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A Semiotic Analysis of the Interface between Evolutionary and Developmental Processes

Eugenio Andrade

Department of Biology
Universidad Nacional de Colombia, Bogotá, D.C.
Mailing address: A.A. 330413. Bogotá, D.C. Colombia.
E-mail: leandradep@unal.edu.co
Phone: 57-1-3165000 Ext. 11313

Abstract: This work proposes the notion of organisms as Evolving Developing Agents (EDA) in order to ground an internalist model in which evolution and development are conceived as aspects of a general transformative tendency driven by organism's need to cope with environmental uncertainty. It is shown how the integration Evo/Devo contributes to an expanded evolutionary synthesis that accounts for divergent evolution in terms of development, without disregarding the role of genes and natural selection. However this integration has to be seen as a specific case that contributes to the contextualization of C.S.Peirce's evolutionary ontology founded on three universal categories and six space/time/function relations, as described by Taborsky. The role played by the EDA is characterized by the *Secondness as firstness* relation for it merges the internal/ external, and individual/population and present/past/ progressive cuts that permeate the discourse of biology.

Keywords: development, evolution, Evolving Developing Agents (EDA), semiosis, Peirce, epigenetic landscape (EL), Developmental Systems Theory (DST).

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1 Introduction

Evolutionary thinking, as it was framed by the Lamarckian, Darwinian, Neo-Darwinian and Epigenetic schools, evokes a scheme of reality that surpasses classical mechanical ontology in breath and depth. This claim is rarely made explicit by students and researchers of biology. In this article I will show how this claim fits with Peirce's cartography of three fundamental categories: *Firstness* (1), *Secondness* (2), and *Thirdness* (3) and the derived six relations of modes of encoding (1-1; 2-1; 2-2; 3-1; 3-2; 3-3) that he originally thought as being a general way to characterize all of existing. I will show how 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.

1.1 The Lamarckian internal/external cut

Lamarck drew a dividing line between "internal" and "external" zones and confined the living to the so created internal space. This distinction was ontological and allowed to frame a specific discourse for biology. Lamarck (1803) postulated a transformation of the form by the influence of circumstances upon the habits of the organisms. In this view, organisms' "inner drive" enabled them to respond to external influences by increasing differentiation of the body parts, while the coherence of the organism´s activity was preserved (Lamarck 1803). The transformations of living forms were likened to embryological processes dependent on intrinsic and extrinsic factors. The former plays the primary role and corresponds to the vital force that tends to make organization more complex in accordance with the Plan of Nature (Burkhardt 1995), that he wished to explain in terms of physical forces like heat and electricity. The latter corresponds 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 (1803) distinguished between organism's inner impulses that produce the basic pattern of the form and the environment that shapes the external secondary features (Burkhardt 1995). Despite the fact that the idea of transformation is put forward, the notion 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 independent events of spontaneous generation.

A number of authors including Darwin related 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). This tight entailment between ontogeny and phylogeny is best expressed in theory of recapitulation.

"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." (Haeckel 1879, cited according to Raff and Kaufman, 1983).

Accordingly, the same laws ruled both the evolution of species and the development of embryos. Haeckel justified recapitulation by asserting that evolution proceeds by continuous additions of new steps to growth. 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 adult form appear earlier in their descendants. Following Richards (1992), Darwin (1836-1844) argued that embryological development evolved by terminal additions produced as a response of the organisms to the external conditions of life. The axis-Y shown in figure 1, divides the internal (left) from the external (right) zones. Individual development corresponds to a transition from "II" (internal individual potentiality) to "I" (external individual completion).

1.2 The Neodarwinian individual-local/population-global cut and the semiotic perspective

Darwin established a distinction between individuals and populations; nonetheless the formal incorporation of this distinction into evolutionary theory was credited to Fisher, who introduced statistical analysis and fostered the idea that individual properties were deviations from statistical averages. Explanation in terms of natural selection became the accepted cause of transformation, assuming that specific variations were retained for their adaptive advantages or positive contributions to problem resolution. Evolution was no longer accounted for in a physical manner but perceived as a series of steps in which only one was favored among different possible options. Therefore, evolutionary theory cannot be predictive. The individual/population or local/global cut brings in a continuous dynamics that opens up to the future within a global evolutionary time.

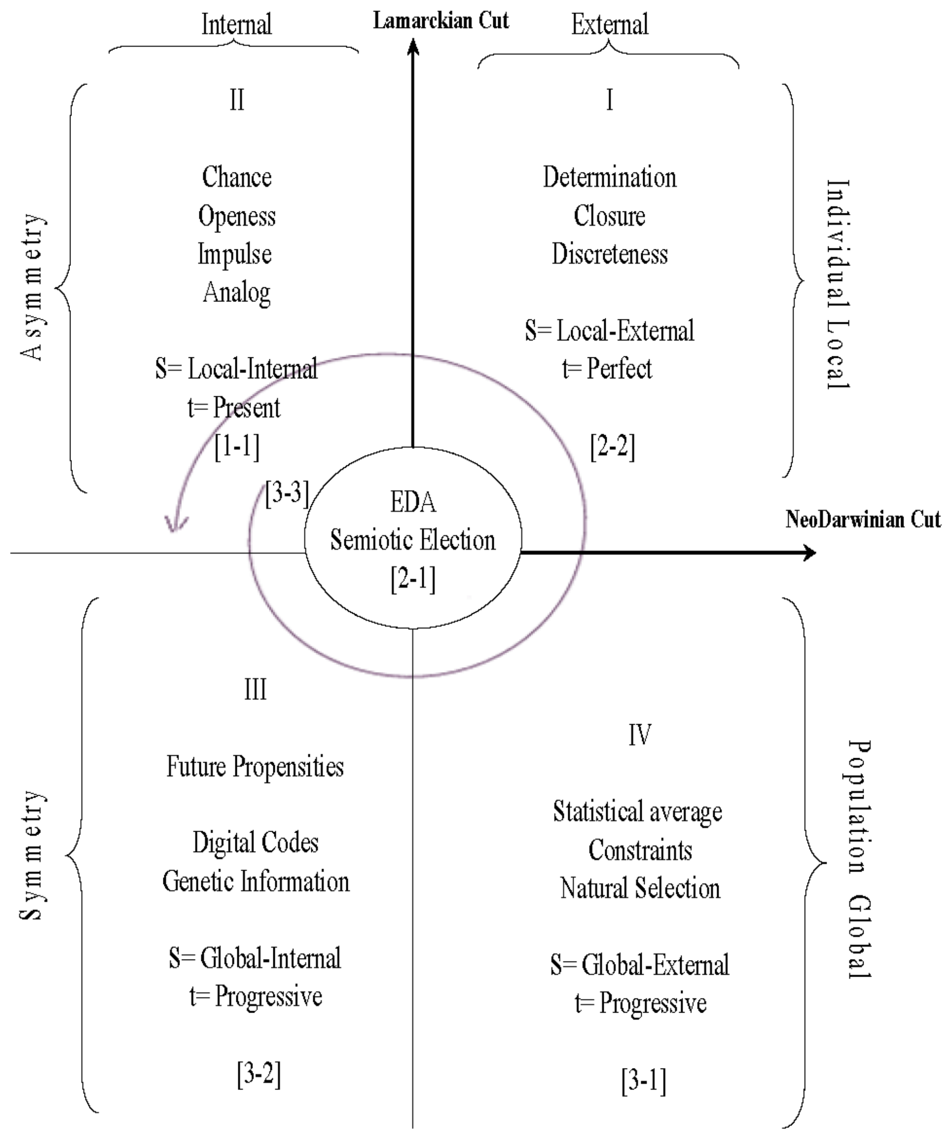

Figure 1: The Lamarckian/Neodarwinian Quadrant (modified after Taborsky 2004). The Y-axis refers to the Lamarckian cut and the X-axis to the Neodarwinian one. This is meant to show how an integrated discourse of biology match the six Peirce relations derived from the three universal categories *Firstness*, *Secondness* and *Thirdness*.

Figure 1, shows the two lower quadrants III (internal/global i.e. genetic information) and IV (external/global i.e. statistical regularities produced by natural selection) created by the X-axis cut. Evolution is depicted as a movement from quadrant IV to III, which is mediated by natural selection whose action is expressed in the progressive time.

Yet according to Weissman, the study of evolutionary influences derived from organism/environment interaction must take into account that the phenotype (P) is determined by the prescriptions encoded in the genotype (G) so that the modifications of P by the action of environment (E) cannot affect G. This reasoning inspired the central dogma of molecular biology in the nineteen fifties. The idea of the gene as a discrete, determined and closed entity led to population evolutionary research on the changes in genetic composition by natural selection. This approach gave outstanding results and furnished evolutionary theory with a mathematical formalism. Nonetheless, it led to the understanding of organisms as non-autonomous entities determined by two opposing causes: G and E. Neo-Darwinians consider that E 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, very few possess an adequate fit to E.

According to this view organisms vary and react randomly without any inner representation of E, so that their problem solving activity in adaptation becomes a metaphor! Insofar as organisms are not understood as agents, random and deterministic factors are confined exclusively to either genes or 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 the concept of individuals' intentionality. With the rise of genetic determinism it was thought that since the embryo was genetically preprogrammed, closed and oriented to a specific goal (the adult stage), it could not contribute to the production of evolutionary novelties. Thence, the embryological approach became a secondary consideration.

The idea of evolution as an open process in which some steps lead to choices among real options had been difficult to accept in the nineteenth century. Nevertheless the continuing idea of evolution as an open process with choice and real options indicated that it was more adequate to conceptualize evolution as an analog of intentional systems.

Darwin had written:

"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).

Following Darwin, it is tempting to see evolution as a process in which the population would play the role of a non local subject, it is in this sense that the individual/population distinction can be equated with Taborsky's epistemic cut. Unfortunately Neo-Darwinians neglected the internal zone (see quadrants I and IV in figure 1), and by restricting themselves to natural selection, ran contrary to the internalist position of Darwin who stood close to recapitulation (Richards 1992, Darwin 1838, 1838-1844 and 1859) 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 postulated the influence of organisms' actions on heredity in his theory of pan-genes (Darwin 1888).

The diversity of evolutionary factors proposed by Darwin was the reason that moved Peirce to see the triad, Variation, Heredity and Selection, as an outstanding case in which his own three universal categories manifested (C.P. 1.398-1.399). *Firstness* corresponds to spontaneity, inner drives, chance, randomness, pure potentiality and evolutionary variation; *Secondness* corresponds to reaction, discreteness, determination, actuality, heredity of stable and fixed characteristics; and *Thirdness* corresponds to mediation, agency, habit, continuity and natural selection. *Thirdness* is associated with processes that generate regularity and symmetry, or the manifestation of an evolutionary law considered as a generalizing tendency to take habits. *Thirdness* so considered is the equilibrating tendency that is produced as a consequence of the open systems' drive to attain states far from equilibrium. 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 (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" (C.P. 7.515).

Peirce's scheme goes beyond the Cartesian mind/matter dualism and in consequence overcomes the ensuing dualisms internal/external, individual/population, local/global, and temporal cuts present/perfect/progressive, because semiosis explicitly rejects the existence of absolute substances but instead postulates a mind-matter continuum that manifest a network of relations. There are six basic relations that are generated from the three Peirce's universal categories, (Taborsky 2002, 2004): 1) *Firstness as Firstness* [1-1], defines the local internal field in a present time. It corresponds to impulses, drives, unbound information, chance, spontaneity, potentiality existent at present time. It is an internal analog code represented in figure 1 by quadrant II. 2) *Secondness as Secondness* [2-2], defines the external local field in a perfect time. It corresponds to what is determined, 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 figure 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 state that allows the analog/digital code conversion (Andrade, 2002) and promotes the establishment of couplings 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 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. It corresponds to future propensities and possibilities generated by encoded digital information. 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. It is represented by the spiral in figure 1.

Following Taborsky (2004) morphological units like organisms are functionally selected signs composed by three of the six relations in which at least one 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 (mutation) or from without (environmental fluctuations). The analytic dissection of these six spatial-temporal-functional zones would permit to examine the relationships between ontogeny and phylogeny.

2 Developmental Systems Theory and Evolving Developing Agents

Scientists 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 individual variations, so neglecting the influence of development in their production. Mainstream biologists affirm that embryos develop according to a genetic program encoded in Hox genes, a standpoint that overlooks the existence of developmental factors other than genes. But to what extent, is ontogeny a deterministic process guided by the information contained in the genes? To what extent is ontogeny influenced by factors other than genes? 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, however one of the advantages of semiosis is that it frees ontogeny from interpretations grounded on natural philosophy. Thus, ontogeny is explained as a non-programmed open ended process. The traditional preformists vs. epigeneticists dispute reappears today as the “Evo/Devo” debate over the roles that must be assigned to genetic information and epigenesis in the production of living forms. Oyama (2001) asserts that genetics is preformism in a new guise inasmuch as development is thought to be a gene programmed process in which the formative factors preexist in an encoded way. On the other hand, epigeneticists 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 (the nature of the organism) or by nurture (the conditions of life) (Andrade 2004). Likewise, it would bridge micro and macro evolution.

Waddington (1957, 1961) visualized the *canalization* of development, as a ball running down through the valleys of an epigenetic landscape (EL) whose features are shaped by both a genetic network and the environment. He argues that G and E do not cause phenotypic traits directly; instead as development goes on the EL opens up new routes and deepens some others. The EL is a dynamic interface between the genetic endowment of the egg and the environment and is permanently tuned by the developing organisms (Waddington 1961). (See figure 2).

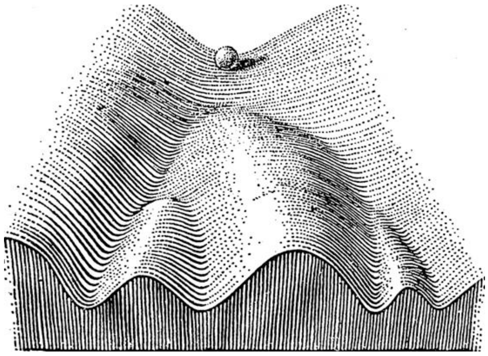

Figure 2: Waddington’s epigenetic landscape interpreted as a dynamic interface between genes and environment

The concept of “genetic assimilation” (Waddington 1957) accounts for the fixation of genetic configurations that reinforce the effect produced by external stimuli on individuals. In early stages of development the epigenetic process are influenced by external morphogenetic factors that act on cellular aggregates (Goodwin 1994, Ho et al. 1979, Jablonka et al. 1995, Jablonka et al. 1998, Newman et al. 2000). Here, external determinant morphogenetic factors can be 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 the production of constitutive proteins. In other words, genes came late to consolidate epigenetic processes (Newman et al. 2000, Salazar-La Ciudad et al. 2003).

Molecular processes like protein (Balbin et al. 2004) and RNA folding (Fontana et al. 1998a, 1998b) are highly sensible to environmental influences that modify the free energy landscapes. Proteins fine tune their free energy landscape as they interact with other molecules found in the intra cellular milieu. Evolved RNA (Fontana et al. 1998a, 1998b) 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 (see figure 3).

In this case the genetic variants that streamline folding pathways by minimizing the number of intermediary steps are most likely to get fixed (Balbin et al. 2004).

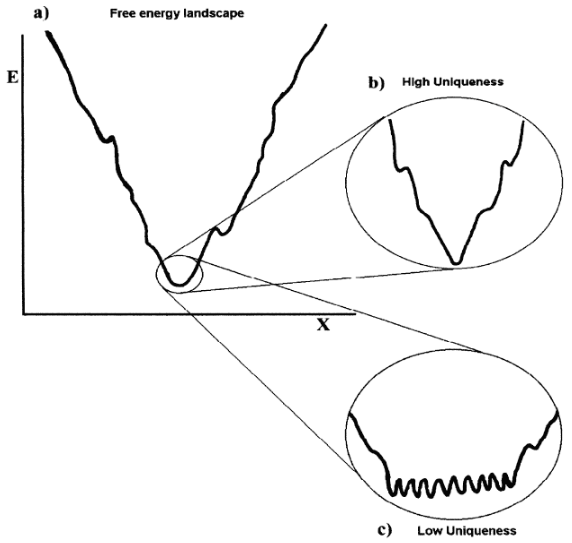

Figure 3: Energy is plotted on the vertical axis and structural conformations on the horizontal axis. A free energy landscape is depicted by a funnel-like shape (a). The details of the landscape surface around the bottom of the valleys would be determined by the uniqueness of the native structure. Proteins with high uniqueness would be found in a smooth bottom landscape (b) while structures with low uniqueness would be located in a rugged bottom landscape (c).

In like manner 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 due to the influence of different factors, such as stabilization of gene networks, guidance of early ontogeny by ovule factors, presence of cytoplasmatic factors, etc.

Developmental Systems Theory (DST) explains phenotype construction within the context of epigenetic and environmental interactions. P is the developing organisms' analog record that cannot be decomposed into separate G and E contributions, or the structure of an organism that determines moment by moment its way of interactions to E in the course of its ontogeny (Andrade 2004). The reconstruction of the bridges between ontogeny and phylogeny will explain divergent evolution in terms of development without disregarding the role of genes and natural selection.

Ontogeny depends on analog information (Hoffmeyer at al. 1991, Hoffmeyer 1996) that according to figure 1 can be divided into external and internal zones encoded in the [2-2] and [1-1] modes respectively (see figure 1, quadrants I and II). Analog information refers to the recognition of patterns by structural motifs of the agent within a continuous threshold of variability. It implies that agents recognize through structural complementarity, so leading to the establishment of non-random reversible interactions (Root-Bernstein et al. 1997, Andrade 2002). These interactions among inner constitutive components preserve coherence of the individual as it interacts with E. Analog recognition of external factors guides the internalization of information by interactions and measurements (Andrade 2004). The internal and external analog zones are connected through the epigenetic inheritance system (EIS) (Jabonka et al. 1992, Jablonka et al. 1998, Smith et al. 2001) since an adjustment to an external factor implies a readjustment of inner states; that is the reason EIS can be represented by the epigenetic landscape interface (see figure 2).

By contrast, digital information (DI) is encoded information in a text-like record composed of basic symbols (DNA); its discontinuous variations produced by mutation, recombination, permutation give rise to potentially different functional content. In figure 1 DI is encoded in the [3-2] mode, which is associated with the definition of future propensities. Genes do not belong to the relation [2-2] because their discreteness is a Mendelian approximation that does not hold at the DNA level since they overlap, are physically discontinuous or intervened by other sequences, can be found within other coding sequences, and their continuity is observed only at the RNA level. Instead, genes make up part of a functional informational network 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 E, that is the survival of the best encoders of environmental information.

Currently, these two dualities (internal/external) and (individual/population) are 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 et al. 1994, Oyama 2001).

A semiotic approach asserts that there is a real interpretation of all informative resources by the developing organisms. I propose the notion of Evolving and Developing Agents (EDA) as a way to formalize a theory of organisms as systems of interpretance that choose between alternative ways in order to relate with external factors. The term merges development and evolution to the extent that both processes are mediated by the agency of the organisms themselves.

The upper quadrants in figure 1 correspond to asymmetric relations while the lower ones account for symmetry or regularities that are properties of *Thirdness*. Considering the potentiality derived from DI (quadrant III), ontogeny is the transformation from G to P 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 P to G by means of an interpretation of the ecological niche by the population or lineage (Hoffmeyer 1996).

Ontogeny and phylogeny are tightly entailed. To grasp the complexity of these processes requires the specification of the internal/external and individual/population interface encoded in the [2-1] mode that I dub as Evolving Developing Agents (EDA). Agents explore, starting randomly with measurements of the possibilities of E, and as information is being gathered measurements get more oriented. Measurement is any kind of interaction between an observer system and an observed one that generates a simplified functional description of the latter by the former (Pattee 1995, Andrade 2000). Nonetheless, there will never be enough information that assures the best choice, so that EDA are compelled to make choices in order to minimize risk. EDA pick up input information in order to enhance adaptability and capacity to promote individual diversity, so opening up future possibilities.

EDA 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 G and E resources that leads to the availability of many options. DI 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*, through the relations [3-1] and [3-2]. By capturing free energy, they link to the relation [1-1]. The interface [2-1] interacts for network construction. And the relation [2-2] is mechanical and does not contribute to information exchanges. The interface [2-1] is always being trespassed in either direction: 1. Environmental uncertainty decreases by means of measurements. 2. Environmental uncertainty increases with record erasure and environmental change.

EDA must be studied simultaneously in two time-frames (ontogenetic and evolutionary) so explaining ontogeny and phylogeny common characteristics such as: 1. Self-reference. 2. Information increase. 3. Open-endedness. 4. Lack of a prior program. And 5. Irreversibility. In both cases, the record reflects their knowledge about the state of the system. The ontogenetic (analog) record is given by P and has two measurable parameters: (1) Specificity (how specific is its relation with a particular environmental factor); (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.

Noteworthy, EDA's activity in ontogeny defines and canalizes 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, in agreement with the recapitulation theory according to which 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 became pushed back to earlier ontogenetic steps became part of a descendant species *Bauplan* (Wagner et al. 1993, Wimsatt 2001).

The central dogma of molecular biology states the impossibility of modifying G by the action of P during individual life cycle, but it does not preclude the change of G in populations by selection of the fittest P. Besides, the increment of information during individual life time expressed as modification of Epigenetic Inheritance Systems (EIS), does not violate the central dogma.

Organisms as EDAs are information encoders (G) and niche constructors (E). G and E partially specify the ontogeny of their offspring, in other words, as development goes on, the P in permanent contact with the E modulates EL and regulates gene expression. The internalist approach highlights the inseparability between subjective and objective reality as EDA permanently shape E while are being imprinted by it, in other words they encode information from an E 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 (*Umwelt*), so accounting for an unavoidable non-formalizable self-referential loop in the relation organism/environment. In a living world composed of EDA, ontological chance (observer independent) is the agents' epistemic uncertainty (observer dependent). Chance as a property of *Firstness* refuels evolutionary potential and life's 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).

A system that can only be defined by making reference to the context or totality it belongs, a totality that can only be defined by specifying the object we want to define to start with, cannot be mathematically computable (Rosen 2000). Therefore, 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 highlights the need to consider the influences of E on P and of P on G or of downward causality E → P → G. Likewise, the origins of body patterns, adaptations, evolutionary variations and in general the major evolutionary transitions are undeniably influenced by E in two senses, as a direct contributor to the form by means of physical forces, and indirectly through organisms' needs to cope with uncertainty (Andrade 2004).

The neodarwinian approach to evolution and the central dogma of molecular biology did away with closed causal loops in favor of a linear reasoning. Yet development and evolution make part of a mutually entailing loop that refers to the transformation of life forms.

3 EDAs measure in order to cope with environmental uncertainty

I aim to substantiate the following proposition about a General Transformative Tendency. *Ontogeny and phylogeny are aspects of the same General Transformative Tendency that is driven by EDA interactions with environmental factors and results in a functional compromise between: (a) Increments of the phenotype's uniqueness (stability and specificity), and (b) Anticipation of environmental changes. In consequence 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 P and 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 figure 4).

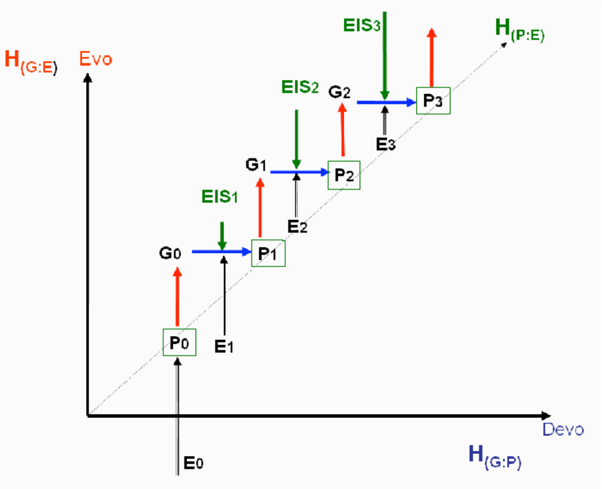

Figure 4: The dashed diagonal shows increment in mutual information content between P and E in an stable E. P_i stand for phenotypes that go from low to high uniqueness. This vector can be decomposed into two: the vertical axis shows increments of mutual information content between G and E along evolutionary 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 or Thompson's forces (Thompson, 1942) 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.

An EDA interacts (measures) 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 (E) by the former (EDA) (Pattee 1995, Andrade 2000). By means of measurement, EDA filters and picks up the relevant information from E. An event of measurement requires: (1) Recognition. (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 plasticity producing more unique and individualized states. Then, P adjustments register a simplified functional description of E 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, the more regularities are detected, the shorter the description. Phenotypes lack evolutionary memory and are sensitive to external influences that threat their stability; thence G buffers P. EDA strive to cope with E, and by means of reciprocal adjustments create a network, in which mutual information content between P and E 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 (Balbin et al. 2004).

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 predicts evolution by neoteny and other departures from a strict interpretation of recapitulation (according to which every ontogenetic step should reflect phylogeny). Also branching evolution is facilitated by the addition of new steps over processes in which the late stages had been removed. Notwithstanding recapitulation is fulfilled and observed in the establishment of organization patterns of growing complexity (Arthur 1997 and 2002, Ekstig 1994).

Following Von Baer, development is a process of modification from general to specific. The number of states that can be accessed diminishes under stabilizing E conditions, given that measurements incremen the uniqueness of P. The smoothing of EL speeds up ontogeny and shortens developmental steps by interacting with E factors. Internalization of these factors constitutes a symbolic representation that stabilizes a state of structural uniqueness while the number of neighboring conformations dynamically connected in a morpho-space varies. 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 EL, its P becomes more restricted, canalized, while new ever shallower routes branch down the road, so generating individual intra-specific variations. Consequently *chreods* run deeper; a fact that makes ever more difficult further shortening of development. In other words, EL is shaped as some phenotypes are functionally retained, so creating deep *chreods* that canalize ontogeny. EDA themselves demarcates the path and constantly shape the EL. Deeper *chreods* correspond to compressed descriptions, high structural uniqueness and entrenchment (Wagner at al. 1993, Wimsatt 2001), while the shallow valleys correspond to redundant descriptions (i.e. low uniqueness and high plasticity).

To summarize, EDA(s) identify E regularities that get encoded in condensed records: (1) Analog condensation is inferred by incremental minimization of developmental steps needed to construct the phenotype. (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.

4 Conclusions

The notion of EDA 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 inner drive within an evolutionary law given by *Thirdness*.

The relations between ontogeny and phylogeny 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 model I have presented facilitates the formalization of Developmental Systems Theory, so highlighting Oyama's (2001) valuable contribution.

Taborsky's 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 Muller (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 EDA's 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 factors that minimize the risk of implementing semiotic choices with insufficient information.

References

Andrade, E. (2000) From external to internal measurement a *form* theory approach to evolution. In: BioSystems, 57. pp 49-62.

Andrade, E. (2002) The organization of Nature: Semiotic agents as intermediaries between digital and analog informational spaces. In: SEED Journal (Semiosis Evolution Energy Development), 2(1). pp 56-84.

Andrade, E. (2004) On Maxwell's demons and the origin of evolutionary variations: and internalist perspective. In: Acta Biotheoretica, 52. pp 17-40.

Arthur, W. (1997) Animal Body Plans, A Study in Evolutionary Developmental Biology. Cambridge University Press.

Arthur, W. (2002) The emerging conceptual framework of evolutionary developmental biology. In: Nature, 415. pp 757-764.

Balbin, A., Andrade, E. (2004) Protein folding and evolution are driven by the Maxwell demon activity of proteins. In: Acta Biotheoretica, 52. pp 173-200.

Burkhardt, R.W. jr. (1995) The Spirit of System. Lamarck and Evolutionary Biology. Cambridge/Massachusetts, London/England. Harvard University Press.

Darwin, C. 1838 Notebook E, MS pp 83-84, In: P. Barret, P. Gautrey, S. Herbert, D. Kohn and S. Smith (Eds.) (1987) Charles Darwin Notebooks, 1836-1844: Geology, Transmutation of Species, Metaphysical Enquiries. Ithaca. Cornell University Press. pp 418.

Darwin, C. 1836-1844. Red Notebook, MS pp. 127-130 and Notebook B, MS pp. 163, In: P. Barret, P. Gautrey, S. Herbert, D. Kohn and S. Smith (Eds.) (1987) Charles Darwin Notebooks, 1836-1844: Geology, Transmutation of Species, Metaphysical Enquiries. Ithaca. Cornell University Press. pp.61-62, 211.

Darwin, C. (1959) The origin of species, First edition. London. John Murray.

Darwin, C. (1888) Animals and Plants under Domestication. 2nd edition, Vol. 2. Londres. John Murray.

Ekstig, B. (1994) Condensation of developmental stages in evolution. In: BioScience, 44. pp 158- 164.

Fontana, W., Schuster, P. (1998a) Continuity in Evolution: On the Nature of Transitions. In: Science, 280 (1998). pp 1451-1455.

Fontana, W., Schuster, P. (1998b) Shaping Space: the Possible and the Attainable in RNA Genotype-Phenotype Mapping. In: Journal Theoretical Biology, 194 (1998). pp 491-515.

Griffiths, P.E., Gray, R.D. (1994) Developmental systems and evolutionary explanation. In: Journal of Philosophy, 16. pp 277-304.

Goodwin, B. (1994) How the leopard changed its spots. London. Weindelfeld and Nicolson.

Haeckel, E. (1879) Evolution of Man. Quoted by R.A. Raff , T.C. Kaufman (1983) Embryos, Genes, and Evolution. The Developmental-Genetic Basis of Evolutionary Change. Indiana University Press. p.13.

Ho M. W., Saunders, P. (1979) Beyond neo-darwinism. An epigenetic approach to evolution. In: Journal Theoretical Biology, 78. pp 573-591.

Hoffmeyer, J., C. Emmeche (1991) Code-Duality and the Semiotics of Nature. In: Anderson, M., Merrell, F. (Eds.) On semiotics of Modeling. New York. Mouton de Gruyter. pp 117-166.

Hoffmeyer, J. (1996) Signs of Meaning in the Universe. Bloomington. Indiana University Press.

Jablonka, E., M. J. Lamb (1995) Epigenetic Inheritance and Evolution. The Lamarckian dimension. Oxford. Oxford University Press.

Jablonka, E., M. J. Lamb (1998) Epigenetic inheritance in evolution. In: Journal of Evolutionary Biology, 11. pp 159-183.

Jacob, F. (1982) The Logic of Life. A History of Heredity. New York. Pantheon Books.

Lamarck, J.B. (1803) Zoological Philosophy, Hafner, translated by H. Elliot and reprinted in 1963, New York.

Newman, S. A., Müller, G. B. (2000) Epigenetic Mechanisms of Character Origination. In: Journal of Experimental Zoology, 288. pp 304-317.

Oyama, S. (2001) The Ontogeny of Information. 2nd revised edition. Durham. Duke University Press.

Pattee, H.H. (1995) Evolving self-reference: matter, symbols, and semantic closure. In: Luis Rocha (Ed.) *Communication and Cognition - Artificial Intelligence* (Special issue Self-reference in biological and cognitive systems), 12 (1-2). pp 9-27.

Peirce, C.S. (1965) Collected Papers. Cambridge MA. Belknap Press. In: Obra Lógico Semiótica tr. and ed. Armando Sercovich, Taurus Ediciones, Madrid, 1987.

Peirce, C. S. (1931-1958) Collected Papers of Charles Sanders Peirce. Vols.1-8. C. Hartshorne, P. Weiss, and A. W. Burks (eds.). Cambridge, MA. Harvard University Press. CP 1.409. 1.415. 1.416.

Richards, R.J. (1992) The Meaning of Evolution. The Morphological Construction and Ideological Reconstruction of Darwin's Theory, Chicago. University of Chicago.

Root-Bernstein, R.S., Dillon, P.F. (1997) Molecular Complementarity I: the complementarity theory of the Origin and evolution of Life. In: Journal of Theoretical Biology, 188 (1997). pp 447-479.

Rosen, R. (2000) Essays on Life Itself, Complexity in ecological systems series. New York. Columbia University Press.

Salazar-La Ciudad, I., Jernvall, J., Newman, S. (2003) Mechanisms of pattern formation in development and evolution. In: Development, 130. pp 2027-2037.

Smith, J.M., Szathmary, E. (2001) The Major Transitions in Evolution. New York. Oxford University Press.

Taborsky, E. (2002) The Six Semiosic Predicates. In: SEED Journal (Semiosis, Evolution, Energy, Development), 3(2). pp 5-23.

Taborsky, E. (2004) The Nature of the Sign as a WFF – A Well-Formed Formula. In: SEED Journal **(**Semiosis, Evolution, Energy, Development**),** 4(4). pp 5-14.

Thompson D'Arcy (1942) On Growth and Form. Cambridge. Cambridge University Press.

Waddington, C.H. (1957) The Strategy of the Genes. London. Geo Allen & Unwin.

Waddington, C.H. (1961) Genetic assimilation. In: Advanced Genetics, 10. pp 257-293.

Wagner, G.P., Misof, B.Y. (1993) How can a character be developmentally constrained despite variation in developmental pathways?. In: Journal Evol. Biology, 6 (1993). pp 449-455.

Wimsatt, W.C. (2001) Generative Entrechment and the Developmental Systems Approach to Evolutionary Processes. In: Gray, R., Griffith, P., Oyama, S. (2001) Cycles of Contingency. Boston. MIT Press.