

The Interrelations between Genotype/Phenotype/Environment: A Semiotic Contribution to the Evo:Devo Debate

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Abstract

Seemingly opposite views of evolution and development that conflict over the role assigned to either or structure/function, genes/environment, random/directed variations, innate/acquired characteristics, instructive/selective information, self-organization/natural selection, are still hotly debated. This conflict results from the self-referential loop present in the ontic (internal/external) and epistemic (individual-local/population-global) cuts, that together contribute to integrate developmental and evolutionary theories. It is assumed that development and evolution are non-programmed open ended processes of information increase. Organisms are modeled as Evolving Developing Agents that codify environmental information and possesses a general transformative tendency to 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 parallel and interwoven scales: individual life cycle (ontogeny) and species time (phylogeny) respectively. Developmental terminal additions along with the minimization of developmental steps must be positively selected. This approach shows how the six Peircian space/time/function relations described by Taborsky provide a conceptual framework that favors this unifying view.

Keywords: Genotype (G), Phenotype (P), Environment (E), development, evolution, information, self-reference, Evolving Developing Agents (EDA), semiosis.

1. Introduction

The Lamarckian internal/external cut:

The problem about the manner in which the relations between organisms and environment influence evolutionary change goes back to the birth of modern biology with Lamarck's distinction between internal and external realms. A divide made on the assumption that a spontaneous rupture of homogeneous symmetry was associated with the generation of life and the environment. This distinction was a *sine qua non* condition for the foundation of biology as a natural science by providing it with an object with intrinsic lawful properties. This is equivalent to the ontological cut (Atmanspacher 2002, Tabor-sky 2002, 2004), for it defined a biological realm as ontologically distinct from the physico-chemical inorganic world. Organisms were, then, conceived as sentient beings with inner impulses and organized structure that enabled them to respond to external environmental influences. The *Inner Sentiment* or capacity to act in a coordinate way was directly dependent on organization (Burkhardt 1995). The increasing differentiation was associated to an ever higher sophistication of the systems of inner coordination so that the activity of the organisms as a coherent and cohesive whole was preserved (Lamarck 1803). The transformations of living forms were perceived as embryological processes for which nature employed intrinsic and extrinsic factors. The former is the *inner sentiment* that by means of heat (*vital force*) tends to make organization more complex. The latter corresponds to the conditions of life or the environment that exert a direct action on the structure and heredity of living beings (Jacob 1982). The Lamarckian ontological cut is between organism's inner impulse and their environment that shapes their external appearance through a process of irreversible transformations that makes time the essential dimension of organic reality as the world of possibilities in the here now (present tense) brings forth actual realizations (perfect tense). The upper quadrants in figure 1, illustrates individual development as a transition from II (internal individual potentiality) to I (external individual completion).

In agreement with an embryological perspective, Darwin postulated a close relationship between the birth of species and individuals. From birth onwards a series of structural modifications are incorporated into the germ and at a certain time when the organization is still flexible (childhood) such modifications became fixed as if added to old individuals during thousands of centuries.

For the embryo is the animal in its less modified state; and in so far it reveals the structure of its progenitor. ... Thus, community in embryonic structure reveals community of descent. ... As the embryonic state of each species and group of species partially shows us the structure of their less modified ancient progenitors, we can clearly see why ancient and extinct forms of life should resemble the embryos of their descendants, our own existing species. Agassiz believes this to be a law of nature; but I am bound to confess that I only hope to see the law hereafter proved true. It can be proved true in those cases alone in which the ancient state, now supposed to be represented in many embryos, has not been obliterated, either by the successive variations in a long course of modification having supervened at a very early age, or by the variations having been inherited at an earlier period than that at which they first appeared". "Thus, as it seemed to me, the leading facts in embryology ... are explained on the principle of slight modifications not appearing, in the many descendants from some one ancient progenitor, at a very early period in the life of each, though perhaps caused at the earliest, and being inherited at a corresponding not early period. Embryology rises greatly in interest, when we then look at the embryo as a picture, more or less obscured, of the common parent-form of each great animals (Darwin, 1859).

Following Richards (1992) Darwin's argument at this stage of his intellectual development can undoubtedly be labelled as Lamarckian and recapitulationist since for him embryological development evolved by terminal additions produced as a direct response of the organisms to the condition of life. The recapitulation theory expresses the tight entailment between ontogeny and phylogeny.

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. (Haeckel 1879).

Although the processes of the transformation of individuals and species undoubtedly share common properties they ought to be differentiated because an approach founded solely on the internal/external distinction confuses individual and population levels. A new cut conceives a more subtle distinction within the ontic realm.

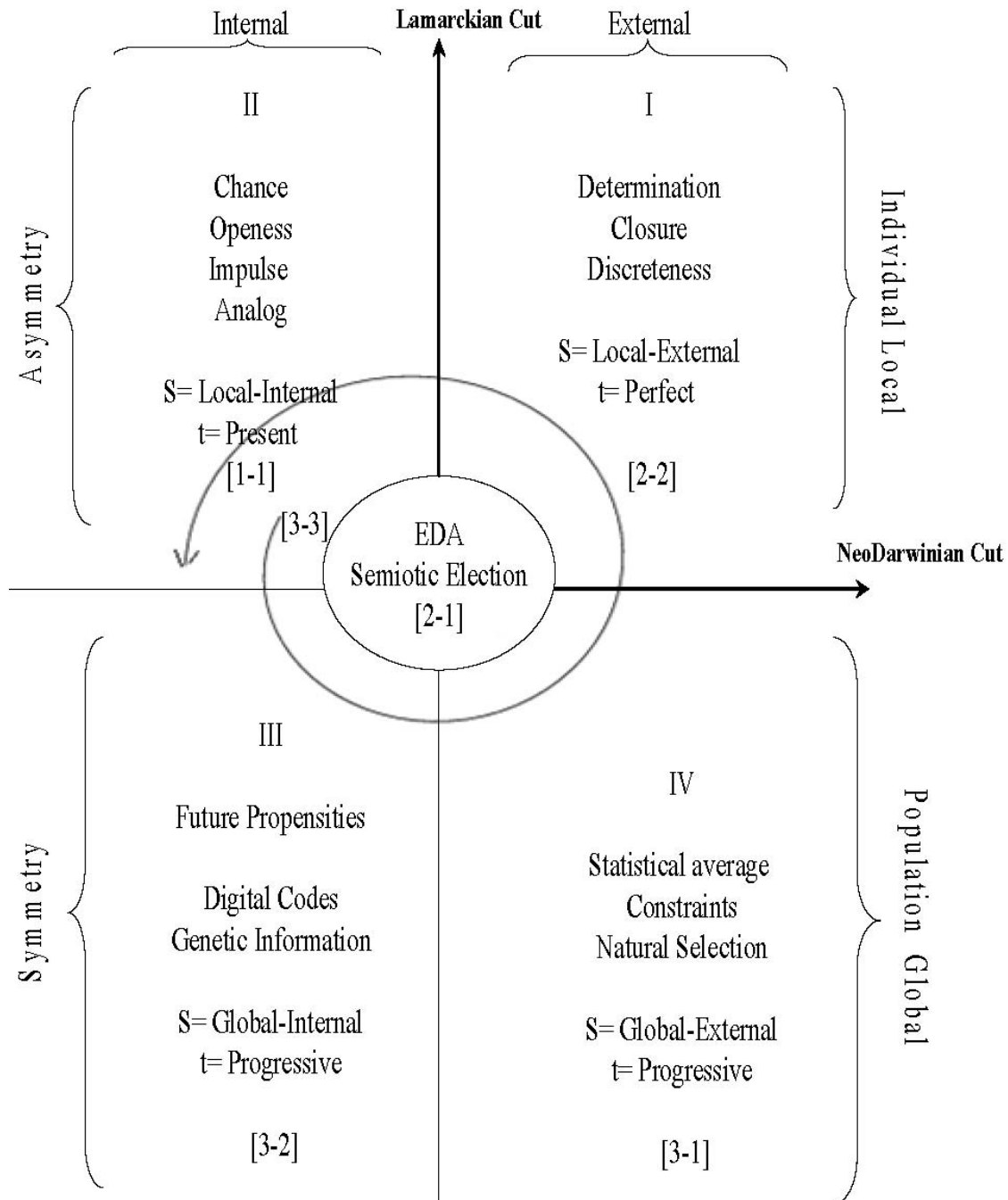


Figure 1: The Lamarckian/Neodarwinian Quadrant (modified after Taborsky 2004). The Y-axis refers to the Lamarckian (ontic) cut and the X-axis to the Neodarwinian one (epistemic). The left upper quadrant (II) corresponds to the internal individual zone

The Neodarwinian individual-local/population-global cut:

This is a distinction for which Darwin has been rightfully credited. Nonetheless it had to wait the incorporation of Boltzmann-Fisher statistical analysis to the nascent genetic

revolution for its real incorporation into evolutionary theory. I equate this cut with the epistemic cut (Atmanspacher 2002, Taborsky 2002, 2004), for it establishes that individual properties are estimated as statistical averages of the population in a given environment. Figure 1, shows the two lower quadrants III (internal/population i.e. genetic information) and IV (external/population i.e. statistical regularities produced by natural selection) created by this cut. These two zones are associated with processes that produce regularity and symmetry while providing a combinatory potential for the emergence of new configurations. Population statistical approaches account for a digital encoding of information and make possible the creation of mathematical computational models of mental process. The quadrants III and IV in figure 1, correspond to manifestations of an evolutionary law considered as a generalizing tendency to take habits characteristic of Peircian *Thirdness*.

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, 1898. C.P. 7.515).

Genetics rests on a foundation given by the existence of a Weissman's barrier, according to which the phenotype was determined by the prescriptions encoded in G so that the modifications of P by the action of E cannot affect G, a way of reasoning inspired the central dogma of molecular biology in the nineteen fifties. Thus, the G/P duality became the new version of the internal/external duality where the self was identified with the gene as an individual and as a population. Accordingly Neodarwinians focused on the shift in the genetic composition of the population by the effects of natural selection.

In consequence, individual organisms were stripped of all autonomy and came to be imagined as determined by two opposing causes, an efficient cause operating upwards from the lower levels (G) and a final cause operating downwards from the higher levels (E). Neodarwinism considers that the environment poses challenges that are to be solved by the organisms, in a process of adaptation in which it is *a priori* assumed that among

the random variants, very few preexist in a population that possesses an adequate fit to the environment. This is depicted as a movement from quadrant IV to III in figure 1, which is mediated by the ever going action of natural selection in the progressive time.

Natural Selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. (Darwin 1859).

The statistical mechanical conception provides statistical predictability under specific boundary conditions by means of the identification of fundamental units and interaction rules among them. But when the intrinsic dynamics and activity of the individual organisms occurring in the two upper quadrants (figure 1) is neglected, the formulation of an integrated evolutionary and developmental perspective is hampered. So long as individuals are not thought as a real information processing agents, “randomness” and “selection” are exclusively confined to properties of the genetic and environmental factors respectively. With the neglect of individual autonomy, intention and teleological interpretations were drastically eliminated in the workings of nature and in consequence embryology was done away, since it was conceived as preprogrammed teleological dead ended processes.

The Epigenetic View and Developmental Systems Theory (DST):

There is an ongoing debate about the relations between ontogeny and phylogeny; each one at its turn has been postulated to be the efficient cause of the other. The internal domain was the level where coherence was achieved and individual evolutionary variations turn up, but it was easier to assume their random production instead of asking how developmental processes result in individual variants. Mainstream biologists prefer to affirm that embryos develop according to a genetic program rather than being subject to other influences. In the last decades the discovery of Hox genes revived an interest in development among geneticists that manage to subsume development to a higher hierarchy of controlling genes and so placed even less weight to 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 evolution exclusively directed by natural selection in a specific environment? By contrast, the epigenetic perspective considers ontogeny as a process in which some additional information from the environment is incorporated in order to produce the form. Then, the relationship between G and P is sensitive to circumstantial fluctuations under concrete local restrictions. Defenders of the epigenetic view

consider genetics as a new edition of preformism according to which no real epigenesis takes place since all formative factors preexists in an encoded way (Oyama 2001).

The succession of developmental stages from less to higher differentiated forms rekindled the specter of Lamarckian recapitulation because of the fear that phylogeny may be understood in progressive teleological terms. Nonetheless the understanding of ontogeny as a non programmed open ended process places this fear on shaky ground. There are documented proofs of Darwin's commitment with the theory of recapitulation (Richards, 1992), a contribution that has been epitomized as an immature intellectual period before the discovery of natural selection as the allegedly principal formative factor (Bowler, 1992). The Darwinian school which is expressed in Neodarwinism is wholly externalist because the demarcation of the local/global cut was done by ignoring the internal realm and so functions only within the quadrants I and IV of figure 1. However, Darwin had a much broader scope. To distinguish between the author and the school that takes his name is important for sake of clarity and justice to the author. Darwin had a more integrative view of evolution; that is the reason why Depew and Weber (1995) talk about the Lamarckian Darwin, and Richards (1992) about the recapitulationist Darwin as much closer to German Natural philosophy than to mechanical thought, at least during an important part of his intellectual development. His concern with an embryological understanding of variation, his agreement with recapitulation, the possibility of directed variation by use and disuse, his views on habit and instinct, the theory of pangenesis ... etc. offer a diversity of elements for a semiotic integration and that was the reason that moved Peirce (C.P. 1.398-1.399) to make a generalization of Darwin's three categories of Variation, Inheritance and Selection.

The Evo/Devo debate is between preformism and epigenesis that today takes the form of a conflict between the roles to be assigned to genetic information and self-organization respectively. To solve this issue would clarify some lasting discussions that were cast in the following dichotomies: (a) Either the inner nature of the organism or the external environmental conditions as a major cause of evolutionary variations; (b) Individual random variations vs. population statistical regularities.

Waddington's image of *canalization* of development, as a ball running down through the valleys of an epigenetic landscape whose features are both shaped by a genetic network and the environment, remains a fertile concept for understanding development in its relation to evolution within a more integrative perspective. Genes and environment do not directly cause traits; they rather assist in laying out the main features of the epigenetic

landscape and therefore in the pattern of canalizations open to the ontogenetic process. The concept of "genetic assimilation" (Waddington 1957) addresses the question about how specific adaptive genes became fixed, or how was genetic encoding achieved? The epigenetic landscape is a dynamic interface between the genetic endowment of the egg and environmental interactions subject to permanent tuning by organisms that interpret all the informative resources in order to push themselves into developmental pathways while updating their information content (Waddington 1961).

In early stages of development the morphological determinants are epigenetic processes influenced by external forces that act upon primitive cellular aggregates (Ho and Sauderns 1979, Goodwin 1994, Jablonka and Lamb 1995, Jablonka and Lamb 1998, Newman and Muller 2000). These external determinants work as causal factors of development that may be reinforced by chemical compounds genetically specified. So to say, genes are suppliers of basic structural proteins and enzymes but do not exert a direct influence on the resultant architecture. The process of genetic assimilation (Waddington 1961) hooked morphogenesis to a genetic circuit that facilitates the generation of digitally encoded templates for raw materials. Thence genes came in to consolidate previous epigenetic processes (Newman and Muller 2000, Salazar-La Ciudad et al. 2003).

Molecular processes like protein folding (Balbin and Andrade 2004), RNA folding (Fontana and Schuster 1998a, 1998b) are sensible to contextual influences given by the modification of free energy landscapes respectively. Proteins fine tune their free energy landscape as they interact with other molecules found in the intra cellular milieu. Evolved RNA (Fontana and Schuster 1998) 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 2004). I propose that 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. Genetic assimilation explains that the genes most

likely to get fixed in the population are those that produce the same effect that is exerted on the individual by the external stimulus.

DST search for 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 G and E contributions. P is the structure of an organism that determines moment by moment its way of interactions in an environment in the course of its ontogeny. The phenotype is being shaped in the encounter with its surroundings, so that every organism is realized as a totality in its domain of interactions and relations in its P, and lives in a specific P according to its interactions and relations, (Maturana and Varela 1992, Maturana and Mpodozis 1995). Thus, P changes in the course of ontogeny result of both its internal dynamics and its interactions with E.

The semiotic integration:

I will go in depth into Taborsky's model (Taborsky 2004) in which both domains ontic (independent of observer's knowledge) and epistemic (dependent on observer's knowledge) are considered simultaneously and their mutually entailing relations made explicit. Moreover, the acceptance of living systems as inner observers bridges these two cuts and paves the way for an integrated view of evolution and development that highlights the existing parallelisms between them that I list as: 1. Self-referentiality. 2. Autonomy. 3. Open-endedness (divergence). 4. Increase of information. 5. No existence of a prior program. 6. Irreversibility.

Most of the issues that concern the Evo/Devo debate boil down to irreconcilable background assumptions grounded on the dominant Cartesian, dualistic, mechanical and reductionist perspectives. A semiotic paradigm discovers a *raison d'être* beyond the internal/external, individual/population or local/global spatial domains, and present/perfect/progressive time. The six coded modes inspired by Peirce's categories must be developed and put into the biological discussion as an alternative reference frame (Taborsky, 2002, 2004).

To reiterate – the six relations defined by Taborsky are:

Firstness-as-Firstness [1-1]: Internal local/Present time/Possible (Internal analog).

Secondness-as-Secondness [2-2]: External local/Perfect time/Discrete actual (External analog).

Secondness-as-Firstness [2-1]: Borderline interface/Perfect-present time/Attractor phase.

Thirdness-as-Firstness [3-1]: External global/Progressive-present time/Statistical average.

Thirdness-as-Secondness [3-2]: Internal global/Progressive-perfect time/Future propensity (Digital).

Thirdness-as-Thirdness [3-3]: Aspatial/Atemporal/Imaginary.

These six relations function as semiotic codal measurements; when selection is made from these six and linked within a triadic functional set, the result is a morphological reality, a sign. Whether this morphological unit is open or closed, is fuzzy or crisp, is an atom, a cell, a word, an action – it is a sign, a morphological reality, a well-formed-formula.

(Taborsky 2004)

This paper sketches a morphogenetic analysis beyond the dichotomy that conceives determinism on either genetic (internal) or environmental (external) factors, and randomness as originating either from within (mutation) or from without (environmental fluctuations). Although, 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.

The reconstruction of the bridges between ontogeny and phylogeny will contribute to an expanded evolutionary synthesis that would be Darwinian in the sense that agrees with his initial interest of explaining divergent evolution in terms of embryonic development.

Ontogeny obeys instructive information, and evolution obeys selective information; the former is commonly associated with directed variation and the latter with random variations (Jablonka and Lamb 1995, 1998). Instructive information is equivalent to analog information (Hoffmeyer and Emmeche 1991, Hoffmeyer 1996) that can be divided into external and internal zones encoded in the [2-2] and [1-1] modes respectively, (figure 1, quadrants I and II). Analog information is defined as direct pattern recognition by some structural motifs of the evolving agent within a continuous threshold of variability. Analog refers to the fact that this recognition is made either by structural complementarity or by similarity and thus, it permits the establishment of non-random reversible interactions (Root-Bernstein and Dillon 1997). If the motif recognized is external, then interactions and measurements lead to internalization of information. If the recognized motif is internal, we have an interaction among inner constitutive components that preserves

the coherence of the individual as it interacts with the environment. Digital information refers to encoded information in the form of a record that has the structure of a text composed of basic symbols (DNA) that can be modified by discontinuous variations such as mutation and recombination. Digital information is encoded in the [3-2] mode, which is associated with information that acts as a network that defines future propensities. Genes do not exactly belong to the relation [2-2] because they do not have a defined material boundary; they overlap, they are physically discontinuous as they are intervened by other sequences, they can be found within other coding sequences, their continuity is observed at the RNA level. Genes might be thought of as a functional networked unit under the command of the whole organized epigenetic system that interacts with the environment. Genes as informational sources belong to the [3-2] mode. The discreteness of the genes is a Mendelian approximation but it does not hold at the DNA level. To map Mendelian genetics into molecular genetics is almost impossible.

Digital information appears when any structure becomes a symbol that can be permuted giving rise to potentially different functional content. The internal and external analog zones are connected by the epigenetic inheritance systems (EIS) (Smith and Szathmari 2001, Jablonka et al. 1992, Jablonka and Lamb 1998), since an adjustment to an external factor implies a readjustment of inner states. On the other hand, selective information, or Darwinian natural selection operates from without and configures the digital genetic informative record shared by the population. The survivors are the carriers of a more faithful (though outdated) inner representation of their environment, that is the survival of the best encoders of environmental information.

These two dualities Lamarckian (internal/external) and neodarwinian (individual/population) are currently the source of endless “either/or” debates. I will show that semiosis favors a coherent integration that is congruent with more recent developments in Developmental Systems Theory (DST). There is a fundamental symmetry between genes and other developmental resources (Oyama 1985, Griffiths and Gray 1994). The semiotic approach is based on the idea that there is a real interpretation of all informative resources by the developing organisms.

2. Igus As Evolving Developing Agents

The notion of Evolving and Developing Agents (EDA) aims to formalize a theory of organisms as real interpretants that choose between alternative ways to relate with external factors and so encode and incorporate information from the environment. The term

merges development and evolution inasmuch as both processes are mediated by the agency of the organisms themselves. This notion agrees with Baldwin's idea of organisms as participants in their own adaptations by means of organic selection (Baldwin 1896).

The upper quadrants in figure 1 correspond to asymmetric relations while the lower ones account for symmetry or regularities that in Peirce's view are properties of *Thirdness*. If we consider the potentiality inherent to digitally encoded information (quadrant III) one can talk of ontogeny as the transformation from the genetic to the phenotypic 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 interpretant that Hoffmeyer (1996) locates in the egg, since it reads DNA instructions and interprets them to implement an ontogenetic trajectory.

Embryogenesis, or ontogenesis, is a sign operation in the sense that a one-dimensional "DNA inscription" containing a coded version of its parents is converted in a three-dimensional organism... An inscription is not meant to be active, it is meant to be deciphered, and so it is with the DNA inscription. The egg – or the growing embryo – is the some one for whom the genome represents a sign of a specific process of development. (Hoffmeyer 1996)

Likewise evolution as a population phenomenon is usually understood as a transformation from the phenotype to the genetic at the level of population by means of an interpretant in this case the lineage.

Any given lineage interprets its ecological niche as a sign that the DNA pool must be modified. (Hoffmeyer 1996)

The interlocking of these two processes is clearly seen in the fact that every single phenotype that makes 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). However the complexity of the processes involved requires that the internal/external and individual/population interface encoded in the [2-1] mode be specified. I name this interface as Evolving Developing Agent EDA or an Information Gathering and Using System (IGUS) that acts firstly as a random explorer of the possibilities of the environment through measurement and secondly tends to interact or to promote couplings that configure a stable inner record, because structural adjustments to environmental factors involve an inner structural modification. The 'thingness' of the Agent or the System would be evident

only within a triadic morphology that involves a relation in the mode of Thirdness (Taborsky 2004). IGUS pick up input information in order to enhance evolutionary adaptability and capacity to promote individual diversity, so opening up future possibilities. The exploration of the environment by the EDA is close to random only to start with, but as information is gathered it becomes more directed or canalized. As I will show below, there would never be enough information to make a directed successful response, EDA are, thus, compelled to make choices or to risk something.

An IGUS is defined as a physical entity that is interested in free energy or extractable work. As an inner observer it interacts, its cognitive activity is error prone, finite, partial and uncompleted, but good enough to preserve its performance and identity. An IGUS was conceived as a universal Turing machine that can extract work taking into account the balance of entropy production as a result of data processing. In order to estimate the amount of free energy that can be converted into useful work, Zurek (1989, 1990) defined "physical entropy" (S). An IGUS can also be imagined as an agent that probes the surroundings by performing a series of measurements and processes the results in order to optimize the amount of useful work, (Kauffman 2000), (Andrade 2003, 2004). As the number of measurements proceeds, its uncertainty about the environment decreases and the gained information increases the size of the digital record (see figure 2).

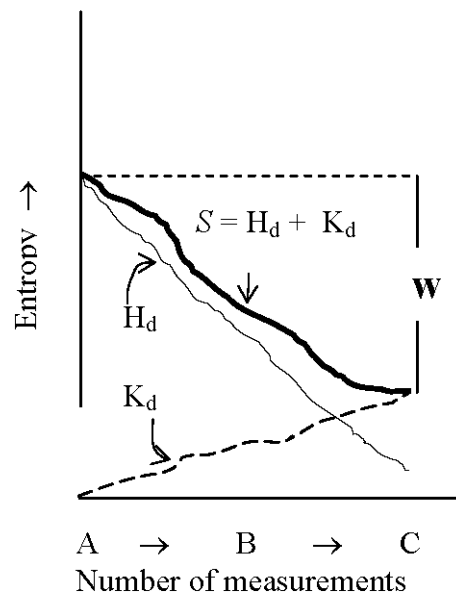


Figure 2: Zurek's physical entropy $S = H + K$ variations against the number of measurements performed by an IGUS in a far-from-equilibrium environment. Bold curve represents the variation of S . Faint curve repre-

sents variations of H with the number of measurements. Dotted curve represents the variation of K with the number of measurements. W stands for the amount of work that can be extracted by the IGUS. From left to right A, B and C stand for one cycle of an evolutionary process. Stage A: Early evolution / openness / prevalence of H. Stage B: Intermediate stage of evolution / partial closure / maximum conversion from H to K. Stage C: Stabilizing evolution / closure / dominance of K.

Physical entropy (S) is equal to the sum of two independent quantities: Missing information (H)¹ plus Chaitin's algorithmic complexity (K) of the string that records the known data. Therefore, for any state of the system $S = H + K$. An IGUS acts as the converting agent of missing information into known randomness (K) of the record². Measurement decreases the ignorance about surroundings, but increments the size (algorithmic randomness) of the record that encodes the obtained information. The model explains how the amount of energy that can be used by the IGUS is dependent on the algorithmic complexity of the record, since the more compressed the record (the lower K), the higher the amount of work (W) that can be extracted. The difference between ΔH and ΔK determines the net gain of work. Far-from-equilibrium, ΔH is greater than ΔK , and a quantity of net work can be extracted, by contrast in equilibrium ΔH would be equal to ΔK and no net work can be extracted. The net work (ΔW) obtained at temperature T is given by the sum: $\Delta W = \Delta W^+ + \Delta W^-$. Where ΔW^+ is the work gained due to the change of H , given by $\Delta W^+ = T (H_f - H_i)$. ΔW^- is equal to the cost of observer's memory updating that replaces the outdated record r_i about the initial state, with the record r_f that describes his knowledge about the final state, given by $\Delta W^- = T (K_f - K_i) = T ([r_f^*] - [r_i^*])$. $\Delta W^- = K_{i/f} = r_{i/f}^* = [r_i^*] - [r_f^*]$. Let $r_{i/f}^*$ be the size of the minimal program that computes r_i given r_f^* . The extraction of energy becomes possible only through compression of the record (r) that is dependent on efficient encoding, or the IGUS' ability to comprehend his experienced world in term of regularities. But the maximal efficiency in energy extraction can only be attained by the IGUS when $r_{i/f}$ is the minimal program $r_{i/f}^*$, that can only be accomplished when the number of steps used to find r^* , tends to ∞ in conformity with the

¹ Shannon's information (H) measures missing information or ignorance remnant in the observer. It is the observer's uncertainty relative to the number of possible messages that can be emitted by a given source. It is a statistical notion that refers to total number of elements of a set, or collection of microstates that are compatible with a macro state. It is given by $H = \log_2 P$ for P events with equal probability and $H = -\sum p_k \log_2 p_k$ for k elements with different probability and equal to p_k .

² Minimal programs are the smallest programs capable of generating a particular series in the output tape of computer C ; the sizes of these programs are measured in bits and their values correspond to the algorithmic randomness or algorithmic complexity of the series (Chaitin, 1975). Algorithmic information content of a binary sequence s , is the size of the minimal program S_u^* , which computes sequence s on the universal computer U ; $K_{u(s)} \equiv [S_u^*]$. The introduction of universal computer reduces -but does not eliminate - the thermodynamic importance of subjectivity. $[r^*]$ indicates the size of the minimal program in bits.

halting theorem of computation. In order to be able to extrapolate this model to developmental biology, I assume that: (1) H is the number of possible configurations that an EDA can attain by virtue of its structural organization as such. (2) K is the (specificity and stability) uniqueness of the phenotype. (3) $K_{i/f}$ stands for (Algorithmic randomness of $r_{i/f}^*$) the average number of intermediary developmental states adopted by the EDA before it acquires the mature structure. (3.1) K_f is the structural uniqueness of P . It would be a function of the number of branching decisions that were made along evolution in order to obtain a particular body plan from a more general structure to a more specific one. (3.2) K_i is the structural uniqueness of P at the onset of development or the primitive conformations. Uniqueness refers to the probability distribution of alternative conformations present in a given state. There are two extreme possibilities: each P is equally likely (one G to many P) or a single P is specified with full certainty (one G to one P).

An EDA measures, classifies and registers environmental features (Andrade 2004, Balbin and Andrade 2004). Measurements reduce EDA's uncertainty about E (Shannon entropy H), proceeding from an initial state given by high uncertainty (high H value), to a final state or mature P (analog information record) with low H value. Measurement outcomes can be estimated in terms of decreasing H and increasing K . Therefore, EDA is an intentional system that minimizes the cost of memory updating by the mechanism of records compression (K). The second law is not violated because the missing information sets the limits for work extraction. The conditions that permit the operations of an IGUS are: 1. Openness. 2. Far-from-equilibrium. 3. Memory (Zurek 1989a, 1989b, 1990).

In reference to the IGUS, the differentiation between ontic and epistemic levels of description is problematic (Atmanspacher 2002). H (statistical entropy) can be interpreted as an ontic description of intrinsic structural probabilities that can be attained by the IGUS. However, at the same time H can be regarded as epistemic for it refers to IGUS' environmental uncertainty, the very fact that H diminishes with measurements means that it is epistemic, (Burbano 2005). In the same way K (algorithmic complexity) is necessarily epistemic because it refers to what is known by the IGUS, however K becomes ontic as long as it can be identified objectively as an analog and/or digital record, P and G respectively. To summarize in a universe composed of semiotic agents such as living entities ontological chance is nothing but the epistemological uncertainty of actually existing agents. If Peirce's *tychism* or chance is an objective reality that is operative in the universe (ontic), then the objective existence of semiotics agents becomes a necessary condition for the understanding of the most fundamental interactions in the natural world. Chance as a property of *Firstness* refuels the evolutionary potential and creative impulse

of nature, however its manifestation and renewal takes place within the continuous, atemporal and aspatial dynamics of *Thirdness*.

This problem has reinforced my conviction about the correctness to extrapolate the IGUS concept to organisms for they exist at the boundaries: (a) “Outside/Inside” since it converts external uncertainty into inner knowledge by measurement; (b) “Local/Global” since individual’s explorations of the environment are converted into digital codes shared by the population (c) “Present tense” potentialities/“Perfect tense” actualities because organisms’ ever going actions in the “progressive” time mediate between them.

IGUS refers to objective entities that partially know their immediate environment. They dwell in the ontic and epistemic realms simultaneously as long as they are the organized material structure that results from mind operations and consequently the instrument for further mind operations. Its mindfulness is always in connection to [3-1], [3-2] and [3-3]. Moreover, the internalist perspective, modeled in the manner of a semiotic agent brings together the ontic and the epistemic realms. This heuristics helps to understand the inseparability of subjective and objective reality, because it asserts the existence of organizing agents that act as participants (subjective reality) in a permanent coevolutionary unfolding with their environment (objective reality), since agents shape their environment while are being imprinted by it. In other words, organisms encode information from an environment that is being modified by their activities that exert an impact on it.

The mode [2-1] shows that the interface is always being trespassed in either direction. An IGUS passes from uncertainty (H) to certainty (K) by measurement, while uncertainty (H) increases as a result of either record erasure (decrease in K) or environmental change. Agency refers to the fact organisms regulate and buffer genetic (G) and environmental (E) influences. Structural adjustments in which some configurations are preferred in accordance to specific environmental conditions is one of the distinctive features of cognition. Thus the autonomy of the EDA depends on contingent evaluations and interpretations of both G and E resources that lead to unpredictable phenotypic outcomes. The evaluations and interpretations made by the EDA are beyond what an external objective observer can predict and so constitute the real source of logical non-predictability.

Digital information in the [3-2] mode provides multiple options through the participation of the EDA that manifests as a material entity partially closed, partially open, individual in a population context only when it operates in connection to *Thirdness*. Organisms are transient manifestations of processes and relations. All relations collapse into the [2-1] only as a material organization that tend to individualization, but simultaneously the

same relations remain diffused in the [3-3] mode to the extent that without them individualization is not possible. Reality is not pure matter, nor pure mind but something that manifests as an interface in a dynamic relation that as it tends to closure we identify as [2-1], as it remains open is identify as [3-3], that is why [2-1] and [3-3] do not fit properly into the Cartesian quadrant. The Cartesian quadrant is useful for it helps to show this limitation.

The interface [2-1] cannot operate alone. As long as it gets localized it makes part of the physical material world, but as long as it is part of the population it interacts with the relations [3-2] to facilitate work extraction. The captured free energy connects again with the [1-1] relation. The relation [2-1] is able to establish interactions to construct the network, while interactions based on [2-2] are only mechanical and do not contribute to the network of information exchange and processing. IGUS accounts for network expansion because they are partially open, the isolated closed entities in the [2-2] mode cannot do that.

Thus, an EDA must be studied simultaneously in two time-frames, ontogenetic and evolutionary. In both cases, the record reflects its knowledge about the state of the system. [Note: From here onwards, I will refer to the IGUS exclusively as EDA.] The ontogenetic (analog) record is given by the phenotype and it 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 of every individual phenotype.

However, 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. The key concept of recapitulation theory is that free living 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*. The nature of the evolutionary record is dual: (a) Analog – that refers to evolutionary information that can be inferred from the sequence of ontogenetic paths; (b) Digital – that refers to evolutionary information that can be inferred from DNA sequences.

The duality replicator/interactor (Hull 1978, 1980) evokes the difficulty to split what is ontic from what is epistemic, replicators are ontic since they are entities that pass on

their structure by copying a template, and epistemic since replication is done by means of interaction with their environment. In the case of the EDA, the intimate association between these two aspects is one of the consequences of their information processing activity. Like the genotype/phenotype duality, the evolution/development duality is a specific case of a more general analog-digital code duality (Hoffmeyer and Emmeche 1991). In the same vein, to be a replicator implies to have generated a digital record that can be copied, but the generation of a digital record is an analog operation. Beyond this duality we find a deeper underlying unity: Analog-Digital-Semiotic work-actions (Andrade 2002, 2003).

3. Self-Referentiality is an Intrinsic Property of Genotype/ Phenotype/ Environment Interrelations

... all life is founded on self-reference. ... Would the organism not then be regarded as the DNA analog's self-description rather than the DNA's being the organism's digital self-description?. (Hoffmeyer 1996. Pp. 42 and 44)

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

The Weissman's barrier and the central dogma prevent the influence on the G by the P during individuals' life cycle, but not necessarily at the population evolutionary time where selection on P determine the genetic pool (G) for the next generation. In addition the fear of violating the central dogma should not stop us from acknowledging that during individuals' life cycle there may be gain of information from the environment expressed in modification of analog Epigenetic Inheritance Systems (EIS).

A theory of organisms as EDAs or information encoders and niche constructors, falls into an unavoidable self-reference circuit because the observer (the interacting P) is included into the digital (G) description. Organisms participate in the creation of the environment that acts as an informative source for them, so to say that P as a natural observer participates actively in the production of both G and E. Both together G and E partially specify the ontogeny of their offspring, in other words, as development goes on, the P in ever going consult with the E participates by tuning and coordinating gene expression throughout the ontogenetic trajectory. Organisms through niche construction and interactions among them actively participate in the formation of their own inner experienced environmental representations or *Umwelt*, so accounting for an unavoidable non-predictable self-referential loop in the relation organism/environment. According to Rosen (1990) non-predictable statements are circular because what is defined is included

in the definition. In other words, something is not predictable if it 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. Circular thinking contributes to intelligibility but it certainly does not favor predictability. Living entities are a particular case of non-predictable systems whose behavior is partially reflected by P/E, G/P and G/E dualities.

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 from environment on the phenotype and from the phenotype on the genotype. Similar to the origin of body patterns, the origin of adaptations, the origin of 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 environmental uncertainty.

The neodarwinian approach to evolution and the central dogma of molecular biology did away with closed causal loops in favor of a linear reasoning. Development and evolution make part of a mutually entailing loop that refers to the transformation of life forms. An EDA is explained in terms of its information processing agency that defines the interactions within the same level of organization and the relations with the adjacent lower and higher levels (Andrade 2003). EDA self-organizes by profiting the potential derived from the interpretation of genetic and environmental informative sources. Evolution and development are non-linear processes that take place in a moving trajectory that unfolds within a continuum of different spatial and temporal dimensions, but in order to discern whether a process takes place within inner/external, individual/population zones, it is desirable to identify for each transition the mode in which analog and digital informational processes overlap. The continuity of these natural processes is given by the [3-3] mode, a mode that was anticipated by Aristotle when he referred to the continuity of causal agencies. Considering nature as a developing process that actualizes *form*, the *formal cause* or *form* is the cause of movement because it mediates between final and efficient causes, (Aristotle. Phys. III, 1). The efficient cause (source of change) is a *form* operating *a tergo*, and final cause a *form* operating *a fronte*. In many cases *form*, source of change, and end, coincide because when a *form* is a source of change, it is a source of change as an end. In other words, Aristotle implicitly states the need to close the circuit from Final to Efficient causality, but this circuit is necessarily beyond formalization.

4. EDAs Execute Measurements in order to Cope With Environmental Uncertainty

My aim is to substantiate the following propositions:

1. Ontogeny and evolution are aspects of the same General Transformative Tendency.
2. This General Transformative Tendency is driven by EDA interactions with surrounding elements that result 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 or the minimization of developmental steps must be positively selected.

This general transformative tendency describes a vector of an inherent driving force to increase mutual information content between Phenotype/Environment that can be decomposed into two vectors: developmental and evolutionary. The former describes increases in Genotype/Phenotype mutual information content, while the latter describes increases in Genetic/Environmental mutual information content.

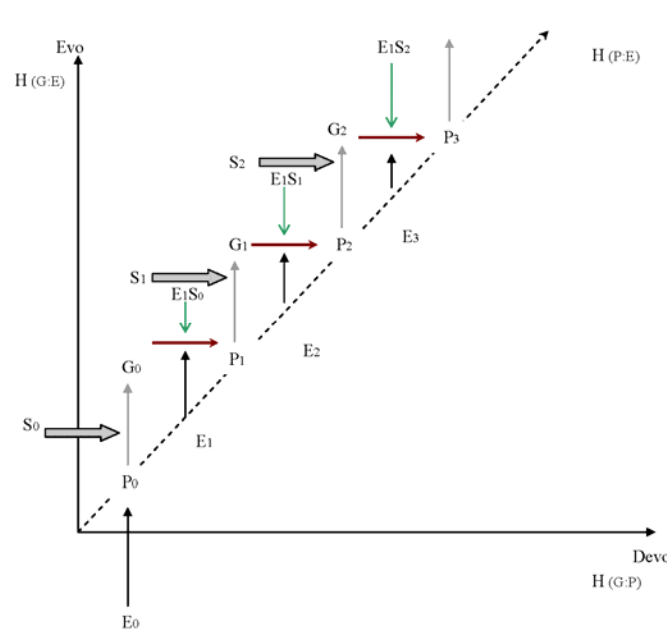


Figure 3: The dashed diagonal shows increment in mutual information content between P and E, as a permanent action in progressive time. P_i stand for phenotypes in which EDA live that go from low to high uniqueness. This vector can be decomposed into a vertical and a horizontal one. The vertical axis shows increments of mutual information content between G and E along evolutionary time. 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: $EIS_0 > EIS_1 > EIS_2 > EIS_3$. S_i corresponds to selection pressure. 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 in order to acquire and to process information that is used to modify the strategies of free energy extraction from surroundings. Measurement is any kind of interaction between an observer system and an observed one that requires classification of the latter by the former (Pattee 1995). The process of classification narrows the initial set of alternatives or choice of possibilities. Measurement is logically irreversible because it establishes a mapping of the kind "many to one" (Pattee 1967), and so generates a simplified and functional observed system's description (Pattee 1995). In other words, classification is a process in which the relevant elements of an observed system are selected by the observer that neglects those that are unimportant. An event of measurement requires two steps: (1) Recognition, (2) Adjustment. Recognition is mediated by structural complementarity that uses a structure as a measuring standard of classification used to compare a variety of external factors. Recognition induces structural readjustments that narrow the set of conformations, so that the number of different individual conformers for the uncoupled state is higher than for coupled states. Interactions reduce phenotypic plasticity inasmuch as the specificity and stability of P depends on environmental conditions. Phenotypic adjustments register a simplified functional environmental description that corresponds to the set of configurations for the coupled state; this is, thus, the record of E as it was recognized by EDA. Recognition is evident in the interaction between EDA and its E in both evolutionary time and ontogenetic time. Therefore, EDA decide based on measurement outcomes since their autonomy and activity depend on the gathered information from E. Encoding efficiency is a function of the ability to "model" the experienced world in terms of regularities.

Phenotypes are the actual interacting structures that lack evolutionary memory and are sensitive to external influences that can affect their own stability. Since they are open to perturbations by E, G encoded information becomes a decisive stabilizing factor of P. EDA permanently strive to cope with E by means of reciprocal adjustments and so creates an interacting network, in which mutual information content between P and E tends to increase while retaining a wide span of fluctuations and flexibility expressed as conditional information. Like individuals living in like conditions tend to act in a similar way, and this tendency defines the range of deviations from the habitual norm produced by the uniqueness of P interactions. Though the adjustment phase is still reversible (in the sense that the character can still disappear when the E stimulus is removed), it becomes a selective condition for genomic variants that fix the record in an irreversible encoding. Organisms produce unforeseen E perturbations as they try to cope with E, thus, the increasing inner coordination makes it more capable of dealing with a wide range of E changes.

The fact that developmental processes can be both extended by addition of terminal stages and condensed in the sense that features tend to appear earlier than they first came up explains why the recapitulation of basic patterns of organization is observed as one focuses on processes of growing complexity (Arthur 1997, 2002, Ekstig 1994). However it cannot be expected to take it literally as if every step in phylogeny should appear in ontogeny as a linear succession of stages since besides terminal additions, there may be also terminal deletions, intermediate additions (insertions), intermediate deletions, repetitions, inversion, regressions, etc. In all instances changes that affect late stages of development are more likely to be selected for they do not affect the entrenched early stages of development. The point is that developmental pathways are subject to two seemingly opposite forces that result from EDA semiotic activity: (1) *Thirdness* manifests as a compressing or shortening force that removes redundant developmental steps without affecting functionality. Also *Thirdness* is responsible for condensing the time required for each developmental step. (2) *Firstness* is the expansive force that tends to add new developmental steps and randomize existing structural modules. The joint actions of these two forces manifest in EDA's semiotic choices or unpredictable adjustments that generate context dependent developmental modifications that account for departures from strict recapitulationism.

The results of EDA's activity are tracked along the interface individual/population since the P is the record (K) generated at a twofold time scale, in ontogeny, it characterizes the individuals; and in phylogeny the species (the type). The individual record is represented by its P; whereas the population record is given by the probability distribution of the attainable P for every individual that depends on the specific adaptive landscape. Moreover, individual interactions (measurements) change the population record by incorporating environmental information, which modifies the probability of EDA's accessible states. EDA modifies the adaptive landscape as it evolves, and at its turn the adaptive landscape constraints the possible available P accessible to the individual by evaluating the population's performance in the environment. On the other hand the interaction with some environmental factors can modify the individual EL and defines the new states available for the population. It is in this sense also that EDA are located at the inter-phase individual/population. The EL is a product of the individuals' activities where new developmental and evolutionary pathways are opened up.

Development and evolution are the non-programmed process of successive configurations from general to specific that streamlines the production of individual P. The number of states that can be accessed diminishes under stabilizing environmental conditions. As

well, measurements bring forth an increment in uniqueness. It is always possible to smooth the passage from one P to another by means of their interaction with external factors. This reduction in roughness of the EL speeds up the ontogenetic path. Since ontogeny involves analog information, shortening of developmental paths (compression of $K_{i/f}$) can only be accomplished in evolution if the presence of the surrounding factors is guaranteed. Internalization of these E factors in the form of a symbolic representation accomplishes a state of structural uniqueness while simultaneously the number of neighboring conformations dynamically connected in a morpho-space may increase.

The reduction of redundancy is mostly achieved by taking over a functional redundant structure in order to execute a new task. By this means, an EDA may augment accessibility to new neighboring tasks and reduce ontogenetic time simultaneously. The argument goes as follows, the increase of the fraction of dynamically connected P improve the memory updating efficiency by the EDA ($K_{i/f}$), thus, tendencies to gain stability and to improve energy extraction are simultaneously fulfilled. As a result there are observed increments of structural uniqueness. The P is a stationary state within a defined stability threshold of energy barriers (Andrade 2000), work must be done in order to overcome energy barriers in order to attain more stable states, that is to shorten K and to increase uniqueness. As the organism rolls down the EL, it becomes more restricted, canalized, while new ever shallower routes branch down the road, so producing individual intra-specific variations. Consequently its *chreod* down the epigenetic landscape will run deeper; a fact that makes ever more difficult further shortening of K. In other words, EL was shaped as some P was retained for functionality, stability and uniqueness, so creating deep *chreods* that drive ontogenetic pathways on its own. It is as if the EDA itself demarcates the path as a truly semiotic agent. As a result of this activity EL are constantly in the process of shaping, the deeper *chreods* correspond to shortened descriptions (high structural uniqueness, and fast developing), while the shallow valleys correspond to unstable redundant descriptions (low structural specificity and stability or plastic phenotypes that accept developmental changes). To summarize: EDA's act as a *formative cause* that identifies environmental regularities and patterns, some of which may be encoded in a compressed manner in two ways: analog (reduction of intermediary states to achieve P), and digital (genetic non redundant description).

This hypothesis provides a unifying explanation for the following observations and arguments: (1) Primitive life forms consist of few developmental stages, and fluctuate among different conformations, so that additional steps were required in order to acquire a more stable form. (2) The elimination of redundancy streamlines development and in-

creases structural uniqueness. (3) There is a strong tendency to diversify configurations in early stages of evolution by the terminal addition of developmental steps. (4) The evolution of Hox genes has proceeded from dispersion to clustering while increasing in number, their co-linearity found in most vertebrata expresses the tendency to optimize encoding.

5. Development And Evolution Are Processes Of Information Increase

According to the foregoing discussions EDAs produce an analog record that is being permanently updated and leads to increasing values of mutual information content, $H_{(\text{organisms:environment})}$. Analog records are the condition for the creation of digital record that register ensuing changes in mutual information content between genotype and phenotype $H_{(\text{genotype:phenotypes})}$ and between genotype and environment $H_{(\text{genetic:environment})}$.

The phenotype/environment relation:

Following Wagensberg (2000), an EDA tends to free itself from the uncertainty of the rest of the world and in so doing reacts to E fluctuations. The point, however, is that the ability to anticipate environmental fluctuations is related to increasing degrees of internal coordination and plasticity. The organism's striving to cope with environmental challenges originates a tendency to increase mutual information content between P and E, if this information is incorporated into the genetic record, higher mutual information content between G and P, and G and E would be observed. While P adjusts to E at the level of the individual, the relations G/P and G/E are detected in the population. The relation P/E is mediated by the organism's behavior, modeled as an open cognitive system. This is a permanent ongoing functional interaction (progressive time) that produces structural adjustments or analog encoding since to adjust to an external environmental stimuli implies rearranging an internal state.

In other words, every ontogeny as an individual history of structural change is a structural drift that occurs with conservation of organization and adaptation. We say it again: conservation of *autopoiesis* and conservation of adaptation are necessary conditions for the existence of living beings; the ontogenic structural change of a living being in an environment always occurs as a structural drift congruent with the structural drift of the environment. This drift will appear to an observer as having been "selected" by the environment throughout the history of interactions of the living being, as long as it is alive. (Maturana & Varela 1992)

Let us consider EDA's phenotype (P) and Environment (E) as informative sources. According to Shannon one obtains the following equation (Eq. 1), (Wagensberg, 2000):

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

Let $H_{(P)}$ (1) stands for diversity of phenotypic states accessible to the organism independently of E. $H_{(P|E)}$ (2) stands for conditional information or the variability of EDA when E is fixed. It refers to phenotypic plasticity or EDA's anticipatory capacity to E changes. It is the condition for evolvability. $H_{(E)}$ (3) stands for the diversity of states accessible to E. $H_{(E|P)}$ (4) stands for environment sensitivity, impact, or capacity of being changed by EDA. It corresponds to variability of E when the P is fixed. $H_{(P:E)}$ (5) stands for structural complementarity between P/E or the information that circulates between organism and environment. It is the condition of the existence for living entities.

The higher $H_{(P|E)}$, the higher the independence to E uncertainty; the fit organisms/environment is expected to be somewhat loose in order to maintain evolvability. 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 make a semiotic election that opens up a new developmental and evolutionary path. EDA achieves 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. A state of equilibrium is characterized by the absence of constraints between the inner and outer regions, a situation that occurs when the individual is isolated from matter and energy transference. Therefore, an isolated system (individual or population) cannot be influenced from without and changes until it can no longer change in equilibrium. By contrast, every EDA tends by its own activities to remain far from equilibrium. EDA independence is paid by exporting to the outside the effects of its inner activity, so that the ensuing increases of E uncertainty manifest as selective pressures that forces it to change the constraining values at the interface internal/external. As E uncertainty increases, the viable EDA increase their phenotypic plasticity or capacity to choose and so produce further unpredictable environmental change. In consequence the need to cope with E uncertainty is the developmental and evolutionary potential that promotes growing differentiation.

Evolution and development proceeded from primitive low uniqueness P to present day stable and specific P, by means of the acquisition and internalization of environmental information. The plasticity of primitive life forms was buffered by environmental

information that shaped the native structures so reducing H (uncertainty), but as evolution went on plasticity was lost due to 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 or complementary interactions between EDAs' structural modules and environment, thus, EDA enhance its discriminating ability by means of the diversification of its structural modules, (incrementing $H_{(P)}$ and $H_{(P|E)}$ values simultaneously). In other words, variability enables to recognize more features from the environment, thus making it more predictable for the EDA. Therefore, the increase in diversity is needed in order to obtain a more stable and unique P. Remarkably, the transformative drive of the EDA is to increase structural uniqueness by means of creating conditions for the incorporation of variations that are congruent with these tendencies.

There will always be environmental potential information not relevant to the organisms that could be made part of their *Umwelt* as a consequence of new explorative behaviors that may become encoded in the form of *habit*. Besides, an EDA may also give up some of its individual identity in exchange for increasing independency to E uncertainty by increasing its dependence on other similar individuals leading to the emergence of a more complex level of organization. For instance the development of multicellular organisms may have started by cooperation among individual cells as a way to decrease individuals' E uncertainty (Wagensberg 2000).

To summarize: (1) EDA strives to incorporate environmental information as a way to increase phenotype uniqueness. (2) Development and evolution do not depend solely on adaptation to a stable environment, but on independence from a changing environment by maintaining the organisms' ability to make a semiotic choice. (3) In ontogeny, information increases are detected as a modification in developmental pathways mostly by the addition of terminal steps. (4) In phylogeny, the increases of information are due to selection for phenotypic or developmental plasticity.

The genotype/phenotype and genotype/environment relations:

An individual EDA acts within a network of EDA(s) that are part of the E. The point is that the mode [2-1] cannot be dealt with in isolation for it is only the material expression of an acting mind in the [3-3] mode. The interface (P, EDA, IGUS) is active, not a passive boundary.

Increases in mutual information content between P and E are the prior condition for further increments in both mutual information content between G and P, and G and E. Specifically, the tendency to increase the content of mutual information between the digital record (DNA sequence or G) and the analog record (structure or P), $H_{(G:P)}$, is the means to enhance the autonomy of EDA in constant E. As it was proposed above, structural uniqueness rises at the interface individual/population that permits the genetic assimilation³ of innovations in evolutionary time that convert analog into digital information (Andrade, 2002, 2003, 2004). The digitalization of information manifests as increases in $H_{(G:P)}$ and $H_{(G:E)}$ that depict a growing function of time that lags behind $H_{(P:E)}$ changes. In short, the uniqueness of the P was evolutionary achieved by internalization of information from the E 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 congruent with E changes. These processes, in as much as they contribute to streamline ontogeny, exert a pressure to minimize the increment of G (digital record) as well. Thence, an EDA becomes more dependent on its history and less dependent on the E to the extent that $H_{(G:P)}$ and $H_{(G:E)}$ was internalized in evolutionary time into the genetic record.

To summarize: The relations G/P and G/E are mediated by genetic assimilation. Genetic assimilation explains the incorporation of environmental information into the genetic record. The evolution of ontogeny is a process of information gain expressed as increases of mutual information content between G and P, though P never gets to be fully determined by G. Likewise phylogeny is a process of information gain expressed as increases of mutual information content between G and E, though E information is only partially incorporated into G. Equation (1) can also be applied to understand these relations: $H_{(G)} - H_{(G|P)} = H_{(P)} - H_{(P|G)} = H_{(G:P)}$ and $H_{(G)} - H_{(G|E)} = H_{(E)} - H_{(E|G)} = H_{(G:E)}$,

³ Gathered information enhances evolutionary potential after being copied into a digital format (genetic record). The problem is how information about E gets recorded in such a digital format. This is a known problem in biology (the inheritance of acquired characteristics) that is explained by Waddington's genetic assimilation. Only the digital is inherited in the standard Mendelian way. Other kinds of variation can be transmitted by means of epigenetic inheritance systems EIS and its contribution to evolution depends on its further 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. So that analog records are reversible and unstable, nonetheless they favor the fixation of mutants that produce the same feature that the organisms develop in presence of the external stimulus. Once it is incorporated the organism develops the feature even if the stimulus is removed from the E, because it has become constitutive. It all boils down to say that the evolutionary contribution of individual storage of analog information must not be overlooked.

where $H_{(G)}$ stands for genotypic complexity. $H_{(G:P)}$ stands for genetic information that contributes to the phenotype. $H_{(G|P)}$ stands for genes that are not informative for P construction. Conditional information reflects the flexibility of G with regard to P, for instance the capacity to include neutral mutations and adopt new encoded functions. $H_{(P|G)}$ stands for features of P that are not dependent on G, because they are influenced by E. $H_{(P)}$ stands for phenotypic complexity.

Likewise, $H_{(G:E)}$ stands for environmental information that has been incorporated into the genome. $H_{(G|E)}$ stands for anticipatory capacity based on the existence of duplicated redundant sequences. $H_{(E|G)}$ stands for E features not recorded by EDA, though some of them are likely to be recorded in the future. $H_{(E)}$ stands for environmental complexity. Noteworthy all these relations are mediated by the EDA that lives in its phenotype encoded in the [2-1] mode.

The study of the interrelations between G, P and E explains how the evolution of life cannot depend on sheer random variations, but on the joint action of internal/external and individual/population factors that converge to give a more or less directed response based on a semiotic choice that minimizes 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 fixed and preprogrammed where no original innovations take place, no room for freedom and creativity. Both mistakes are associated with a mechanical view of nature. Chance is ignorant, variations are the very products of semiotic choices neither directed, nor random but canalized. This is a model that minimizes chance without falling into the opposite mistake, a goal directed evolution. Chance is only the unpredictability for an external observer of EDA semiotic choice. Choices are made within a somewhat restricted span of possibilities but which one will be selected depends on EDA's evaluations. But this choice brings forth new possibilities that were unforeseen before the choice was made. At this moment potentiality [1-1] is renewed.

6. Peircian Relations And Genetic, Epigenetic, Behavioral And Environmental Informative Resources

An EDA experiences and probes its world as an individual that captures energy by encoding and decoding analog and digital information, so pulling itself through a developmental trajectory. The understanding of living entities as EDA becomes an alternative to genetic reductionism, by means of which Developmental systems theory (DST) can be interpreted. Oyama defines a developmental system as a “mobile set of interacting influ-

ences and entities” comprising “all influences on development” at all levels (Oyama 1985), and Griffiths and Gray (1994) affirm that it involves a whole matrix of resources and interactions that permit the reconstruction of ontogenetic and developmental information in each generation. Likewise, I propose that the fundamental unit of evolution is not the gene, but the interacting EDA that by measuring and recording is responsible for information updating in each life cycle.

But, to what extent does the EDA depend on self-organizing processes driven by analog interactions? And to what extent does the EDA depend on inherited encoded digital information? To answer this question one must recall Salthe’s developmental stages, (Salthe 1993: 9, Salthe, 1995): (A) Immature, (B) Maturity and (C) Senescence. Each stage can be characterized by the relative weight attributed to each one of the six modes of codification.

A) Immature stage of “openness”:

This phase is suited for modeling the major evolutionary transitions i.e. the origin of life, the origin of the eukaryotic cell, the Cambrian explosion. However at the very earliest before the emergence of life the distinction organism/environment has no meaning. This is the [1-1] mode of full potentiality. It represents all the possibilities at the point where no interactions have yet taken place since the symmetry and homogeneity of an excited undifferentiated matter has not been broken. Nonetheless it helps to understand the burst of diverse and disparate forms achieved in early life history, with no requirement for differential fitness or competition. Once the boundary inside/outside was achieved, life and the environment came into being. The [1-1] mode codes all possibilities of the individual given its inner drives, creative urges and the available energy. For a protein, it corresponds to the state of maximum uncertainty given by the set of all possible attainable conformations from the unfolded state. For an undivided egg, it would be the set of all possible differentiated cells that can be produced by divisions and differentiation, the starting point of a life cycle from unicellular stage towards multicellular organisms. For a primitive life form, it stands for all the possible states or forms that can stem off from it.

Characteristics of phase A:

1. It is induced by an environmental catastrophe; in consequence the emerging EDAs are uncertain about their E, a situation that corresponds to a minimum of

- shared informational content between EDA and environment and a maximum of conditional information.
2. Low connectedness is found between inner components, and between emerging EDA and E factors.
 3. Non-random interactions are being established between inner constitutive elements.
 4. Outline of the very basic *Bauplan*.
 5. Extrapolating Zurek's model this phase corresponds to high uncertainty (H) and low digitally encoded environmental information (K). (Fig. 2 stage A).
 6. For evolved life forms evolutionary innovations are very unlikely in this phase for it would affect early developmental steps, but if successful, would lead to abrupt intense changes.
 7. The following modes of encoding overlap: [1-1], [3-3], [3-1].

The asymmetric expansive and creative impulse [1-1] is offset by the habit taking mode [3-3] that through interactions with environmental resources forces a statistical average [3-1] that opens the way for the creation of an interface [2-1].

Early immature stage: prevalence of internal analog information [1-1] with increasing potential for efficient analog/digital conversion. At this stage environmental information has not yet been incorporated into the genetic record, thus, it is a phase of a strong structural dependence on external circumstances, for instance, forms being shaped by external physical forces. D'Arcy 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). The neodarwinian and Mendelian modes of shaping life had to wait for the appearance of encoded information (Newman and Müller 2000). Organization patterns must be inferred prior to the action of natural selection (Kauffman 1993, Goodwin 1994, Denton et al., 2003). In evolution, this phase corresponds to chemical prebiotic evolution, for instance Fox's micro spheres and Kauffman's first autocatalytic networks before the emergence of DNA and genetic code.

Late immature stage: it is defined by the appearance of an internal digital redescription of the self in the form of a genetic record in evolution so that thereafter the EDA interprets genetic messages and makes use of gene products. P has a low dependence on

G, and the internal analog information plays a role as a cohesive internal factor. There is an abrupt increase of $H_{(P:E)}$ followed by slowly rise of $H_{(G:P)}$ and $H_{(G:E)}$. Associated increments in $H_{(G)}$ bring forth the augment of structural motifs of the EDA that by conferring enough internal variation permits further internalization of information about the transformed environment.

Embryos, thus, correspond somehow to earlier life forms that were and are no longer open to the influence of external environmental factors, in agreement with the view that the modification of developmental routes in free living primitive forms opened up novel evolutionary paths. It is in this sense that ontogenetic variations create long term phylogenetic canalizations.

... 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)

Although Richardson et al. (1997) has shown that even 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, still one can consider today's embryos as structurally closed or buffered to E influences while PLF were open to them. Structural closure of today's embryos resulted from the digital symbolic internalization of E information. To say that PLFs were more open than today's embryos, means that they were more flexible and had dynamic structures which adopted a great number of alternative conformations with varying affinities for environmental elements. In every moment, the number of external factors is a function of the number of conformational states (according to the reaction norm) that characterizes P. The constancy, stability and convergence characteristic of ontogenetic early stages within classes is due to two factors, first the re-edition of previous environmental conditions that act as internal Epigenetic Inheritance Systems and secondly genetic information. Nevertheless gene expression is dependent on signaling systems that make up part of the EIS. For example, the control of early development is exerted by maternal environmental factors that in due time turn on their own genes. PLF with less complex genetic process are unstable, they do indeed show higher phenotypic plasticity because they are more susceptible to environmental influences. They are less constrained. This phenotypic plasticity that may have acted as an evolutionary potential in PLF, is not shown in the earlier stages of ontogeny because the environ-

ment of the developing egg is more homogeneous and less complex than the environment of PLF

B) Intermediary mature stage between “openness and closure”.

This phase on a developmental scale corresponds to the realization of the juvenile and young adult form and on an evolutionary scale to the consolidation of basic body patterns (Ediacaran explosion of body plans followed by a second explosion around the base of the Cambrian 545 my) and functional adaptation in populations. Maturity is characterized by active encoding of digital information by means of the combined influences of behavior, EIS and cooptation by genetic assimilation of random genetic variations that result in the maximum efficiency analog/digital conversion. At this stage, selection brings forth encoded adapted motifs and the consolidation of the most important structural domains of present day phenotypes.

This phase is characterized by:

1. Rapid increasing mutual information content between P and E that drag subsequent increases in $H_{(G:P)}$ and $H_{(G:E)}$.
2. Increasing connectedness among inner subsystems.
3. Adaptive evolution.
4. Decreasing E uncertainty to a level in which enough plasticity is maintained.
5. Consolidation and fine tuning of structural *Bauplan*.
6. Extrapolating Zurek's model, this is a phase of decreasing uncertainty (H) and low increases in mutual information content between EDA and environment (K). (Fig. 2 stage B).
7. For evolved life forms, evolutionary innovations due to modifications of intermediary stages of development are more likely to occur and lead to less abrupt and intense changes with regard to phase A.
8. The following modes of encoding overlap: [3-3], [3-1], [3-2], [2-1].

The following modes of encoding are found, depending on the ways EDA deal with external constraints [3-1] and the interpretations of the genetic information [3-2], the interface [2-1] shifts towards a state of local discreteness in the form of a truly differentiated entity [2-2]. This phase oscillates between “openness” and “closure”, due to EDA's measurements that happen as a permanent action in the progressive mode [3-3].

When the EDA moves towards openness it can expect to find fairly adaptive evolution encoded in [2-1] and [3-1] modes characterized by a rapid and continuous coupling between organism and environment. Potentiality remains as long as new behaviors or

new manners to interpret the environment are being proposed by EDA, some of which are interiorized in Epigenetic Inheritance Systems. In consequence the following can be observed: 1. Directed behavioral innovations. 2. Refueling of organisms' drive to cope with uncertainty. 3. Enhanced variability of developmental pathways. 4. Increasing mutual information content between G/P and G/E.

When EDA moves towards closure it can expect to find slow adaptive and nearly neutral evolution given by the prevalence of the [3-2] and [2-2] codes. In consequence one can expect to find: 1. nearly neutral genetic variations and increasing redundancy, 2. diminished capacity to anticipate possible environmental changes, 3. stabilization of developmental pathways, 4. decrease of mutual information content between EDA and environment.

C) Senescence stage approaching "closure":

The developmental stage of senescence reveals itself as stabilization and decay. On the evolutionary scale, senescence manifests as an ever slower change of terminal adaptation to a stable environment and increasing neutral genetic variations.

This phase is characterized by:

1. Maximum value of encoded information or mutual information content between G/P and G/E.
2. Decreasing capacity of EDA to cope with E changes, loss of flexibility or capacity to react creatively to external stimulus due to lowering of EDA's conditional information.
3. Overconnectedness among component subsystems.
4. Neutral evolution and random genetic variations.
5. Extrapolating Zurek's model, this is a phase of minimum uncertainty (H) and maximum values of K as in (1). (Fig. 2 stage C).
6. For evolved life forms evolutionary innovations by terminal modification of development are more frequent but manifest as minor modifications or gradual transitions.
7. The following modes of encoding overlap: [3-3], [3-2], [2-2].

There is an overlap of the modes of encoding [2-2] that is revealed as increasing closure and discreteness, and the mode [3-2] that manifests as a stabilizing of genetic information. The phase of senescence leads in ontogeny to the following outcomes: *i*) Individual decay and death after completion of life cycle. *ii*) Reenactment of the juvenile form: the modifications of developmental routes are possible by opening up to new ways to

interpret the external environment by young adults' creative behaviors. For instance: neoteny (early sexual maturity that makes it unnecessary to continue the whole developmental cycle) may bring forth plastic younger forms that lead to novel ways to explore the environments. These outcomes are paralleled by the following evolutionary outcomes: *i*) Species extinctions. *ii*) Modified developmental routes that lead to evolutionary branching. This branching will consolidate through the exploration of variants that become functionally coupled to external influences. Notice that in (*i*) cases, though the fate is death, individuals while still alive make a contribution to the permanent remodeling of the epigenetic and *Umwelt* landscape. After death they favor the continuity of life by recycling of components. In (*ii*) cases, new life forms and lineages may spring forth.

In senescence the dependence on digital information follows increasing closure. The specialization of the realized structures occurs as $H_{(G:P)}$ increases towards maximum. At this phase, G undergoes minor modifications that serve to fine-tuning or terminal adaptation, within an already stabilized genetic network. $H_{(G)}$ shows a tendency towards minimum increments but paradoxically, its growth can only be minimized by incorporating more information from the environment. New measurements result in ever smaller changes congruent with ever diminishing entropy production as EDA approaches equilibrium or the point of minimum extraction of available energy.

7. Conclusions

The G/P/E interactions lie as a substrate that accounts for the relations between ontogeny and phylogeny which are not of cause/effect but rather of mutual entailment. If it were 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 using 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, it 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, considering that the self-referential loop does exist in nature I have preferred to justify the idea of a general transformative tendency that manifest at two different time frames. This model does justice to Oyama's valuable contribution while making it more amenable to formalization by making the analogy between a Developmental System and an IGUS or EDA. On the other hand Taborsky's cartography of Peirce six modes of encoding becomes a brilliant philosophical perspective that sheds light on deeply felt scientific problems by providing a way to interpret empirical data. The material embodiment of the EDA is

encoded in the analog [2-1] and [2-2] modes but as an agent of interpretation its activity is associated to [3-1] and [3-2] modes of being. Notwithstanding the differences with previous models is that cognition is not a property exclusive to the population/global realm but also to the individual/local, a fact that is best expressed in the idea of the EDA located at the interface internal/external, individual/population, present/perfect.

EDA is the phenotypic attractor state where environmental and genetic information are instantly interpreted, the interaction with the environment becomes recorded in 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) asserted that the relationship between genes and form is a derived condition, a product of evolution, a statement that I hope to have explained in depth by pointing out that it is the outcome of EDA semiotic choices.

This model explains also why there should be a tendency to retrieve developmental programs that are as short as they can be. The presence of non-redundant developmental programs is best accounted by a semiotic process mediated by a system sufficiently complex such as to be able to rid some steps off. This phenomenon becomes also the reason why strict recapitulation is unlikely to happen, though the core of the hypothesis is preserved, that is that novel evolutionary variation arose as organisms' reaction to environmental modifications in free living ancestors in their juvenile stages through changes in behavior that paved the way for major modifications some of which became genetically fixed. To conclude, natural selection favors EDA that is able to implement semiotic choices.

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