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Abstract:

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In contrast with some theoretical approaches in evolution, like neo-Darwinism, the approach presented here is not focused on the transmission and change of hereditary information that can be copied (like in the case of DNA). Instead, multiple mechanisms by which a system can generate offspring (with and without copy) and by which information in it affects the structure and evolution of its offspring are considered.

The first part of this article explains in detail these new concepts. The second part of the article explains how these concepts are directly applicable to the diversity of systems that can evolve. The third part introduces hypotheses concerning: 1) how different mechanisms of generation and inheritance can appear from each other during evolution 2) how the existence of several inheritance mechanisms in an

organism affects its evolution and 3) how the origination of inheritance mechanisms may give rise to parasites.

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She has been working in the evolution of inheritance systems for many years and has many important papers on it. My work makes a lot of reference to it

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He has been suggesting some concepts similar to some of the concepts introduced in my article but not exactly equal.

Evolution in biological and non-biological systems under different mechanisms of generation and inheritance

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Abstract:

The majority of definitions of life and evolution include the notion that part of an organism has to be copied to its offspring and that this includes some form of coded information. This article presents the thesis that this conception is too restrictive and that evolution can occur in systems in which there is no copy of information between generations. For that purpose this article introduces a new set of concepts and a theoretical framework that is designed to be equally applicable to the study of the evolution of biological and non-biological systems. This article focuses on the effect that these different mechanisms can have on the forms and rates of evolution of different kinds of evolutionary systems.

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Keywords: Inheritance mechanisms, generative system, development, cultural evolution, origins of life

Introduction:

In living organisms a part of an individual, the genotype, is copied into its offspring. This genotype interacts with other cellular components inherited from the parent (or parents) and the environment to lead, over time, to the production of an adult that is able, in its turn, to produce other offspring. Evolution is normally regarded as the change in the structure of organisms over generations. This change is due, ultimately, to the accumulation of DNA changes in the genotypes that are copied between generations (although not exclusively (Oyama, 2000; Jablonka and Lamb, 2005)). In that respect the majority of definitions of life and evolution (Palyi et al, 2002; Cleland et al., 2002; Ruiz-Mirazo et al., 2004) incorporate the notion that part of an organism has to be copied to its offspring and that this includes coded information (Schrödinger, 1944; Morowitz, 1992; Santos et al., 2003, Gánti, 2003). This article presents the thesis that this conception is too restrictive and that evolution, under some circumstances, can also occur in several kinds of systems in which there is no copy of information between generations. This article also tries to identify which are the minimal requirements for a system to be able to evolve. For that purpose this article introduces a new set of concepts and a theoretical framework that is designed to be equally applicable to the study of the evolution of known biological and non-biological systems. In that respect this framework has the dual motivation of helping in understanding the evolutionary process across systems and helping in the understanding of some non-biological systems by using an evolutionary perspective.

In contrast with some theoretical approaches in evolution, like neo-Darwinism, the approach presented here is not focused on the transmission and change of hereditary information

that can be copied (like in the case of DNA). Instead, multiple mechanisms by which a system can generate offspring (with and without copy) and by which information in it affects the structure of its offspring are considered. This article focuses on the effect that these different mechanisms can have on the forms and rates of evolution of different kinds of evolutionary systems.

This article simply introduces a new nomenclature and perspective. It does not present any new results or tests but helps reinterpreting evidence in biological and non-biological systems from a unified perspective. However, this article proposes new evolutionary hypotheses. These, however, are not tested. Instead, only some circumstantial evidence is presented to support them.

The first part of this article explains in detail some new concepts. This article also uses specific definitions of some commonly used concepts such as evolution, evolutionary system, non-biological and biological system. In this first part concepts are arbitrary and thus they can not be proven to be wrong or right, as far as they are not contradictory with each other. Some examples are discussed in that part but only to clarify concepts that may seem, otherwise, rather abstract. The second part of the article discusses how these concepts are directly applicable to the diversity of systems that are able to evolve. An extensive review of these systems is outside the scope of this article. However, example systems able to evolve will be presented only to exemplify the utility of the new concepts. In the third part of the article, the presented concepts are used to elaborate a set of hypotheses about how different mechanisms of generation and inheritance, including the ones found in living beings and others, differentially affect evolution. This is: 1) how different mechanisms of generation and inheritance can appear from each other during evolution 2) how the existence of several inheritance mechanisms in an organism affects its evolution and 3) how the origination of inheritance mechanisms may give rise to parasites.

While the second part tries to explain the applicability of the presented concepts to many different biological and non-biological systems the third part focuses only in those systems and conditions in which long lasting and complex evolution is possible.

Definition of generative system:

This article deals with generative systems. Generative systems are arbitrarily defined systems that fulfill the following requirements:

1) A generative system (the parent system) is able to generate (alone or with other generative systems), in a given environment, another generative system (the offspring system). For the purposes of this article this means that some information existing in a parent generative system (called the *kernel information*) is causally responsible, at least, for the information in the offspring system that allows it to be a generative system (*kernel heredity information*).

2) A generative system is physically independent from the parent(s) system(s). Physically independent means, in here, that changes occurring in the parent system do not necessarily have an effect on the offspring system. This definition allows for a clear distinction between generation, development and evolution. Generation is the process by which a generative systems ends up producing an independent offspring system. This involves recruitment of material elements from the environment and their organization in specific spatio-temporal patterns (the offspring system) through interactions with the organization of the parent(s) and the environment. The changes (if any) occurring in the offspring system from the moment it becomes physically independent to the moment in which it is able to produce other offspring systems is called in here the development of the offspring system. Generative systems can thus produce a sequence of successive offspring, offspring of offspring and so on. A *Lineage* is the set of ancestors of a given generative system. Lineages do not need to be lineal sequences since a generative system can have several parents and multiple offspring.

The use of information and causality requires some clarifications:

Information as organization:

Information is used in here as synonymous to organization or organizational pattern, as a specific pattern of arbitrarily defined relationships between arbitrarily defined elements. For example, spatial patterns (as distributions or configurations) of neighborhood between cell types in an animal, a specific pattern of friendship relationships between individuals in a club or a specific sequence of nucleotidic bases in a RNA molecule. Thus, for example, two different spatial patterns of cell types are told to have different information. Given a common definition of states and their relationships, the amount of information in two or more generative systems can be quantitatively compared by using relative statistical measures as for example joint information or mutual information (Shannon, 1948). How this information is measured and compared is not of vital importance for the ideas presented in this article.

Information in here relates to the patterns of configuration of parts in a whole (for example which atoms bind to which in a molecule) without consideration on the nature of these parts (although at a lower level the nature of these can come from the organization of its parts). This definition does not consider coding, as for example in DNA, because, as it will be proposed, coding is an advanced outcome of evolution and not something required for it. Since this article focuses in the later question, a definition that does not presuppose coding is preferred. In addition, this concept does not implicitly consider whether one information has an effect (or has meaning by interpretation) on information in another generative system because the aim is, to some extent, to identify the possible diversity of way by which this could happen. In that sense, other more complex definitions of information (Jablonka, 2002) are comparable to concepts based on the present meaning of information like causality (see later) but not to information as used in here.

This article loosely refers to complex phenotypes as phenotypes with a large diversity of different elements and relationships between them or to some related measures (like mutual information and others (Shannon, 1948)). It is important to note that this definition of information does not imply the existence of any kind of code, as for example the genetic code, nor the existence of a molecule with an intrinsic informational function as the DNA.

An organism phenotype can be described as information: For example as its cells types and their spatial relationships (which cell is next to which) or their molecules and their spatial relationships. It is important to note, however, that the existence of a phenotype does not imply, in this paper, the existence of a genotype and that in any case the genotype of living beings is part of its phenotype (its DNA phenotype). Then, unless it is explicitly stated, statements about the phenotype of a generative system also apply to its genotype (in the case the generative system has one).

Heredity or hereditary information is all the information in the offspring system that is caused by information in the parent(s) systems (this later information called *parental hereditary information*). Note that the heredity in a offspring system is not necessarily the same information than its parental hereditary information (that is when that offspring systems acts as a parent of another generative system). One clearly leads to the other, but other influences (for example from other parents, from the environment or from informational transformations inside a generative system) can also affect the parental hereditary information and can even make that this information is different at different moments during the existence of a generative system.

An *Inheritance mechanism* is defined in this article as any set of physical interactions (and their spatio-temporal organization) by which a parent can change or generate information in the offspring. The process of generation implies the existence of an inheritance mechanism but some inheritance mechanisms may not be associated with the process of generation itself. For example human parents can affect their offspring's information by teaching them some ideas (or

modifying their bodies) but these ideas may not be required for the offspring to be born (although some of them may be required for offspring's survival in specific environments). *Reproduction* is understood in this article as the generation of offspring system that resembles the parents. Then, as it will be explained, all reproduction is generation but not all generation is reproduction.

Causality:

"Causally responsible" means in this article that the kernel information is strictly required for the offspring system to be produced and that variation in it would lead to variation in offsprings kernel heredity. Notice that the definition of causality in this article requires the existence or possibility of variation. This causality does not imply sufficiency nor unicity. In other words, several parents may be required for the production of an offspring system (the kernel heredity then being caused by several different kernel informations). In that respect there is three main types of generative systems: *Informational parasites* are generative systems that require some external information in the environment to be able to generate the offspring system. This external information can come from another generative system or not. A clear example of that are viruses. To produce other viruses a virus requires the transcriptional, transductional and replicative machinery of the host cell. This machinery does not only provide the energy necessary for the production of new viruses but the structural information required for such a process to be possible (this is the spatio-temporal arrangement of the molecules involved in the transcriptional, transductional and replicative machinery). Note, however, that even if the host is strictly required for the production of offspring viruses its variation does not normally produce a change in the structure of the offspring viruses and thus can not be considered as a parent system. *Energetic parasites*: are generative systems that require some energy income from some other generative systems to produce the offspring systems. *Autonomous generative systems*: are generative systems

that are not parasites. In addition, *nested generative systems* are generative systems that are part of another generative system and are informational parasites of it (some examples are later presented).

Since the process of generation involves information changes (even in the case of copy, elements from the environment have to be taken and organized to form the copy itself) it follows that generation involves changes in energy. If the information changes involved in the generation process do not increase universe's entropy, then generation requires an input of energy from the environment (Prigogine and Nicolis, 1977). In that case generative systems are open dissipative systems that require energetic and material inputs. These material inputs can be information in itself that can be incorporated into the generative system. For example all living beings incorporate molecules from the medium (for example through food). Some of these are transformed and some are not but the configuration of these molecules is required for its proper functioning in an organism. Some of these molecules may be required for development and later reproduction even if they may not be part of heredity. Humans for example, as many other animals, are unable to synthesize many essential vitamins. These are often produced by bacteria and acquired through aliments. These vitamins do not provide energy as such but some molecular organization that is required for body growth and eventually reproduction (for example vitamin C is required for collagen hydroxylation a process essential for the formation of tissues such as cartilage and blood vessels (Peterkofsky, 1991)). In that sense most or all living beings can be considered informational parasites.

For the offspring system to be a generative system it is required that the information that, in it, is caused by parents kernel information is also causative of the generation of the offspring's offspring. This implies that the kernel heredity in the offspring's offspring is indirectly caused by its grandparent kernel information and so on. Thus generative systems imply a transgenerational chain of causation. Note that only causality is required. It is not required that any information is passed or transmitted from generation to generation, but that, simply, information in

one generation leads, causally, to information in later generations. Later sections would explain how that can be achieved without copying of parental information into the offspring system.

Evolutionary systems:

The concept of generative system allows introducing what is meant in this article by evolution. *Evolution* is change in the information (this is the phenotype) of the generative systems in a lineage over generations. Individual generative systems can not be considered to evolve, but to develop. The definition of generative system implies the existence of a lineage and, in a way, this definition of evolution is equivalent to: change in the structure of individuals through a lineage.

It is often the case in living beings that parents and offspring are far from being identical. In obligate sexual animals each gamete receives only a subset of the parent's genotype. This subset arises by the recombination of the genotypes inherited from the grandfather and grandmother. Each individual thus only shares around 50% of its genes with each of its parents. The pairing of chromosomes during meiosis and mitosis produces that normally each offspring receives a copy of every gene from each parent. However, this is again imperfect because father's and mother's genome may have non-homologous recombination. 50% of genetic similarity does not imply, however, 50% of phenotypic similarity because mother and father gene products often interact to repress each others or to produce an outcome that is not necessarily the average of the parents (dominance). Even without dominance the intricate genetic and epigenetic interactions between genes that are required for development ensure that 50% of genetic similitude does not linearly ensure 50% of phenotypic similitude. Environment can also affect the phenotype in such a way that even in asexual organisms the phenotypes of the offspring and parents can be substantially different (West-Eberhard, 2003). In fact, experimental measurements in quantitative genetics show that, in general, the heritability of phenotypic traits can be very variable (Carlborg and Haley,

2004). In other words, even if the offspring get their genomes by copying part of their parents genomes they are not always very similar to them. However, even when heritabilities are very low, evolution is still possible (although it is slower and less effective).

In living beings, where evolution is better understood and accepted as a phenomenon, DNA copying occurs between successive generations in a linage. In that case evolution is still understood as change in the phenotype of individuals (this being the genotype and the rest of the phenotype) over generations. Thus, although there is copying, what counts as evolution (or which aspects of the phenotype are regarded as evolving) is what changes between generations (so what is different from ancestors and not what is common). This is why, in here, evolution is concerned with change in lineages and does not depend, in its definition, on the mechanisms by which lineages are generated. Thus, evolution does not require copying but the existence of a lineage (thus causality between generations and the possibility of change in it over generations). In that respect, this definition of evolution is general and includes what happens in living beings while at the same time can consider, as it will be explained, evolution occurring in other kinds of lineages.

An evolutionary system is a generative system that is in an environment where its offspring evolves over time. Thus, the classification of a system as evolutionary is dependent on the environment. The same occurs for the definition of generative system, a system would be able to generate generative systems depending on the environment (for example if the essential energetic and informational resources are available). Therefore the classification of a system as generative or evolutionary should be regarded as a hypothesis about a system's lineage behavior in the future (in a given environment). In this article the term biological systems arbitrarily includes all the kinds of living beings known to science (monera, protista, animalia, plants, fungi) and also viruses and viroids.

Evolutionary systems and the environment:

The environment of a generative system is defined in this article as anything that is not the generative system itself. The evolution of a generative system can be affected by the environment in two major ways: *mutational environmental effects* are environmentally induced changes in the parental hereditary information or kernel information of a generative system (the change itself called *mutation*) while *non-mutational environmental effects* are environmentally induced changes that do not affect the parental information of a generative system. In living beings mutations can be changes in the genotype that have an effect on later development. In generative systems without a genotype, as it will be explained, the mutation itself is a phenotypic effect but this leads to different phenotypic effects later in development.

The phenotypic effects of a mutation are defined as the phenotypic consequences of this change in the subsequent development of a generative system. Mutations clearly affect a lineage's evolution by changing the information that is causal between generations. Non-mutational effects can also affect evolution by affecting the probabilities by which a generative system will give rise to offspring systems. Non-mutational effects can be, for example, the relative abundance of some informational resource or energetic resource or any other factor (like predators or destructive accidents) that affects the probability of generation. Thus, non-mutational effects can lead natural selection. In living beings, but not necessarily in other kinds of generative systems, what is normally considered as somatic mutations and environmental effects on development can also be considered as non-mutational environmental effects.

The range of mutational effects possible in an environment has a strong influence in the evolution of a lineage. This range depends on the environment and on the structure of generative systems (in fact in the interaction between those). The *total variational properties* of a generative system is the set of different offspring systems arising from all possible mutations in a given

environment. The *variational properties* of a generative system are a subset of the total variational properties that includes only the mutations that occur more often in a given environment.

The evolution of a generative system and its total variational properties can be finite and predictable. This does not seem to be the case for living beings but it is likely to be the case for some simple generative systems placed in simple environments. In that respect this article is not only concerned with evolutionary histories that started in the past and are still going on (like in living beings) but also considers hypothetical or real started-and-ended evolutionary histories and evolutionary histories that start and end many times and very fast. Examples of that will be provided in the next section but in general three different types of evolutionary histories for a lineage can be described: *monotonous evolutionary histories*: The repertory of changes occurring in a lineage of generative systems during evolution is finite and predictable. *Recombinant evolutionary histories*: The repertory of changes in an evolving lineage is not finite but it can be understood as the combination of a finite number of basic changes. *Open evolutionary histories*: When none of the previous applies. This categorization is similar to that of limited and unlimited heredity (Maynard Smith and Szathmary, 1995) except that it includes aspects about the environment and variational properties.

The concept of generative systems is vaguely reminiscent of that of reproducers (Griesemer, 2000). A reproducer is a unit of multiplication, hereditary variation and development in which a parent generates a offspring that is able to develop to generate its own offspring (as in here). However, what is meant by heredity is not defined as in here and it seems to imply some kind informational transmission (like something identical is passed from parents to offspring) and it does not considers informational transformation between generations (as in here). Here generation, instead of multiplication, is required. Generation is more general than multiplication, although clearly, multiple offspring generation is likely to be selectively advantageous over single offspring generation. Generation or multiplication is not defined on the bases of physical independence,

kernel information and causality. Material overlap is not required for generation in generative systems but it is required in reproducers. This allows applying the concept of generative systems to non biological systems as it will be later explained. In summary, reproducers could be an instance of generative system (or following the trend in terminology a generator). In addition, it has been suggested that replicators (units of copying and variation as in DNA) are evolutionary ancestors of reproducers (Szathmary, 2006) while here it will be argued that generative systems are evolutionary ancestors of replicators (but also descendants).

The next section discusses some examples of generative systems to clarify the concepts presented until this point. Additional concepts would be introduced during next section. These are easier to understand after the discussion of concrete examples.

Examples:

Five kinds of examples are going to be discussed throught this article: living beings, parts of living beings, psychological, computer-based and chemical. Many of these examples are not very well understood, many are not usually considered from an evolutionary framework and others have never been found but are used for the purpose of clarifying some concepts.

Chemical generative systems and closed mutations:

Some chemical systems could provide the simpler examples of generative systems. A system of reactions in a chemostat, where reactants are steadily supplied and some products evacuated, can, in some circumstances, be considered to be made of generative systems. An example could be a reaction in which a molecule A reacts with an externally supplied reactant R_a to produce a molecule of B and P_b (a product that is evacuated) and B reacts with R_b to produce a

molecule of A. The molecules A and B can be considered as generative systems if there is at least one possible mutation (for example due to some lateral reaction or some external radiation) that transforms A into another molecule A' and this molecule A' reacts (with R_a) to produce a molecule B' (and P_b) that reacts (with R_b) to form a molecule A'. This is because the change in A (to A') is responsible for the change in B (to B') and this change also affects the information in B that is required to make its offspring generative system A (that then changes to A'). In other words, the change in every molecule (for example from A to A') is, from the definition herein, a change in its information (typically the nature and spatial arrangement of atoms). Thus the informational change in a generative system A (to A') is responsible for the variation in information in system B (to B'). This change in B clearly affects the information in B that is required to produce its offspring system because B' produces A' instead of A or nothing. In that sense there is a transgenerational causal chain.

This kind of mutation is called in this article a *closed mutation*. An *open mutation* is a mutation in which, for example, A' will lead to B' but B' would lead to A (instead of A'). Open mutations, thus, have no effects on future generations while closed mutations have. From the definition of generative system it follows that any generative system should be able to suffer at least one closed mutation in its kernel information (otherwise there is no causality between the information in a system and the information in its offspring).

Another example mutation that can help to understand the nature of generative systems is a mutation in which A' leads to B' and B' leads to A'' and A'' to B'' and successively A^n leads to B^n and B^n to A^{n+1}. This is also a closed mutation. In fact, there is nothing in the definition of generative system that forces a member of a generative system lineage to resemble any of its ancestors. In this example the causality link between information in generations is not broken at any point. In fact, a lineage of systems in which A^1 leads to A^2 and A^2 leads to A^3 that leads to A^4 and successively A^n leads to A^{n+1} is a lineage of generative systems as far as there is, in a given

environment, some possible closed mutation (leading, for example, to a lineage in which $A^{n'}$ leads to $A^{n'+1}$).

To my knowledge no chemical system has been reported to be a generative system. Some artificial self-catalytic chemical systems have been studied in relationship to the origins of life (von Kiedrowski, 1986; Terfort and von Liedrowski, 1992; Sievers and von Kiedrowski, 1994; Bohler et al., 1995; Pitsch et al., 1995; Wintnet and Rebek, 1996; Lee et al., 1997). These have generation, as autocatalysis, but they do not seem to have the capacity to accumulate changes that lead to changes in the offspring (closed mutations). Then these systems can not be considered to be able to evolve (nor are they generative systems).

Although no artificial or natural chemical generative systems have been reported some studies provide indirect evidence of its existence. In a recent study (Ashkenasy et al., 2004) it is shown that a polypeptidic molecule (T1) can be catalyzed from two other polypeptides (N and E1) by another T1 molecule. A T1 molecule is made of an N and an E1 molecule bound by a peptidic bond. In T1 catalysis the N part of T1 interacts with an N molecule while the E1 part interacts with an E1 molecule, this positions N and E1 in a favorable spatial arrangement for the formation of a peptidic bond (thus a new T1 molecule is catalyzed). This kind of autocatalytic reaction is also possible in 9 other polypeptides (T2 to T8) from N and 9 precursors (E2 to E9). All the E polypeptides are very similar: they differ only in one or few aminoacids. Each T molecule can catalyze the synthesis (from N and a specific E) of several other kinds of T molecules (but not all of them). This pattern of cross-catalysis is indeed rather complex (Ashkenasy et al., 2004). This pattern allows, however, identifying generative systems. For example, in a chemostat with only molecules of T2, N, E2 and E5, only T2 molecules reproduce. However, if one mutation can transform T2 into T5, then T5 molecules would also be produced. In that sense a T2 molecule is a generative system because it can generate other generative systems (other T2 molecules) and also have closed mutations (when T2 becomes T5, T5 can generate T5 offspring systems and not T2

systems) that change the kernel heredity of the offspring (T2 is changed to T5 and then can catalyze the production of T5) and produce a different generative system. Both T2 and T5 can catalyze the formation of other T molecules if the appropriate E molecules are present. Thus, T molecules do not copy themselves (see later definition of copying) but simply re-make themselves. In that sense these generative systems are generative systems without copy. In principle, these kinds of systems may not be dramatically interesting because they are unlikely to lead to monotonous evolutionary histories.

In practice it is likely that many generative system without copy are possible and then the critical question may not be whether generative systems exist but which of them, and under which conditions, can produce many different kinds of closed mutations (and potentially lead to non-monotonous evolutionary histories) and how they relate to living beings.

Biological generative systems:

Most biological organisms fall into the category of generative systems here introduced. However, not all biological systems are generative systems. For example sterile organisms (like for example hybrids between biological species) are not generative systems. This distinction is similar to the one introduced by Gánti between life and evolution units (Gánti, 2003). The are many difference between evolutionary units and generative systems is that the later do not presumes the existence of copying in generation process. Similar differences hold for the concept of unit of selection (Lewontin, 1970).

Nested biological generative systems:

Some parts of living beings can be considered as nested generative systems. For example, cells extracted from animals and keep in cell culture (Rubin, 1992) can be considered as generative systems in the limited environment of the culture itself. Each cell gives rise to daughter cells that are in their turn able to generate other daughter cells. In addition, these cells are able to evolve in the sense that genetic mutations accumulate over generations (Rubin, 1992). This does not imply that these changes are adaptive although it is expectable that in conditions of finite resources and space some kind of natural selection is likely to occur.

A more natural example at the cellular level is cancer. In cancer a cell or group of cells starts to proliferate in excess and independently from the body extracellular regulatory signals. These de-regulated cells can have an increased mutation rate (Chow and Rubin, 2000). Mutants that increase proliferation rate and independence from body's signals increase their frequency. Mutants that can penetrate body's mechanical and chemical barriers to spread around the body (producing then metastasis) have access to more resources and can increase their offspring and relative frecuencies. If the body is taken as the environment each cancer cell can be considered as an evolutionary system for which there are clear selective pressures. This evolution has a predictable end with the death of the host body but this certainty does not affect the classification of cancer as an evolutionary process (simply each cancer has a started-and-ended evolutionary history).

A similar example can be found in the evolution of genes, plasmids, transposons and DNA sequences in general. If the environment is taken to be the genome of a living being and all its offspring, then any gene, transposon, plasmid or (in general) any DNA sequence that can be copied by cells machinery can be considered as an informational parasite nested generative system (note that nested means that they are at the same time parts of and parasites of the organism). They are causative for their offspring sequences and their changes. As in the case of cancer these sequences can evolve under clear selective pressures (increase in its frequency in host's lineage) that are not always compatible with the selective pressures acting on the host. A clear example of that are killer

plasmids: plasmids that produce a long lived toxin and a short lived antidote for it. Daughter cells that do not receive a copy of the killer plasmid are killed by the long lived toxin (inherited from the split of mother's cytoplasm) (Gunge, 1986). This ensures the spread of the plasmid in populations. The abundance of transposon sequences in many genomes (especially animal) also suggests the evolution of some gene sequences as evolutionary nested generative systems (Kidwell and Lisch, 2001). In essence these so called selfish sequences (Doolittle and Sapienza, 2001; Hurst and Werren, 2001) can be regarded as behaving as viruses in which transmission is only possible to host's offspring (like if they would be vertically transmitted viruses in contrast to the normal "horizontal" viruses).

Computer based generative systems:

There are several *in silico* artificial life algorithms that implement generative systems. Many of them are artificial life programs, like for example Tierra (Ray, 1991) or avida (Adami and Brown, 1994), that embody artificial organisms as a sequence of computer instructions (Bedau *et al.*, 2000). These are copied, over generations, into the computer memory and mutated. These generative systems compete for memory space and CPU time (or some program-specific analog) and, by doing it, lead to a process of evolution by natural selection. To my knowledge all artificial life studies use copying. However, it is easy to propose computer based generative system without copying that can evolve.

For example an informational parasite computer based "organism" made of a set of mathematical functions. In each generation a function applies to itself (composes with itself) to produce a function as offspring. Selection can be applied by giving an environmental numerical input to the functions in an organism and comparing its output with an arbitrary optimal numerical value. Mutations can be induced, for example, by changing the mathematical operations involved in

a function or by replacing a function with the application of it into another function in the same organism. This organism would be an informational parasite because it uses the CPU time, memory and structure of the computer to make all the calculations required for the process of generation. In this kind of organism the functions in a parent are causally responsible for the variation in the offspring and thus this organism is a generative system. In addition, no copying is involved in the process of generation (although copying could appear through functions that give themselves when applied on themselves). It is interesting to note that, as in cases that we will later discuss, if the optimal output changes over time, copying (by the above mentioned functions) may not necessarily appear as the most adaptive kind of function through evolution.

An imaginary example of a computer based generative system without copying can be introduced to clarify the concept: an intelligent robot that is able to construct other robots that are also intelligent and able to construct other robots. These robots could learn from the environment and produce in each generation offspring that does not resemble their parents and that have different methods and motivations to construct offspring. Since robots characteristics and generative capacities are due to the characteristics and generative capacities of ancestors (but are not a copy but a design based on life span experience) these robots would be clear examples of generative system without copying.

Computer viruses and worms are pieces of computer code that replicate as informational parasites in an environment comprising the computers in the world. This does not imply that viruses and worms are generative systems. For that it is required that they can experience closed mutations. The high reliability of information copying in computers seems to preclude this possibility but, apparently, no systematic studies have been performed in that sense.

Psychological generative systems:

It has been previously proposed that ideas that tend to be transmitted between individuals can be understood as evolving selfish entities (Semon, 1924; Dawkins, 1976). This is assumed to happen, by some authors (Dawkins, 1976), by imitation and then lead to the copying of one idea in one host to the same idea in another host. How to define ideas and which are their mechanisms of generation is a rather complex and controversial issue for which no important conclusions are going to be provided in this article. For the purposes of the article an idea is any neurally encoded information that can be remembered. In here, as in some other work (Sperber, 1996; Jablonka and Lamb, 2005) it is considered that copying is not necessary for the evolution of ideas (as it is suggested for the case of memes; (Dawkins, 1976)). Any idea that is communicated in some way can evolve as far as its lineage can have closed mutations. Thus, some ideas could be generative systems with copying, some without copying and some are not generative systems.

In communication a set of physical changes in the environment (that can be speech, chemicals, body gestures and writings among others) produced by the emitter host are received and interpreted by the receiving host. In this process a new idea arises in the receiving host. This idea is caused by the idea in the emitter host but may not be identical or similar to it. It is a common day experience, in fact, that there is substantial variability in the way an emitted idea is understood by the receiver host. This involves not only possible noise in the environment but also the relative capacities and previous knowledge of the emitter and the receiver. The neurobiological bases of ideas are not currently understood. However, the offspring idea is not necessarily copied and then modified by other ideas in the host. The generation of an idea in the host is influenced (and likely also caused) by the other ideas existing in it. In that respect whether ideas use copying or some kind of recombination is an open question that may accept multiple answers. This in fact, does not preclude the evolution of ideas but, on the contrary, may enhance it (as it will be explained).

Mechanisms of generation:

In this article the mechanisms of generation refer to the physical interactions (and their spatio-temporal organization) that are required in the parent generative systems to give rise to offspring generative systems in a given environment. Even in living beings these processes are not fully understood. This article does not provide an exhaustive list of all possible mechanisms of generation but an incompatible description of some of them. However, even at this coarse level the differences between these mechanisms are large enough to allow tentative inferences about how they may affect the evolution of different generative systems.

Copying:

Until this point the article has made many references to *copying* without providing a definition (although the case of DNA replication has been taken as the paradigmatic example). In copying the parent generative system recruits elements from the environment (for example nucleotidic bases or their chemical precursors) and makes them interact with part of its structure (for example the DNA and the replication machinery) to produce a copy of that part (for example the DNA itself or in general the genotype). In living beings this happens by the replication machinery acting on complementary DNA strands. In computer viruses copying occurs by completely different mechanisms. Information (the virus) as patterns of 0s and 1s is stored as ordered spatial patterns of magnetization states (0 and 1) in a hard drive or some other storage media. Since different magnetization states allow or preclude the pass of current a stored pattern of "on" or "off" current tracks (the 0s and 1s) can be recovered by passing a current over the magnetized media. This way, information (as for example the virus program) is copied without the use of complementary interactions but by making environmental resources (current, free memory and CPU time) to interact with the structure of the parent (the magnetization pattern that describes the parent system in the memory).

The proportion of the phenotype that is copied by copying mechanism can be different between types of generative systems. In computer viruses and in biological viroids (viruses consisting of a naked RNA molecule), for example, the whole phenotype is genotype. In most living beings the genotype is only a small proportion of the phenotype (although the genotype may interact with the epigenetic structure of the zygote to regulate many aspects of the rest of the genotype).

The range of structures that can be copied by a copying mechanism can also be different. In computers only 0s and 1s can be copied while in living beings four configurations can be copied (A, T, G and C). Ideally, however, the maximal rates of evolution by copying would be attainable, if any simple aspect of the phenotype could be copied. In general, copying more complex phenotypes (for example if protein three-dimensional structures, cells or cells spatial arrangements could be copied directly) can be expected to require more complex copying mechanisms. For ideas, for example, the structure of a brain is required (and even then it is not necessarily the cases that all ideas can be copied). In addition, it can be expected that more complex copying mechanisms are also necessary for copying large number of structural changes in a structure (for example to copy nucleic acids with more than four base types).

Re-making:

Reproduction, the generation of offspring generative systems identical or similar to the parent generative system, can occur without copying. By re-making a part of an offspring generative system is identical to a part of a parent generative system but this parent part is not mechanistically involved in the generation process. In re-making the generation process intrinsically works to produce a generative system (lets say A) that is similar to that of the parent. But if the parent changes (to A') it may still produce a offspring system looking like A. Thus, there is no

model part of the parent (like a genotype) that interacts to make a copy. Instead, the offspring system arises only from the dynamics of the generation mechanism of part of the parent generative system.

The simple hypothetical chemical generative system described previously could be an example of re-making. As explained these generative systems can suffer closed mutations but these do not arise because of copying but because of particularities of the generation process itself (note that as explained a close mutation may lead to different phenotypes in different generations). Hypercycles, hypothetical self-catalytic cyclical reactions (Lee et al., 1999) are also an example of re-generation and so are simple cyclic reactions as the formose reaction (Fernando *et al.*, 2005).

Others:

Other generation mechanisms are likely to be possible in the kinds of generative system that are currently poorly understood. In fact, the classification of copying and re-making is not very detailed at the mechanistic level. The rest of the article, thus, considers only the distinction between generative systems with copying and generative systems without copying.

A natural history of generative systems:

From the previous discussion it seems that even if some generative systems without copying may exist most generative systems known to science use copying. This article suggests that, in spite of that, generative systems without copying may be important both as possible precursors, and descendants of generative systems with copying. This section discusses these possibilities from both the evolutionary dynamics of generative systems with copying and generative systems without copying.

The different types of generative systems presented and their mechanisms of generation could be compared in relation to the frequency and variety of adaptive mutations they can produce. This, however, depends on the environment and is too complex to be approached in this article. As a proxy to that, this section compares mechanisms of generation from their capacity to produce closed mutations and also from their capacity to produce complex phenotypes. It is not implied that evolution tends towards increasing complexity. The aim is simply to produce some understanding about how that may happen when it happens. This section is based in the idea that, in general, the likelihood by which a mechanism of generation (or development) is going to be found in the evolution of a lineage depends on the likelihood by which this mechanism can appear due to mutations in past generative systems and the likelihood by which these mechanisms would produce closed adaptive phenotypic variation in a given environment.

Generative systems and the origins of life:

Currently one of the most widely reported hypothesis about the origins of life is the RNA-world hypothesis (Darnell and Doottlitle, 1986; Gilbert, 1986). According to it life would have arisen through self-catalytic RNA molecules. This hypothesis was motivated precisely because some unexpected catalytic activity found in RNA molecules. However, extensive chemical research on RNA and related molecules (Monnard, 2007; Chen et al., 2007) has identified a limited number of catalytic capacities. Other bio-molecules, like polypeptides, can catalyze a much richer range of reactions. However, it seems that there are no straightforward mechanisms by which polypeptides could catalyze their own copy and exhibit closed mutations.

Even the simplest examples of RNA or DNA replication (found in some viruses) require complex enzymes. Life requires (as generation often does) input of energy and molecular building blocks from the environment. Even in the case that early life appeared in an environment

with abundant energy and building blocks, replication would require a minimal metabolism that may not be possible from the limited catalytic capacities of RNA molecules. This metabolism is required to cope with the energetic demands of generation, and possibly, maintenance. Early metabolism is also required to attain a molecular diversity from which complex processes such as RNA copying or copying could arise (Dyson, 1985; Morowitz, 1992). In addition, as it will be discussed, the replacement of a copying mechanism by another (of different chemical nature) is unlikely once some degree of complexity is attained. Thus, both the replication process and life minimal metabolism require a minimal threshold of molecular diversity and complexity. This threshold can be reach, hypothetically, by random molecular events in some early earth special environment. Alternatively it could arise by a process of evolution in simpler generative systems without copying. In other words, systems in which closed mutations can happen without copying should be considered as possible evolutionary precursors of life-like generative systems with copying. Evolution by closed mutations could increase the variability of molecular species found in a lineage over time and eventually the chances of reaching some life-like system with copying. However, this kind of generative system would need many closed mutations. This may also require some threshold of molecular diversity and complexity but it is possible that this threshold is lower for non-copying generative systems. In fact, several researchers have proposed that early life would have appeared in chemical systems, called composomes, that can suffer heritable changes and generation but do not have copying. These systems, thus, fulfill the criteria to be generative system without copying (Segre et al., 2001; Hunding et al., 2006).

The invention of the genotype and its advantages:

Evolution by natural selection can be regarded as a process of learning in a population. In each generation each individual produces a set of offspring variants (trials) and some

of them may fit to existing selective pressures (tests). By the fact that the unfit produce less offspring the population "learns" in which way to change. In many living beings this learning is mostly by trial and error at the genetic level (the trial being produced by random mutations at the genotype level).

Copying can be seen as a mechanism of guessing that future selective pressures are going to be similar to current ones. In generative systems without copying the phenotype of the offspring system can be, in principle, very different from those of the parents. In that later situation adaptation is only possible if the environment changes all the time and in a way compatible with the phenotypic variation encountered in each generation's offspring. For large populations of generative systems originating from the same ancestors this can be possible as far as many different offspring generative systems are produced in each generation (in proportion to the amount of possible adaptive phenotype in a given environment). However, if generative systems without copying and generative systems with copying (assuming that they have similar variational properties) compete in an environment, then, the copying generative systems would be selectively favored if the environment remains constant between generations often enough.

Another important advantage of copying is that it allows closed mutations. In DNA, mutations leading, after repair, to any of the four nucleotidic bases (including deletions and additions) are closed mutations. Thus, DNA copying allows a large diversity of closed mutations (those appearing in any DNA sequence) by a single mechanism. Closed mutations should not be confused with modular heredity (Maynard Smith and Szathmary, 1995), in which, like in the DNA, different parts can suffer mutations independently (modularity does not imply closeness nor its absence).

It is not clear if RNA was the molecule that first allowed copying in early life (in principle other molecules could have been involved and later replaced by RNA) but once some part of a generative system is copied it can be hypothesized that it can drive the subsequent evolution of

its lineage. For that it is required that the genotype is extensible (that it can increase in size due to mutation and still allow copying) and that it can affect processes other than its own copying (for example metabolism). In that situation even a small genotype with a short sequence can be expected to grow (*Genotypic drive hypothesis*) to affect many aspects of the phenotype and be the main factor responsible for its evolution. This drive is not due to copying per se but to the closed mutations it allows and, hypothetically, it would also occur in generative systems without copying that can produce many closed mutations (see next section for possible examples).

This situation can be clarified with a hypothetical example consisting of a pre-biotic system with a metabolism and a membrane-like amphilitic vesicle that splits in two after a threshold size is reached. If a copyable molecule (like some RNA) in it can bind to some reactants to affect their specificity or catalytic activity (even if just slightly) some conservation of catalytic capacities would be ensured between generations (of course other mechanism can also exist at that time). If duplications of this sequence and later mutational divergence of the duplicated sequences allow affecting several metabolic molecules (of the same species or different species) differently, then this enhanced conservation can increase in frequency. More importantly, the effects produced by the RNA molecule on catalysis could suffer closed mutations. If these mutations lead to, at least, slightly different specificities or catalytic rates, then these RNA molecules may increase in number and number of types. This could increase the speed, number and reliability with which a lineage can respond to natural selection. The increasing chances of getting closed mutations would produce that, over time, adaptive variation occurs most often in the aspects of the phenotype that are affected by the genotype. This process can go on as long as the copied molecules (and its mutation) can specifically affect aspects of the metabolism and phenotype in general. It is interesting to note, in that respect, that there are a number of very widespread and conserved enzymes in living beings that require and are affected by RNA molecules (Huttenhofer and Schattner, 2006).

This hypothesis also suggests that early life may not have appeared from a set of self-copying molecules that later acquired metabolism but from a metabolism in which some closed mutations became possible and in which, ultimately, some molecules acquired self-copying ability (or collective self-copying) and then allowed more closed mutations in metabolism. A side effect of this hypothesis is that the function of parts of a generative system that are not affected by the genotype may tend to be replaced by networks of other molecules that are actually affected by the genotype (and perform equivalent functions). This would suggest that in early live evolution, a reduction on the diversity of types of molecules could have temporally co-occurred with the arising of copying. Their functions would have been replaced by molecules that can be affected by the genotype. For example the number of types of aminoacid types in early life (or pre-life) could have been larger than 20. Copying may have driven evolution to be based on a smaller number of aminoacids combining on a large diversity of large polypeptides rather than into a large number of aminoacid types combining into small polypeptides. Alternatively, molecular diversity may not have decreased in early life. In that case the genotype drive hypothesis still provides a possible explanation to why bio-molecules are made of many different combinations of few types of monomers (like aminoacids) and not of few combinations of many different types of monomeres.

The existence of copying makes a system to evolve mainly in those aspects of the phenotype that are affected by the genotype. The mechanisms of copying that are more likely to appear in a lineage are those that require less mutational changes from ancestral members in a lineage. These are likely to be simple mechanisms able to copy only simple aspects of the phenotype and a small number of variations in it. This is because, in principle, it can be expect that simple mechanisms require less mutational changes to appear. For example in living beings only the DNA is copied (not more complex things like protein conformations, cells or whole structure of multicellular organisms) and only mutations that lead to one of the four allowed bases are copied. DNA and RNA copying may have appeared because they were, in early earth, the simplest, or

among the simplest, molecular mechanisms to allow copying (and copying would have been a simple way to allow many closed mutations).

In many living beings, only mutations in a small proportion of the phenotype (those in the genotype) can be used as variation for evolution (mutations in other aspects of the phenotype of living beings tend to be open). Complex multicellular organisms are generated from single cells (an egg) or small groups of cells (as in the blastemas that give rise to gemmation and other kinds of vegetative reproduction). In other words, the complex organization of multicellular organisms is not used to directly generate complex offspring systems but single cell gametes or simple multicellular structures for vegetative reproduction. Instead, offspring is generated from the level at which more closed mutations re possible or the level at which more closed mutations were originally possible. This produces that the offspring has to have a complex development in which genetic encoded proteins and RNAs have to interact with themselves and the epigenetic structure of a single egg or gemmule, to produce a complex multicellular organisms with different molecules and cellular types in different parts. In other words, since mostly simple aspects of the phenotype (the DNA) tend to have closed mutations often, complex aspects of the phenotype have to evolve and develop by multiple indirect interactions between what can be copied (and also between that and the epigenetic information of the egg cell or gemmule). This has been suggested to inevitably lead to a complex relationship between genotype and phenotype that, in many living beings, determines, together with natural selection and genetic mutation, the dynamics of phenotypic evolution (Salazar-Ciudad, 2006). This comes both from entrenchment (Wilkins and Duboule, 1998; the recruitment of a gene in the production of multiple traits leads to the unreachability of an optimal sequence for it due to opposing selective pressures in those traits) and the fact that the developmental mechanisms that most likely appear, by random mutation, exhibit a complex relationship between genotype and phenotype (Salazar-Ciudad et al., 2001, Salazar-Ciudad and Jernvall, 2004). This way of constructing the phenotype may not be exclusive of biological systems. Many complex ideas can

arise through the interaction between several ideas. However, these ideas may be difficult to communicate directly (so then mutations in them are not necessarily closed) and need to be learned by the combination or interaction between other ideas (thus leading to a complex relationship between mutations and their phenotypic effects).

The invention of secondary mechanisms of inheritance:

Evolution by selection of genetic mutations can be described, as mentioned, as a learning process. Learning by trial-and-error is, however, not the more efficient way of learning one could image. Most known living beings can change their development and physiology in response to changes in the environment. This way not only one, but several phenotypes can be exhibited by an individual. This is equivalent to organisms having a memory of some past adaptive phenotypes in a lineage and the capacity to decide, based on environmental clues, which one is more likely to be adaptive in their near future.

A different situation applies if individuals in a lineage or in a population can learn and communicate. In learning the repertory of behavioral changes elicited by environmental changes is itself determined by previous influences from the environment in a generative system (in contrast to plasticity due to internally fixed responses to environmental changes). With communication some information acquired by learning in a generative system can lead to information in its offspring generative systems. Thus, the repertory of responses (as phenotypes or behavioural phenotypes) exhibited in a lineage can change due to genetic mutations but also due to communication with other generative systems. In that way, learning plus communication is a mechanism of inheritance; some times called *cultural inheritance* (Jablonka and Lamb, 2005). Learning plus communication in living beings is a way to have more (closed and open) mutations. Many of them may not be possible or likely from changes in the genotype and in general different inheritance mechanisms may allow

different kinds of changes. Learning itself allows some mutations (notice that notice this does not mean genetic mutations) to happen while communication allows some of these mutations (those that can be learned) to be closed (and at the same time allows the generation of offspring idea generative systems).

A hypothesis (*secondary inheritance mechanisms* hypothesis) of this article is that secondary systems of inheritance are expected in generative systems with copying that have evolved to have complex phenotypes. This is because, as mentioned, during the evolution of complex generative systems closed mutations happens at the level of the copied elements (or at the level of the more closely mutable parts of the phenotype) and then complex phenotypes have to be generated by interactions between these elements. As mentioned, in living organisms complex phenotypes the relationship between genotype and phenotype is complex. The arising of secondary inheritance mechanisms allows more closed mutations (by copying or not) and possibly more complex (or simply other) aspects of the phenotype to be affected by these mutations. This way the arising of secondary inheritance mechanisms could be an event that would make more likely the evolution of complex phenotypes.

Learning plus communication often permits this secondary inheritance (although others exist; see Jablonka and Lamb, 2005). There are many differences and similarities between this system of inheritance and the copying of the genome (Jablonka and Lamb, 2005). The discussion of all of them is outside the scope of this article but some of them are important for the concepts presented in this article. Memes (Dawkins, 1976) are defined as ideas, or cultural elements of inheritance that tend to promote its own copy. This is based on a strong analogy with genes but ideas that are not copied could still evolve (as suggested). Idea generative systems without copying are not necessarily less able to produce adaptive variation. Indeed, humans living in variable and complex environments may have benefited, in some situations, from the fact that received ideas tend to be affected by (or interpreted in the light of) previous ideas. Thus, for example, young

generations may tend to interpret the ideas received from older generations in the light of the current context in which they live (and other existing ideas at the time). On the other hand parents can try to affect the development of specific kinds of ideas in their offspring according to how they think the future is going to be. In that situation the evolutionary guess is more variable than in the case of copying (that selection will be similar in the future). From these perspectives generative systems without copying may provide, in some environments, larger chances of producing adaptive variation in evolution than idea generative systems with copying.

It is not necessarily the case that all ideas can be communicated. It is possible, however, that human languages allow, potentially, for the expression of an infinite number of ideas. This is not necessarily informative about how many ideas a human can mutate. However, it has been estimated that humans have on average 175 mutant nucleotides (Nachman and Crowell, 2000) but less than 3% of the genome codes for genes or regulatory regions. Thus, each human may have on average less than 5 mutations affecting genes or its regulation (not considering synonymous changes). It is likely that an average human receives more than 5 changes in its ideas over his life (in fact, all or most ideas are learned) and thus it seems reasonable to assume that ideas can change, in a generation, faster and in more complex ways than genes.

Another important difference is that learning plus communication allows playing. By playing and individual can explore the environment in a protected context (by protection from the parents directly, or indirectly by a nest or another modification of the local environment) in which the negative effect of mis-adaptive behaviors is minimized. In that situation the offspring has more chances of learning to respond to specific environmental changes. This can substantially reduce the cost of selection. Depending on the environment and the amount of offspring, that may require a lot of time and energy from the parents (compared with the situation in which selective pressures are faced directly by the offspring in early life).

In other aspects genetic and cultural inheritance can be similar. Communication also exists at the level of DNA. Indeed communication at this level can be quite frequent and not restricted to members in a lineage. Thus many bacteria and protista can interchange genetic material. This process is called sex although does not necessarily lead, by itself, to offspring. Many bacteria and some protists can express specific structures to be able to interchange DNA (Madigan and Martinko, 2005). Many can simply acquire DNA molecules from the environment. Errors in the packing of virus DNA can also lead to the transfer of DNA between non-viric hosts. These genetic transfers are possible, although rare, between organisms of unrelated species. This process is also possible because all living beings use DNA for copying and a similar genetic code (there is some small variation in the genetic code between prokaryotes and eukaryotes and within eukaryotes (Fox, 1987)). In the same way communication in animals (especially in humans) is not necessarily restricted to individuals in the same lineage (or close in it).

Conflicts between inheritance mechanisms:

Some researchers have suggested that cultural inheritance allows, at least in humans, adapting to a wider range of environments than genetic inheritance (Jablonka and Lamb, 2005). This would be consistent, as proposed in here, with cultural inheritance allowing more and more complex kinds of mutations (as suggested). This greater adaptability of cultural inheritance may produce that adaptation to selective pressures occurs more likely by changes in ideas than changes in the genotype. As a result evolution at the genetic level could de-accelerate due to cultural evolution. This hypothesis is similar to a secondary inheritance mechanisms drive hypothesis. This time is the second genetic inheritance mechanism that tends to control the evolution of other parts of the phenotype.

More in general it can be expected (without taking into consideration specific aspects of a system functioning), that when two or more inheritance mechanisms co-exist in a given generative system the one that can produce more (or more diverse) closed mutations in a wider range of environments is likely to produce more adaptive variation and drive the evolution of the generative system (although, specifically, that would depend on which mutations each inheritance mechanism can exhibit). This is because the driving inheritance mechanism would make many mutations in other inheritance mechanisms maladaptive (for example genetic mutations increasing aggressiveness may be adaptive in isolated individuals but not in individuals that may benefit from acquiring ideas from other individuals) or obsolete (for example mutations increasing hairiness may be neutral if cloths have been invented).

Although cultural inheritance may, currently, drive human evolution this still depends on the specific environments encountered. As stated by the non-free-lunch theorem there is no single strategy that is the most adaptive in all environments (Wolpert and Macready, 1997). Learning and communication are not always necessarily better than random genetic mutation in finding adaptations to selective pressures. If the only possible adaptations in an environment are too complex to be learned by a given generative system (meaning that it escapes by far the understanding capacities of existing learning generative systems) random genetic mutation may be as good or even better (since they may require less energy and can thus have larger numbers of offspring).

A similar “survival of the dumbest” situation applies if changes occur so fast that there is not time to develop (through learning and communication) a suitable adaptation or if there is no available environmental clues to solve this solution (intelligent guessing relies on the existence of some amount of information in the environment that can be interpreted). In that situation it can be expected that the capacity of learning and/or communication would decrease in evolution because it is costly in time and energy. In fact, there are multiple cases in which intelligence has decreased

during evolution (for example in some salamanders (Roth and Wake, 2001)). It is interesting to note that, in spite of the amount of intelligent researchers devoted to it, pest control is a complicated subject and pests often (by simple mutation) manage to develop resistance to pesticides rather fast. In addition, learning plus communication requires, to be efficient evolutionarily, that the environment itself has some degree of complexity (on a generative systems "eyes"). For example it is dubious that humans will adaptively outperform bacteria if the world would be a simple homogeneous glucose culture.

In general it can be expected (*multiple inheritance hypothesis*) that in complex generative systems multiple inheritance mechanisms co-exist. As mentioned, once an inheritance mechanism exists further evolution in complexity may arise by interactions between aspects of the phenotype that can exhibit closed mutations. Although different mechanisms of development lead to qualitatively different relationships between the genotype and the phenotype (or between closed mutations and its phenotypic effects) it is very unlikely that all aspects of complex phenotypes can be inherited directly. Thus, further increases in phenotypic complexity would lead to very complex relationships between genotype and phenotype or, more in general, between mutations and their phenotypic effects (Salazar-Ciudad and Jernvall, 2004, 2005). At that stage the arising of additional inheritance mechanisms would be quite adaptive, as explained and as suggested, on different grounds, by other authors (Jablonka, 1994). This is more likely than the transformation (or disappearance) of already existing inheritance mechanisms to be able to make more complex aspects of the phenotype to be copyable or closely mutable. This is because many developmental interactions can be based on early inheritance mechanisms and then variation in them is likely to disrupt most of the resulting phenotype. For example a change in the genetic code (and the t-RNAs and associated aminoacid metabolism) leading to codons with four bases (and then, potentially, to many more kinds of aminoacids) is likely to be more disruptive in current living beings (specially in

the more complex ones in which many more developmental interactions are based on previous ones in developmental time) that the addition of new inheritance mechanisms.

New inheritance mechanisms, like the cultural one, are less likely to interfere with the already existing development and are thus more likely to be adaptive. This way complex phenotypes would often arise by the progressive acquisition of inheritance mechanisms dealing with more and more complex aspects of the phenotype. For a while, once a new inheritance mechanism is attained, further complexity may be based on interactions between elements from the new inheritance mechanism that can have closed mutations. But eventually this system may also lead, as in the case of genetic inheritance, to entrenchment and to a complex relationship between mutations and their phenotypic effects. Thus further evolutionary increase in complexity (when it occurs) may require additional inheritance mechanisms. Other researchers have suggested that the acquisition of new inheritance mechanisms may constitute the most important transitions in evolution (Jablonka and Lamb, 2005). It is also likely that the acquisition of new inheritance mechanisms often leads to the origin of new kinds of nested generative systems (like it is the case for ideas).

Conflicts between generative systems:

In humans, and in some other animals, genes and ideas are both the main aspects of the phenotype that can have closed mutations. At the same time they are both parasite nested generative systems of a host generative system (the organism). So, as mentioned, in nested generative systems the parasites are part of the host generative system and also generative systems themselves. This situation of interdependence between hosts and parasites can lead to a complex set of cooperation and conflict between parasites and their hosts. There is some research on the evolution of genetic conflicts (Maynard Smith and Szathmary, 1995) and about the diversity of dynamics of co-evolution existing between parasites and their hosts (Gilchrist and Sasaki, 2002;

Gandon et al., 2002). There are also some studies of these conflicts for the case of memes (Dawkins, 2006) and cultural and genetic evolution (Cavalli-Sforza and Feldman, 1973a, 1973b).

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