionary law given by *Thirdness*.

Organisms' interactions with the environment account for the relations between ontogeny and phylogeny, which are not of cause/effect but rather of mutual entailment. If it were merely a matter of breaking up this logical loop, as mainstream science has done by placing variation prior to selection, and genetic information prior to form, then following the same logic ontogeny should be considered prior to phylogeny. This priority expresses the fact that ontogeny is the source of individual evolutionary variations and also is a process in which a digital text is translated into an analog representation. Therefore, one would be forced to assert that ontogeny is the causal agency of evolution. However, in keeping with

the self-reference between ontogeny and phylogeny, I would rather justify the idea of a general transformative tendency that manifest at two different time frames.

The cartography of Peirce's six relations (Taborsky, 2002, 2004) not only helps to understand how the discourse of biology came to be structured but also provide the ontological framework for the interpretation of empirical data. The physical organization of EDA is encoded in the analog [2-1] and [2-2] modes but its agency is associated to [3-1] and [3-2] relations. EDA are the phenotypic interface where environmental and genetic information are instantly interpreted; the interaction with the environment provokes physiological, behavioral and EIS adjustments that switch on and off existing genes while creating condition for further assimilations of new genes.

Newman and Müller (2000) assert that the relationship between genes and form is a derived condition, a product of evolution; genes came late and became the informative source that open up new possibilities, some of which will be actualized by EDAs semiotic elections. This model explains also why there is a tendency to retrieve developmental programs that are as short as they can be, and which minimize increments of developmental steps. This phenomenon explains why strict recapitulation cannot happen, though the core of this hypothesis is preserved, that is to say, that novel evolutionary variation arose as organisms' reaction to the environment in free living ancestors in their juvenile stages through changes in behavior that paved the way for the genetic fixation of some modifications. To conclude, natural selection favors EDA phenotypic plasticity as a factor that minimizes the risk of implementing semiotic choices with insufficient information.

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