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Evolution of Natural Agents: Preservation, Advance, and Emergence of Functional Information

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Abstract Biological evolution is often viewed narrowly as a change of morphology or allele frequency in a sequence of generations. Here I pursue an alternative informational concept of evolution, as preservation, advance, and emergence of functional information in natural agents. Functional information is a network of signs (e.g., memory, transient messengers, and external signs) that are used by agents to preserve and regulate their functions. Functional information is *preserved* in evolution via complex interplay of copying and construction processes: the digital components are copied, whereas interpreting subagents together with scaffolds, tools, and resources, are constructed. Some of these processes are simple and invariant, whereas others are complex and contextual. *Advance* of functional information includes improvement and modification of already existing functions. Although the genome information may change passively and randomly, the interpretation is active and guided by the logic of agent behavior and embryonic development. *Emergence* of new functions is based on the reinterpretation of already existing information, when old tools, resources, and control algorithms are adopted for novel functions. Evolution of functional information progressed from protosemiosis, where signs correspond directly to actions, to eusemiosis, where agents associate signs with objects. Language is the most advanced form of eusemiosis, where the knowledge of objects and models is communicated between agents.

Keywords Extended evolutionary synthesis · Epigenetic inheritance · Inclusive heritability · Selective reproduction · Plasticity · Levels of semiosis

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Introduction: Informational Nature of Biological Evolution

The notion of biological evolution as a gradual change of the morphology and functions of organisms in sequential generations emerged about two centuries ago. This morphology-based approach was challenged by the discovery of the DNA code, which prompted the synthesis of evolutionary theories with processes that occur in cells at the molecular level. However, most biologists have not realized that the discovery of molecular-based heredity requires a new understanding of the nature of life. It appears that *life has informational nature*, and therefore, evolutionary theory should be focused on both information and morphology. If information change is an important component of evolution, then we have to answer some basic questions about the nature of information and its relation to matter and life. What is the meaning of information? How did meaningful information emerge at the origin of life and how was it preserved and improved by living organisms? In biology, information is viewed as a useful metaphor rather than reality, and most biologists are busy studying molecular interactions and DNA sequence, which seem more real than the meaning of information. Similarly, cybernetics studies the quantity of information but usually avoids discussions on its meaning.[1]

There are philosophical reasons why the meaning of information is neglected in biology. Information can be seen as "knowledge" that is used by organisms to perform their functions and follow their goals. Thus, the meaning of information cannot be separated from intentionality of organisms who use it. The success of science is heavily based on the Newton's way of separating the physical world from human intentions. In physics, intentionality is represented by constraints or boundary conditions that are set before the experiment, and then the dynamics of any system appears passive. Following this approach, most biologists try to avoid the notion of intentionality and describe organisms as fully automatic or even passive systems. The Modern Synthesis (MS) in the theory of evolution (also known as neo-Darwinism) considers organisms as passive tokens selected by nature and then passively copied for the next generation (Dawkins 1986). The activity of organisms is viewed as illusion that after detailed study can be reduced to non-equilibrium dynamics of randomly moving and interacting particles. If any activity of organisms is admitted, then it is treated as externally programmed, which makes organisms equivalent to robots. However, this interpretation of organisms contradicts the very existence of humans who are active and intentional (Emmeche and Hoffmeyer 1991). The MS cannot explain the origin and evolution of *Homo sapiens*, human society and knowledge because it rejects the existence of simpler versions of knowledge in the ancestors of the human species.

In spite of the wide acceptance of the MS, teleological thinking has not disappeared from biology and is often applied to animal behavior, physiology, and molecular biology. Organisms and individual cells are not passive but chose their actions and developmental pathways based on all available information that comes from the environment, internal sensors, memorized experience, and genome. These choices have downstream effects on the function of their progeny via heredity (both genetic and epigenetic) and selective reproduction of organisms with more successful phenotypes and behaviors. Thus, programs do not make organisms passive; instead they facilitate

[1] For semantic theories of information in cybernetics see (Carnap and Bar-Hillel 1952; D'Alfonso 2011).

goal-directed activities by making them more productive. Many biologists work on the revision of the theory of evolution by removing unnecessary dogmas (e.g., no heritability for acquired or behavioral traits, purely random phenotypic variability, passive selection) and recognizing the active role of organisms. This version of the theory, which is known as Extended Evolutionary Synthesis (EES), explores the role of development, behavior, epigenetic heritability, niche construction, and hidden morphogenetic capacities on the directions and rates of evolution (Pigliucci and Müller 2010).

Here I use the methodology of EES to develop an informational approach to biological evolution, which is based on the analysis of *preservation, advance, and emergence of functional information in natural agents* at various levels including individuals, cells, sub-cellular complexes, populations, and symbiotic consortia. Based on this functional semiotic approach, organisms use signs to preserve and organize their functions as well as to disseminate them vertically (i.e., from parents to offspring) and horizontally (i.e., between peers). Organisms are active in interpreting functional information and making choices in their development and behavior. Principles of human semiotics are not fully relevant to the study of biological evolution because functional information often includes primitive signs that do not have many properties of human signs (Sharov and Vehkavaara 2015). Thus, I distinguish two phases in the evolution of signs: protosemiosis, where signs correspond directly to actions; and eusemiosis, where agents associate signs with objects. Language represents an advanced form of eusemiosis, where knowledge of objects and models is transferred horizontally between agents. I hope that this approach will help to transcend the bounds of molecular biology, embryology, evolutionary theory, behavioral sciences, zoosemiotics, and traditional human semiotics and arrive to new levels of synthesis in biosemiotics.

What is Functional Information?

The functional approach to the meaning of information can be traced back to Jakob von Uexküll who wrote: "Everything that falls under the spell of an Umwelt is altered and reshaped until it has become a useful meaning-carrier; otherwise it is totally neglected" (Uexküll 1982: 31). This approach is closely linked with the philosophy of pragmatism, which equates "practical" and "meaningful" (James 1907). I define "functional information" as *a network of signs that are used by agents to preserve and regulate their functions*. Adjective "functional" emphasizes the link with agents and helps to distinguish it from quantitative approaches to information developed by Shannon (1948) and Kolmogorov (1965). Functional information is meaningful for agents because signs stand for specific functions, methods, and tools that are necessary for successful survival and reproduction. Using the terminology of John Locke (1853), functional information does not belong to physics (or *Phusike*, i.e., knowledge of things, as they are on their own), but fits into practice (*Praktike*, i.e., knowledge of things as they are used), and semiotics (*Semeiotike*, i.e., knowledge about knowledge itself as it is attained and communicated) if applied to agents in general. The definition of functional information is modified here from the earlier version (Sharov 2010) as follows. First, instead of *set of signs* I now refer to the *network of signs* to emphasize the connections between signs, both physical (e.g., interaction of signaling molecules in

cells, proximity of DNA sequences, order of word uttering) and semantic (e.g., relations to objects, connotations). And second, the purpose of functional information is changed from *encoding* to *preserving and regulating* of functions (which includes encoding). The term "encoding" appears too narrow because it refers mostly to highly-autonomous construction processes (e.g., protein synthesis) and does not fit well to context-dependent signification or regulation. The pragmatic value of functional information (i.e., functional closure via survival and reproduction) echoes the theory of autopoiesis (Maturana and Varela 1980), however in contrast to this theory, I emphasize the *semiotic aspect of information*. In particular, functional information is a network of signs that interconnects (via syntax, semantics, and pragmatics) otherwise unrelated functional units.

Signs are meaningful only in relation to certain *agents*; where agents are systems with spontaneous activity that select actions to pursue their goals (Sharov 2010). Signs that are meaningful for one kind of agents (e.g., species of animals) may appear meaningless for other agents. Agents include all living organisms as well as artificial devices that are constructed (or recruited) and programmed for performing certain functions (e.g., ribosomes in living cells or computers and robots in human technology).[2] Although all agents carry some externally-supplied programs (e.g., the genome is supplied by parental organisms), the majority of agents, including all living organisms, also have self-generated programs (e.g., epigenetic signs or conditioned reflexes). Goals are considered here in a broad sense, including both achievable events (e.g., capturing a resource, or producing offspring), as well as habits and values (e.g., survival, energy balance). Some goals emerge within the agent, whereas others are set by parental agents or higher-level agents. Although all signs require material carriers (vehicles) they are not material objects because carriers perish but signs persist as long as agents keep their capacity to perceive and interpret them in a meaningful way. In particular, functional information often includes *external signs* (i.e., carried by external objects), which are in fact not fully external because they have to be interpreted internally by agents in order to be counted as signs. In particular, animals have complex sense organs and neural networks designed for image analysis and object recognition, which together process external signs and build internal representations of environment known as Umwelt (Uexküll 1982).

It seems unlikely that functional information can be studied by physics because physics may be applicable to material sign carriers but not to signs. Some physicists believe that quantum mechanics is better equipped for explaining signification since it includes the notion of measurement (Penrose 1989; Bordonaro and Ogryzko 2013). However, measurements in quantum mechanics simply rescale the probabilities of quantum events and have no relationship to agents, goals, or adaptive evolution. Of course, there is always a possibility to use quantum-mechanical terms as metaphors for describing life, although the advantages of quantum terminology are not clear.

Functional information has to be studied in the evolutionary context because each function is a product of evolution (Sharov 2010; 1992). In particular, we need to study the origin of agents and their functions; an approach that is generally ignored in cybernetics. Interestingly, *agents are always constructed by other agents of comparable*

[2] For definition and classification of agents in the context of Artificial Intelligence, see (Franklin and Graesser 1996).

or higher functional complexity. The reason why the probability for agents to get self-assembled by chance is extremely low is that agents carry substantial functional complexity. It takes long times for agents to develop each new function via trials and errors; therefore, simultaneous and fast emergence of multiple functions is very unlikely. In other words, functional complexity cannot increase fast but can be lost rapidly (e.g., in cases of narrow specialization). Thus, the statement that all agents are products of parental agents with a higher or comparable functional complexity can be viewed as informational equivalent of the *principle of gradualism* (Sharov 2009b). This principle, however, does not exclude variations in the rates of morphological evolution over time as it is assumed in the hypothesis of punctuated equilibrium (Gould and Eldredge 1977), or sudden changes of morphology due to macro-mutations (Goldschmidt 1940). Indeed, organism morphologies may remain stable in the absence of external perturbations but molecular (invisible) evolution is likely to go on even during periods of apparent stasis. The novelty of macro-mutations should not be overestimated; observed sudden changes of morphology represent the release of already existing developmental capacities of organisms, and not associated with a substantial increase of complexity. In some cases, evolution resulted in the integration of simple agents into more complex super-agents (e.g., emergence of multicellularity or symbiogenesis). However, even these cases are consistent with the principle of gradualism because (a) redundant components and functions do not increase the overall complexity, and thus a colony of identical or similar cells is only slightly more complex than a single cell; and (b) in simbiogenesis, we have to account for combined complexity of both parental organisms. The origin of life also does not contradict the principle of gradualism because primordial agents were extremely simple. According to the "coenzyme world" hypothesis, life may have started with a single function and then continually accumulated additional functions (Sharov 2009a).

If signs are not material, then how do we recognize that a certain object is a carrier of a sign? There is no universal "sign detector" machine that can help us, although we can easily detect already known signs. We have to study how objects are handled by living organisms, cells, and molecular subagents, and how living functions change as a result. If the change is forced deterministically by an object, then it is not a sign carrier.[3] However, if the object triggers a signaling pathway that tends to be beneficial for an agent, then it is likely to be a sign carrier. Additional evidence of sign function comes from evolutionary studies: it is necessary to show that the capacity to detect and interpret a sign has evolved in the lineage of ancestral agents. Sign carriers can be isolated objects (e.g., Ca^{++} ion) or parts and variations of large objects (e.g., phosphorylated aminoacid in a signaling protein), but usually we do not distinguish these cases for simplicity. Saying that some object is a sign carrier means that it contains at least one part that plays the role of a sign. Examples of signs carriers in living cells include nucleic acids (DNA and RNA), transcription factors, histones with various modifications, hormones, secondary messengers, and chromatin remodeling complexes. But molecular tools and resources are not signs per se if they are sufficiently abundant and do not regulate cellular functions on their own. If some

[3] Here my understanding of signs differs from Peirce: if an object releases a mark, then this mark is not a sign yet. It belongs to "hidden correlations" in the outside world unless it is detected and utilized by some agents as a sign.

cellular function is slowed down or halted due to the lack of resources in experimental conditions, this effect is forced and purely physical. However, tools and resources may serve as signs if they have been designed by evolution to regulate cell functions in a meaningful way. For example, the UCP2 protein converts the pyruvate (a resource for the Krebs cycle) into lactate, and in this way effectively switches cell metabolism from oxidative phosphorylation to glycolysis, which is important for stability of pluripotent stem cells (Shyh-Chang et al. 2011).

Functional information is inseparable from the structure and function of evolving agents. Although programmed agents are often viewed as non-semiotic systems (Barbieri 2008), this view is not consistent with the fact that execution of programs is a part of semiotic activity of all agents, and agency is not possible without it. We (humans) are programmed genetically by ancestors, behaviorally by the family, and culturally by the society, but this does not make us robots (Sharov 2013). Moreover, programs should not be viewed as purely external because they are products of the human species and human ancestors; they did not come from aliens or gods. These programs define our identity, help us to survive, reproduce, work, enjoy life, and disseminate our knowledge. There is also a feedback from organism activity to the functional information passed through generations: organisms with better phenotypes and behaviors preferentially pass their genes to the progeny via selective reproduction, and acquired programs can be transferred via epigenetic inheritance and parental effects, as assumed in the EES.

Preservations of Functional Information

Preservation may seem too static to be considered as an aspect of evolution. However, preservation of functional information is an *active task* because functions have to be maintained despite of various external and internal changes, including transient short-term disturbances and long-term irreversible shifts. In fact, *evolution would not be possible without reliable preservation of functional information*. Any function of an agent requires specific organs or subagents to perform it, as well as resources, energy, and control pathways that coordinate actions with the environment and other functions. To preserve a function, agents have to perform other functions that include making and repairing organs, producing resources and energy, and controlling actions through signaling pathways. Agents are *functionally closed*, which means that every function (including construction of subagents, resources, tools, and copying of encoded programs) is performed by internal subagents that are supplied with necessary tools, scaffolds, resources, and control programs (Rosen 1970). If some resources are not provided internally, then agents need a capacity to capture or recruit them outside. All these functions are preserved in the lineages of living organisms (i.e., inherited) because they are encoded and controlled via heritable information that is transmitted across generations.

Explaining the phenomenon of heredity is one of the greatest challenges in biological sciences. According to the widely accepted MS theory, genes fully determine the phenotype of organisms, and therefore, heredity is explained solely by faithful DNA copying and separation of identical sister chromatids between daughter cells. The only admitted complication in this process is generation of gametes (oocytes and sperm) via

meiosis followed by fertilization that combines haploid fractions of parental genomes. However, this model of heredity is oversimplified in many respects. First, the phenotype is not constructed in its final form (as in 3D printers) but emerges via embryogenesis, which is a self-organizing process regulated by numerous internal and external signals and feedbacks (Lickliter 2014; Sharov 2014). In particular, phenotypes exhibit phenotypic plasticity by which organisms adjust their morphology and functions to the environment. Thus, the major opposition to the MS came from embryology resulting in "evo-devo" theory, which stands for a synthesis of evolutionary and developmental biology (Brakefield 2011). Second, the MS does not account for non-genetic factors of heredity that include epigenetics and parental effects (Danchin et al. 2011). And third, the dominant role of environment in evolution (assumed by MS) should be reconsidered because organisms often modify their environment, which is known as niche construction (Laubichler and Renn 2015).

The recent update to the model of heredity was the introduction of the notion "inclusive heritability" (Jablonka and Lamb 2005), which is an important component of the EES (Laland et al. 2015). In this model, total phenotypic variation is partitioned into transmitted (i.e., heritable) and non-transmitted components. Transmitted variation includes both genetic and non-genetic components, and non-genetic heritable variation is based on parental and non-parental effects (Danchin et al. 2011). Non-parental heredity includes information that comes from the environment and from other organisms (e.g., horizontal gene transfer in bacteria or social interactions in higher animals). Then, inclusive heritability equals the proportion of phenotypic variation that is transmitted by all these channels. It has been also suggested that non-parental components of transmitted variation should not be combined with parental effects which represent the continuity of information flow from parents to the offspring (Prasad et al. 2015). However, it seems more logical to keep the non-parental transmitted variance as a part of inclusive heritability because parents experience almost the same effects from the environment as their progeny, and both are capable of interpreting these external signs. In other words, an evolutionary lineage is a sequence of contextually-placed and responsive organisms rather than abstract "organisms in vacuum".

Living beings include multiple levels of subagents such as organs, cells, organelles, and functional molecular complexes. All these subagents have some phenotype (i.e., structure, function, and relation to lower- and higher-level agents) which is dynamic and depends on the interplay of deterministic, stochastic, and sign-dependent changes. The latter kind of change is different because it is based on activating or modifying *pre-existing internal capacities* of agents, which has been designed in the process of adaptive evolution. For example, a ribosome may start synthesizing a specific protein when supplied with a program in the form of mRNA molecule. A ribosome is an example of externally programmed agent because most of its functional information comes from outside, whereas internal information is limited to the ability of recognizing the mRNA and aminoacyl-tRNA. Mitochondria and plastids are programmed both internally by their own genome and externally by the genome and epigenetic signs of the host cell. Many mitochondrial proteins are encoded in the nucleus, and then synthesized by ribosomes of the host cell. Interestingly, the majority of these externally encoded mitochondrial proteins are synthesized near the surface of the outer mitochondrial membrane. Mitochondrial localization is driven mostly by mRNA-binding proteins that have affinity to bind the outer membrane as well as nascent polypeptide

synthesized on the ribosome (Fox 2012). These proteins are then translocated into various compartments of mitochondria: membranes, inter-membrane space, and matrix. Cells and organisms are examples of internally programmed agents because they carry the bulk of their functional information in their genome and epigenome.

One of the most fundamental capacities of living organisms is self-reproduction. However, the notion of "self-reproduction" may be confusing if interpreted literally, because (a) offspring organisms are never identical to their parents even in the case of cloning, and (b) reproduction is seldom done by a parent alone without any external help. Self-reproduction is assumed to be successful if all essential functions are transferred from parents to offspring without loss of efficiency (see details below). Also, most organisms reproduce by taking advantage of interaction with other organisms used as food, habitat, or subordinate agents. For example, viruses are agents that reproduce only in specific host cells via reprogramming their ribosomes and other molecular subagents, but in this process viruses preserve their identity as agents (Villarreal and Witzany 2010). Individual genes are also agents capable of self-reproduction, and their evolutionary history is partially independent from the phylogeny of whole organisms. However, genes are not just passively-copied "replicators" as viewed by Dawkins (1978); they also include RNA and proteins produced from the corresponding DNA sequence and all functions performed by RNA and/or protein in various cellular compartments. As the life cycle of an insect includes an egg, larva, pupa, and adult; the life cycle of a gene includes a DNA phase, mRNA or non-coding RNA (ncRNA) phase, and protein phase. Protein (or ncRNA) is the active phase, which is comparable to a larva or adult insect, and the DNA is mostly a passive phase comparable to an egg. Genes within the same cell can be compared to workers within a factory each specialized in certain operations. Collectively they complete the task of copying all DNA-encoded genes together with selected functional proteins and RNA and placing them into a newly constructed cell. Each gene somehow facilitates this process, because otherwise it would tend to degrade via neutral evolution. Despite of the collective nature of gene reproduction, it is still possible to track the evolutionary lineages of genes because the major portion of functional information of a newly constructed gene (i.e., DNA sequence) comes from its parental gene.

Preservation of parental functions in the offspring requires transfer of a seed of the parental functional information (or inheritome[4]) to the newly built organism or cell: (1) a copy of the genome, (2) essential epigenetic signs (e.g., histone modifications, DNA methylation, primers of structural elements such as membranes and centrioles), and (3) a minimal set of subagents capable of interpreting inherited information and constructing/modifying other components (e.g., DNA- and RNA-polymerase protein complexes and ribosomes). The genome is duplicated via direct copying whereas epigenetic signs are replenished via combination of template-based protein construction, autocatalysis, and cross-catalysis. For example, new histone molecules (i.e., vehicles of epigenetic signs) are first synthesized by ribosomes and then become decorated with various chemical marks by chromatin-remodeling protein complexes. This process can also be called "indirect copying" (not to be confused with direct

[4] The term *inheritome* (i.e., heritable information passed from parents to offspring) was suggested by Prasad et al. (2015).

copying of nucleic acids[5]) because chromatin-remodeling complexes include sensors that bind to specific parental histone marks and effectors that apply the same kind of marks to new histones included into the chromatin (i.e., DNA wrapped around histone tetramers) just after replication of DNA.

Based on acquired functional information, a new organism starts building itself from the initial zygotic phenotype and sequentially constructs components that are necessary for the execution of each function: tools, resources, scaffolds, subagents, and signaling networks. This process is highly flexible and context-dependent. Each cell in the embryo attempts to communicate with neighboring cells by secreting cytokines, hormones, and growth factors, as well as by establishing physical contacts. Eventually, the direction of cell differentiation emerges as a *consensus* among communicating cells, and those cells that do not match the consensus either crawl away or die.

Prescriptive (i.e., top-down) control of functions is most efficient at the lowest hierarchical levels of living systems (e.g., in protein synthesis), but becomes entirely futile at higher levels because of the exponential increase of the number of downstream subagents. As a result, prescriptions cannot be effectively generated, and subsequent actions cannot be fully coordinated. As analogy, consider the task of washing dishes. One way of doing it is to specify exact movements for each finger and each muscle in a time-dependent manner, or even send nerve impulses to individual muscle cells. Another option is to tell your son "wash the dishes" and he will do it in his own way. Similarly, some portions of the genome encode non-algorithmic commands like "grow an eye" without specifying the details of how it should be done. Embryonic development may even include elements of learning at the cellular level where successful habits become encoded epigenetically and then reproduced on demand (Ginsburg and Jablonka 2009; Sharov 2013). In addition, populations of cells are subject to intra-organism selective reproduction such as in the immune system and neural system (Edelman 1987). Because of abundant non-algorithmic components of embryo development, it would be a mistake to view the genome as a *blueprint* of the adult phenotype. A much better metaphor of a genome is a *switchboard* that coordinates the action of various construction processes within growing organism (Sharov 2014).

Genomic information is often called "digital", and DNA copying is portrayed by the MS as a passive and deterministic process. However, being digital is not a property of the DNA molecule, but rather a property of active molecular agents that support replication. The process of DNA replication is not deterministic in a physical sense (i.e., it is not a physical law); instead it simply has evolved to be fast and almost errorless. The replication machinery is highly selective allowing only 4 specific nucleic bases to be assembled into the newly synthesized DNA strand, and only one kind of base is allowed to match with the nucleotide on the opposite reverse-complementary strand of the DNA. If a wrong base is accidentally attached, then the DNA polymerase stops and corrects the error. The complementary pairing of nucleotides happens only within the context of DNA (or RNA) molecule, where nucleic bases keep exact orientation via rigid 3′ and 5′ links to cyclic sugars. This orientation is one out of many

[5] DNA replication is a *direct copying* because new nucleotides come into direct contact with matching parental nucleotides. In contrast, new histone modifications are added without direct contact with parental histone marks.

options, which apparently was selected in evolution for the purpose of supporting replication. Thus, DNA copying is a kind of simple interpretation in the sense that it is not entailed by physical laws.

Besides copying, information can be transferred via *coding*, where output signs are generated from a different kind of input signs.[6] The most common example of a code is the genetic code, where triplets of nucleotides in the messenger RNA (mRNA) are used to guide the synthesis of proteins on ribosomes. Barbieri (2003, 2007) developed a theory of "organic codes", which explains the physiology and self-reproduction of cells by the combination of DNA copying and various kinds of coding (e.g., genetic code, signal transduction code, and splicing code). These processes are performed by "copymakers" and "codemakers", respectively. However, coding should not be viewed as deterministic mapping between inputs and outputs. Although protein synthesis may appear deterministic, it can be altered in experimental conditions by supplying modified aminoacyl-tRNA complexes. It is also conceivable that the genetic code was more flexible in primordial organisms, when the chemical structure of pre-nucleotides, pre-aminoacids, and pre-ribosomes was selected for better efficiency of polypeptide synthesis and for additional properties such as protein folding and transport.

Barbieri proposed that *coding* is qualitatively different from *interpretation*, which is not deterministic and occurs in the neural system of animals (Barbieri 2009). Although there is no doubt that protein synthesis and neural processes are qualitatively different in their complexity and flexibility (see "Qualitative Steps in the Evolution of Functional Information" section), the separation of coding from interpretation appears confusing. Coding is not entailed by physical laws and is based on "natural convention" (Barbieri 2008); thus, it seems logical to consider coding as a lower-level interpretation that emerged at the early stages of biological evolution and later became complemented by more advanced levels of interpretation including epigenetic regulation and neural processes. In contrast to the mostly automated low-level interpretation of signs, higher levels of interpretation are substantially more flexible and require extensive additional information, which is either stored internally or acquired from the environment to regulate living processes. In summary, although encoded information is digital, its meaning is not fully fixed. It can be regulated in relation to context or environment and become modified in evolution. This indeterminacy does not mean that the metaphor of encoding is irrelevant, as suggested by Bickhard (2005). We just need to reject the idea of genetic determinism and realize that any kind of natural coding is *soft* and provides at least some variability that can be utilized for functional polymorphism and evolutionary change.[7]

[6] The difference between copying and coding is not qualitatively sharp because the input and output are different even during DNA copying, where nucleotides A, C, G, and T are paired with *different* nucleotides T, G, C, and A, respectively. However, copying is reversible and recursive, whereas coding is irreversible, as in protein synthesis.

[7] Here I do not consider human codes that can be fixed by design (e.g., Morse code). However, even human codes that are fixed within our life time may change over millennia together with other cultural features.

Advance of Functional Information

The advance of functional information includes improvement and modification of already existing functions via selection and/or internal trends of variation. Improvement of functions via natural selection is the most well studied component of evolution. However, the theory of natural selection requires modernization because it has been historically linked with the philosophy of neo-Darwinism that emphasized the passive nature of organisms, genetic determinism, and randomness of variation. Darwin presented natural selection as a process similar to artificial selection, where humans intentionally chose organisms for breeding. This comparison may have been useful in the early days of Darwin's theory, however now it brings more confusion than help. Nature is not an agent and cannot select anything; it has no intentionality in contrast to humans who breed animals and plants. Thus, it's time to replace the term "natural selection" with "selective reproduction", which can be equally applied to the evolution in nature and in human-managed ecosystems and can include both genetic and epigenetic changes. Selective reproduction may improve functions and traits of organisms in a sequence of generations only if these functions and traits are heritable. Heritability is a tendency of related organisms to be more similar in phenotypes than unrelated ones. Then, the descendents of survived and reproduced parents tend to have heritable phenotypes that support better survival and reproduction. In particular, functions of organisms can be improved in terms of their reliability, speed, and energy-efficiency.

Although nucleotide substitutions in the DNA are mostly random, the phenotypic consequences of mutations are not random. Instead, phenotypic traits exhibit correlations that are based on the logic of cell differentiation and embryonic development (Waddington 1968). This internal logic often determines potential phenotypic outcomes, and thus may affect the directions of evolutionary change. For example, the variation of leaves in plants can be presented as a combination of several nested elementary patterns (Meyen 1987). Leaf shapes probably have a limited contribution to the survival and reproduction of plants; thus, internal developmental constraints appear more important in their evolution than fitness. Another example of developmental logic is homological series of variation (Vavilov 1935). It appears that different taxonomic groups of plants exhibit similar series of variation; and phenotypes in one lineage can be predicted from observed phenotypes in another lineage.

Emergence in Evolution

Emergence of new functions and traits represents the unpredictable aspect of evolution; however this does not mean that emergence cannot be studied by science. For example, it is possible to analyze conditions that facilitate or inhibit the emergence of new functions. Also, it is exciting to reconstruct evolutionary pathways that may have resulted in the emergence of major novel functions. Obviously, complex new functions cannot emerge from nothing; they are always based on modification of already existing functions, a process known as preadaptation or exaptation (Gould and Vrba 1982). Organs, resources, and control mechanisms should be almost ready for a new function; what is needed is to invent a new way of using them. Thus, emergence of novel

function is not associated initially with a profound change of functional information. Instead, small modifications/additions are needed to *change the interpretation* of a large amount of already existing functional information.[8] For example, mammals originated from terrestrial reptiles, but several lineages of mammals independently switched to aquatic life. The initial switch to a different habitat does not require significant change in the morphology because many animals (e.g., dogs, horses) can walk in the water and even swim without any specific adaptations. Animals only had to learn how to use already existing body parts in the water. However, behavioral adaptation to aquatic life has led to the re-invention of the body because limbs and tails were used in a new way. As a result, the evolution of body parts switched to a new mode with entirely different optimization criteria. For example, the use of the tail for propulsion in the water by beavers, whales, and manatees resulted in a dramatic subsequent change in its shape, skin, and musculature.

Another example is the emergence of insect flight. Wings did not appear as an adaptation for flying because there was no flying function yet. However, wing-resembling appendages may have helped insect ancestors to glide when they dropped down from trees.[9] This new behavior (gliding) initiated genetic selection that resulted in the modification of the size and shape of the appendages. As gliding progressed, insects apparently changed their behavior again and started bending their pre-wings for steering in the air. This created a fitness gradient for genes affecting corresponding muscles and cuticle thickness at the base of pre-wings, which again changed the fitness landscape. Finally, the muscles became stronger and could partially support forced flight, which led to subsequent specialization of these muscles. As follows from these examples, the emergence of new functions is strongly facilitated by behavioral plasticity, a phenomenon that is known as Baldwin effect (Baldwin 1896).

Functional plasticity exists even in molecular mechanisms, allowing molecules to change or expand their functions. For example, the initial function of actin protein is likely to be making a cytoskeleton and supporting the shape of a cell. However, in evolutionary advanced organisms actin is used for many additional functions, including protein transport, contraction of muscles, and growth of nerves. Developmental plasticity and modularity offer a powerful support for the emergence of novel functions. Organisms use plasticity to adjust functions to entirely novel environments which provide a chance of function change. Modularity also allows a seamless transfer of developmental programs to new parts of the body. For example, ancient flightless reptiles carried feathers on various parts of the body before the origin of birds who started to use feathers for flight (Jones et al. 2000; Prum and Brush 2002). Another advantage of modularity is the protection of existing developmental programs from external and internal disturbances which may be associated with habitat change and emergence of novel functions. Cohabitation (e.g., symbiosis) and horizontal gene transfer can also facilitate the emergence of new functions due to re-interpretation of existing information in the context of new interactions or assimilation of external functional information.

[8] Note, that I consider emergence as a *semiotic phenomenon* (i.e., change of interpretation by agents) rather than simply an unpredictable thing, event, or a new kind of causation in nature, as discussed by Kim (1999).
[9] Here I do not discuss additional possible functions of wing-like appendages, such as thermoregulation (Kingsolver and Koehl 1985) or sexual display (Dickinson and Dudley 2009).

According to the MS, genetic mutation is the only source to novel phenotypes. In contrast, the EES assumes that developmental and behavioral capacities of organisms determine the spectrum of potential novel phenotypes. New forms can be produced even without mutations (e.g., phenocopies), and some of them are replicated in the progeny via epigenetic inheritance. However, the simplest way to preserve a new phenotype in subsequent generations is to link it with some mutation, or in other words, attach a new meaning to a mutation (Sharov 2014). Each function is controlled by thousands of signaling pathways, and each pathway can be affected by a large number of potential mutations. Thus, the direction and magnitude of function change is primarily controlled by the network of signaling pathways rather than by mutations themselves. In other words, organisms do not have to wait for a specific mutation to change their function. Any mutation out of a large number of alternative options will work equally fine if there is a well-organized network of signaling pathways that has a capacity to generate a new phenotype that is beneficial in current conditions. Similarly, mutations that cause non-functional or lethal changes can be neutralized by the network of signaling pathways via selecting another counteracting mutation (one out of thousands of mutations with the same effect).

It is difficult to evaluate quantitatively the prevalence of the "emergent mode" of evolution, but paleontological records indicate that mammals had much higher rates of evolution than mollusks (Simpson 1953), which can be attributed to increased probability of emergence events. Apparently higher rates of emergence events in evolutionary-advanced lineages (e.g., birds and mammals) may be related to increased ontogenetic plasticity, modularity, and learning capacity. One of the factors that facilitated emergence in evolution was evolutionary transition to more advanced memory carriers: from non-writable DNA, to re-writable epigenetic memory, and finally, to the mental memory of animals equipped with a brain (Jablonka and Lamb 2005).

Qualitative Steps in the Evolution of Functional Information

The complexity of functional information increased in parallel with the evolution of living organisms. Besides a quantitative increase in the number of supported functions, these changes were associated with qualitative reorganization of the meaning of information, which are often described as levels of semiosis. For example, Prodi (1988) suggested a term "protosemiosis" for primitive forms of sign processes at the molecular level. Krampen (1981) used the term "phytosemiosis" for sign processes in plants. Barbieri (2009) distinguished between code-based semiosis at the cellular level and interpretational semiosis that includes representations and requires brain activity. Kull (2009) described three levels of semiosis: vegetative, animal, and cultural, which he linked with three types of signs defined by Peirce: icons, indexes, and symbols, respectively. Sharov and Vehkavaara (2015) combined approaches of Prodi, Kull, and Barbieri, and suggested to distinguish *protosemiosis*, where signs are linked to actions of agents either directly or via simple logical gates, and *eusemiosis*, where signs are linked with classifiable objects and only then - with possible actions.

Protosigns that operate at the protosemiotic level differ substantially from higher-level signs because they do not correspond to objects (Sharov 2013). This is not easy to comprehend because brains are trained to think in terms of objects. It seems natural to

associate a triplet of nucleotides in the mRNA with aminoacid as an object. However, a cell does not have internal representation of aminoacid, which is not perceived as object by a cell. Instead, a triplet of nucleotides in the mRNA is associated with an action of a ribosome that appends an aminoacid to the elongating polypeptide.

Molecular interactions in living cells can be alternatively described as chemical reactions; thus, a question arises: why apply semiotic terms to systems that seem to be just chemical? This question is best to discuss in the context of the origin of life: i.e., where is a threshold zone that separates chemical and biological systems? Kull (2009) proposed that it corresponds to the emergence of the first functional cycle, which is a self-reinforcing cycle of perception and action (Uexküll 1982). Obviously, primordial systems were too simple to make a full-scale functional cycle with sensors and effector organs. Thus, we need to consider a simpler version of a functional cycle. Earlier I proposed a model of a self-propagating system which supports unique internal conditions to facilitate its functions, and functions are targeted on supporting internal conditions (Sharov 2009a). In particular, coenzyme-like molecules can establish and enhance their own autocatalysis by colonizing oil microspheres (i.e., hydrocarbons of abiotic origin) and changing surface properties via oxidation. Changing surface properties of oil microspheres is a function that may have been beneficial for coenzyme-like molecules if it helped them to multiply and then colonize other oil microspheres. In such a system, it can be said that coenzyme-like molecules encoded surface properties of oil microspheres. Moreover, this system has a capacity for evolution because it can assimilate additional coenzyme-like coding molecules with novel functions (e.g., helping to capture or store resources). Although individual chemical reactions in these systems can be well described by chemical kinetics, the integration of these reactions into a coordinated and evolving agency is certainly beyond the sphere of chemistry.

As the number of protosigns increased in evolution, they became integrated into networks via logic gates with contextual control. For example, transcription of a gene is often activated by simultaneous binding of two or more transcription factors to the promoter of a target gene. However, this innate logic is still fixed genetically and cannot be modified within the life span of an organism even if it fails to produce beneficial effects. To overcome this limitation, organisms developed epigenetic mechanisms for modifying logic gates on demand. For example, a gene with multiple regulatory modules in its promoter may initially carry open chromatin at all modules. However, after some "memory triggering" event, the chromatin may become condensed at all regulatory modules except the one that was functional at the time of the event that had a successful outcome (e.g., captured food). This can be viewed as a primitive mechanism of adaptive learning (Sharov 2010).

As organisms advanced in perceiving internal and external signals, they eventually acquired a capacity to integrate them into meaningful categories representing real objects and situations (e.g., food items, partner agents, and enemies), and predict events using models. These classifications and models comprise the knowledge of an agent about itself and its environment, which belongs to *eusemiosis*. Following the terminology of Uexküll, this knowledge is the Innenwelt and Umwelt of an organism (Uexküll 1982). Information processed at the eusemiotic level does not necessarily induce physical actions of an organism. However it still can be called "functional information" because it involves mental functions (e.g., accumulation of knowledge) and it may affect future

physical actions. This preparedness for future actions was called "disposition to respond" (Morris 1964).

Memory of animals is not heritable, and cannot be transferred directly to the next generation. However, the accumulation of individual knowledge is facilitated and directed by heritable features of the body, such as effector organs (e.g., legs, tail, and mouth), sense organs, and neural system that connects all organs with the brain. The structure, sensitivity, and resolution of senses determine which patterns an animal can learn in its individual life. The size of the body, life span, and movement speed also contribute to the perception and interpretation of the world. Thus, animals of different sizes (e.g., a cow and ant) perceive and use the same environment (meadow) in entirely different ways (Uexküll 1982). Because of these heritable constraints, Umwelten of conspecific organisms are similar to each other, which is a pre-condition for the emergence of language which supports the transmission of knowledge within a society of individuals. Language requires references to abstract objects such as qualities, quantities, and relations that generalize the features of real objects. Thus, it is based mostly on symbols, whereas icons and indexes play only supplementary roles. Language is fully developed only in humans, but higher animals also have a limited capacity for language-like communication (Čadková 2015). In pre-language communication, messages carry information only about the sender (e.g., emitting pheromone means "I am ready to mate") or its immediate environment (e.g., bird's cry means "I see a predator"). In contrast, language allows transmitting information about things that are not perceived but only named. Teaching appears as new kind of communication activity, which supports the development of language skills.

Conclusions: Perspectives for the Semiotic Concept of Evolution

Despite advances in molecular biology and systems science, the evolutionary theory still considers morphology as the main yardstick of evolution. For example, the popular theory of punctuated equilibrium (Gould and Eldredge 1977) is heavily grounded on the fossil records as it was in the times of Cuvier. Biologists have not yet realized that the evolution of life has semiotic/informational nature and that the terminology and main postulates require a qualitative revision. Sequencing of full genomes of eukaryotes confirmed inadequacy of common notions of progress in evolution. For example, the genome of a simple unicellular choanoflagellate *Monosiga brevicollis* appears amazingly similar to complex multicellular organisms (King et al. 2008). It includes 9200 genes which is just a little short of *Drosophila*'s 11,000 genes; its genes are intron-rich and encode cell adhesion and signaling protein domains that are otherwise restricted to metazoans. Obviously, *M. brevicollis* has a far greater functional complexity than it would be expected from its morphology.

The MS captures only most simple cases of short-term evolutionary changes in populations (e.g., allele frequency change) and does not consider other effects related to adaptability, plasticity, habitat change, exaptation, speciation, or the Baldwin effect. Alternative models of evolution are being developed (Jablonka and Lamb 2005; West-Eberhard 2003) but they have not appeared yet in the evolutionary textbooks. Biosemiotics can offer many fresh ideas on how to restructure the evolutionary theory, but will biologists listen? Unfortunately, the integration of biology with semiotics is a

slow process and the major obstacle is the incompatibility of worldviews. Applications of chemistry and physics are heavily promoted in biology, whereas semiotic aspects of evolution are neglected. The semiotic community also resists incorporating biology because principles of semiotics were traditionally applied to human communication, rather than to genes or signaling pathways in living cells. To make biology and semiotics compatible, both parties should adjust their views. On one side, biologists have to assume an extended ontology where there is a place for agents, goals, functions, and signs. The EES provides important theoretical concepts such as epigenetic heredity, dynamic phenotypes, and niche construction that can facilitate the transition of biology to the semiotic understanding of life. On the other side, semioticians should accept that signs are grounded in evolving populations of agents. The meaning of a sign is neither a material object nor a universal eternal idea (as in objective idealism) but a useful heritable association or convention in a population of communicating agents. What should we call such a doctrine? It is close to the pragmatism of James (James 1907) who suggested that truth is grounded in the activity of individuals. But pragmatism over-emphasized the role of utility and underestimated the importance of logic, plasticity, aesthetics, and other factors (Sharov 2009c). Contemporary versions of pragmatism are supported by evolutionary epistemology (Gontier 2006) and constructivism (Riegler 2006). However, these theories also have some problems. Evolutionary epistemology has been strongly associated with neo-Darwinism and is slow in accepting the EES, whereas constructivism is often excessively materialistic (e.g., autopoiesis) and slow in accepting the ideas of semiotics. But no matter what we call this emerging philosophy, it may become the point of convergence of biology and semiotics in the future.

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