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ORIGINAL PAPER

The Great Chain of Semiosis. Investigating the Steps in the Evolution of Semiotic Competence

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Abstract Based on the conception of life and semiosis as co-extensive an attempt is given to classify cognitive and communicative potentials of species according to the plasticity and articulatory sophistication they exhibit. A clear distinction is drawn between semiosis and perception, where perception is seen as a high-level activity, an integrated product of a multitude of semiotic interactions inside or between bodies. Previous attempts at finding progressive trends in evolution that might justify a scaling of species from primitive to advanced levels have not met with much success, but when evolution is considered in the light of semiosis such a scaling immediately catches the eye. The main purpose of this paper is to suggest a scaling of this progression in semiotic freedom into a series of distinct steps. The elleven steps suggested are: 1) molecular recognition, 2) prokaryote-eukaryote transformation (privatization of the genome), 3) division of labor in multicellular organisms (endosemiosis), 4) from irritability to phenotypic plasticity, 5) sense perception, 6) behavioral choice, 7) active information gathering, 8) collaboration, deception, 9) learning and social intelligence, 10) sentience, 11) consciousness. In light of this, the paper finally discusses the conceptual framework for biosemiotic evolution. The evolution of biosemiotic capabilities does not take the form of an ongoing composition of simple signs (icons, indices, signals, etc.) into composite wholes. Rather, it takes the shape of the increasing subdivision and control of a primitive, holophrastic perception-action circuit already committed to "proto-propositions" (dicisigns) reliably guiding action already in the most primitive species.

Keywords Biosemiotics · Semiotic freedom · Learning · Social intelligence · Consciousness · Dicisigns · Peirce

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Introduction

The conception of the world as a *Great Chain of Being*, a continuum of beings emanating in God and stretching all the way down through the variety of angels and living creatures has been a vital element in European religious and metaphysical thinking. From its genesis with Plato and up through intellectual history, this *Great Chain of Being* was generally associated with ideas of *plenitude*, *continuum* and *graduation* as explored in (Lovejoy 1948 [1936]). When the French naturalist Jean-Baptiste Lamarck created, in 1809, the world's first comprehensive theory of evolution[1] he was still under the influence of this idea but he ingeniously conceived the great chain of being not only as a chain in space but also, or rather, a chain in time, where 'more perfect' forms had gradually emerged from 'less perfect' forms.

The issue of perfection, often rephrased as structural or behavioral complexity, has been contentious in Darwinism. In this paper, we shall propose a semiotic measure of that idea. Thus we propose the *great chain of semiosis* with particular emphasis on how the cognitive and communicative potentials of species may be classified according to their plasticity and articulatory sophistication.

The meaning of the term *semiosis* unfortunately is not well known and many, even in academia, tend to burden the concept with mentalistic connotations which it does not imply. S*emiosis* simply means "sign action", i.e. a process whereby a sign induces a receptive system to make an interpretation. Thus a rat, for instance, quickly learns to lift its left hind leg when approaching a distinct spot in the cage where it has repeatedly received an electric chock through the paw of that leg. The rat's avoidance reaction discloses that touching this spot now signifies pain. Surprisingly, perhaps, the avoidance reaction is quickly learnt even in rats where the spinal cord has been severed (Grau 2002, 80). Recognition of the 'electric' spot thus induces a distinct avoidance reaction even in "brainless" rats, implying that semiosis may occur in the absence of brain processes, and, *a fortiori*, of consciousness.

Human linguistic utterances undoubtedly involve mental processes, and one reason why the term semiosis is so often taken to carry mentalistic associations is probably the conception of semiotics as a branch of linguistics. Modern semiotics considers human language as one, admittedly very peculiar, sign system only, among the millions of sign systems that have evolved in natural systems. Songs of birds, croaking of frogs, flashing of fireflies, or spawning behavior of fish are other well known cases of sign systems, but millions of less conspicuous semiotic interactions are active as regulators of organismic activity. Semiosis is an essential regulator not only of intraspecific behavior among conspecifics but also of interspecific behavior as is illustrated in symbiotic interaction such as that of pilot fish with sharks. Pilot fish feed on the parasites they dig out of the shark's skin and, in return, they get protection from potential predators. Pilot fish may even swim inside the mouth of the shark to clean away fragments of food between their teeth. Evidently, very specific semiotic mechanisms are involved here to prevent the shark from swallowing the pilot fish and the pilot fish from fleeing.

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[1] It is often overlooked that central ideas of biological evolution were aired already during the French Enlightenment in mid-18th century, such as Buffon and Diderot (2011), but Lamarck was the first to articulate such ideas in a comprehensive theory.

We consider life and semiosis to be co-extensive (Kull et al. 2009) implying that semiosis has been essential to life from the very beginning. With the appearance of multicellularity during evolution the former autonomous unicellular eukaryote organisms were challenged by a need for cooperation in the multicellular body, and eventually this need even implied that some cell lines had to give up their own reproductive potential, i.e., they had to become somatic cells (not germ cells). In order for this kind of cooperation to happen, strong semiotic interaction would be necessary in the growing embryo, and we hypothesize that *endosemiosis*, the semiotic regulation that takes place inside an organism, is as much a part of *the great chain of semiosis* as is *exosemiosis*, the semiotic interaction between organisms.

To take an example, if e.g. the membrane of a liver cell is hit by a certain threshold number of epinephrine molecules per millisecond, the cell[2] initiates a cascade of biochemical reactions in its interior space resulting in the degradation of polysaccharide (glycogen) to monosaccharide (glucose) which is excreted to the blood to assure the availability of energy resources (primarily in the muscles). Since epinephrine is itself excreted from the adrenal medulla as a response to stress (threats, noise, excitement etc.), and the ensuing muscular action reacts regarding the stress source, the communicative function of this loop of endosemiotic processes is obvious. The stress experience is signaled to the rest of the body and, ultimately, to single liver cells that interpret the hormone message by initiating polysaccharide degradation. Other cells in the body interpret the same hormone-message quite differently, pancreatic cells will decrease their excretion of insulin, fat cells will begin degrading lipids, and smooth muscle cells in the airways become relaxed whereas smooth muscle cells in the arterioles contract, etc.

The overall result of this flurry of bodily activity is to make the body ready to confront the real or anticipated challenges that stressed it in the first place. The endocrine apparatus (the hormone system) involved here should not be seen as an isolated regulatory system, however, but rather as an integral part of both the immune system and the nervous system. Together, these major semiotic systems make the body recognize and respond to whatever situation it happens to meet. Or, to put it differently, these endosemiotic tools are collectively responsible for the interaction of the organism with its social and physical world and constitute the fundament out of which so-called psychological reality, if any, of the organism will emerge.

Semiosis and perception should therefore not be confused. Perception, understood as the process of creating internal models of events or things in the surroundings, is a high-level activity based on the integration of hundreds, thousands or, in some cases, even millions of semiotic interactions in the body and between the body and its environment and facilitates, in higher organisms, comprehensive mental maps of relevant aspects of organism surroundings. Signs in simple organisms typically cover a narrow range of important environmental and inner situations only, and are thus far simpler than full-fledged perception in organisms with central nervous systems (CNS) and the integration of information from various broad-spectered perceptual organs able to perceive a wide range of environment situations. The accusation often leveled against biosemiotics that it is just another kind of panpsychism therefore rests on a poor conception not only of

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[2] The ascription of agency to the cell implied here is not meant to question the sufficiency of enzymatic causality. Enzymatic reactions, however, are operating inside a higher-order functionality determined by the cell as a holistic unit.

semiosis but also of perception. Perception presupposes semiosis but semiosis does not presuppose perception. A web of sign processes, semiosis, is underlying all kinds of cognitive activity in the world from human imagination and down to the lowest level as exhibited by bacteria.

But why do we insist upon calling such comparatively simple processes “signs”? An alternative, widespread idea is to see organismic activity as completely mechanical, up until the stage where consciousness appears in organisms with CNS, implying that true semiosis would presuppose conscious mental representations. The reason why such a metaphysics is unsatisfactory is that it instates a coarse dualism where one single evolutionary event, that of the coming into being of nervous tissue, would distinguish a realm of semiotics from a totally asemiotic realm. But such a dualism simplifies what went before that event, the appearance of CNS, and makes too complex what came after it.

Our idea is that the evolution of nervous tissue and its organization into CNSs served to facilitate simpler semiotic-cognitive processes that were already there. Indeed, each single link of such processes will run according to simple causal dynamics and, yet, the overall cyclic, self-sustaining structure of metabolism in which they partake cannot be reduced to such simple dynamics. The ongoing self-organization of that process makes it prone to cognition: to find the means to get to crucial nutrients, escape predators, find shelter etc. is needed to uphold the process. Self-organizing structures best able to achieve this end would have an obvious selective advantage over less successful self-organizing structures thus favoring the evolution of systems, organisms, equipped with a basic intention, that of self-preservation. Long before the appearance of mental life, organisms and their behavior display this intentional structure, which is why such entities are selectable and evolvable in the first place: Living systems better equipped to sustain essential metabolic cycles survive at the expense at less successful ones. This gives life its local, organism-bound purpose-orientation, its direction towards the best self-preservation (and, in turn, self-reproduction).

Once an organism has perception, of course, higher-level signs may appear in its perceived world in the shape of particular perceived qualities, shapes, events, objects carrying a further meaning. Such signs are central for the behavior, cognition, and communication of higher animals with central nervous systems - but they do not exhaust the class of signs in biology. Quite to the contrary, they constitute a higher-level, sophisticated class of signs, made possible only by the integration of simple lower-level signs, most of them probably without any mental or conscious qualities, in perception.

From Agency to Consciousness

Agency may be defined as the capacity of an agent to act in the world. Until recently, few philosophers or biologists would ascribe agency to non-human life forms on the pretext that natural systems behave according to deterministic causality and that any supposedly deliberate behavior must, in a deeper analysis, come out as a purely mechanistic reflexive activity. Such sharp demarcation lines between human and nonhuman life have dwindled, however, in recent years as the true sophistication of animal cognitive and communicative life has gradually become evident.[3] We are now left with the choice of denying the existence of real agency altogether (eliminitavism)

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[3] Cf. volumes like Bekoff et al. 2002 or Hurley & Nudds 2006.

or explaining where and how true agency gradually occurs during evolution. Our hypothesis is that agency as such is co-existent with life and semiosis (Kull et al. 2009)[4] so that life, semiosis, and agency make up one conceptual complex which, once realized in the wild, constitutes the basis of ongoing sophistication during evolution. Metazoan agency therefore may well be a lot more articulated and expressive than the agency of unicellular organisms but ultimately it depends on the semiotically controlled and coordinated agency of individual metazoan cells.

Biologists discussing the agency aspect of organismic life use terms such as “action selection” (Prescott 2007), “decision-making” (Esch and Kristan 2002), “behavioral choice” (Kristan and Shaw 1987) or “motor program selection” (Kupfermann and Weiss 2001). The instrumental aura of such terms cannot cover the fact, however, that those terms are either meaningless or expressions of a basic agency of living systems. In the absence of organismic agency natural selection would hardly work, since ‘competition’ depends on a plurality of agents striving for the same good. From the very beginning, organisms must have possessed some modest capacity for directing their agency towards a self-sustaining activity. This implies that they must have possessed means for measuring vital parameters of their environments and ‘selecting’ their activity accordingly, which exactly is what semiosis is all about. Semiosis must have been, from the beginning, an important element in evolution, and the sophistication of the semiotic capacity of organisms will have been one basic way of escaping extinction. It is not surprising, therefore, that later stages of evolution have seen the birth of species (such as birds and mammals) that exhibits high levels of semiotic complexity - or semiotic freedom (Hoffmeyer 1992, 1996). The ambitious task before us now is to begin to sort out the essential stages along the route which has lead from the simple semiotic agency of bacteria to the cognitive sophistication of human beings. We conceive of the charting of the appearance of semiotic capabilities during the process of evolution to be one of the major aims of the nascent discipline of biosemiotics, and we can but make an initial hypothetical overview here. When and where, in evolution, did central semiotic competences appear?

The enumeration of elleven steps of cognitive evolution discussed below is tentative and should be seen simply as an attempt to initiate the construction of a taxonomy of evolved semiotic forms that has so far been absent. We are aware of the incompleteness and somewhat haphazard character of this enumeration, thus a major objection to this ordering of semiotic competence into a linear scale is that evolution follows parallel tracks. Some of the steps may be taken more than once during evolution.

Steps on the Evolutionary Route to Human Consciousness

Molecular Recognition

Molecular recognition probably is the most basic instrument in the semiotic toolbox. As used in biochemistry, the term refers to the ability of a system to ‘select’ or bind specific molecules without necessarily entering into full chemical reaction with them. Weak

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[4] To explain how semiosis and agency could have evolved in the course of prebiotic evolution is a major scientific challenge (for some current work in this area see (Deacon 2012; Kauffman and Clayton 2006; Kull et al., 2009).

molecular forces (short range forces such as hydrogen bonds or van der Waals interactions) which do not destroy or fundamentally change the molecules involved, account for the specificity of the recognition process, and the process itself serves to control i.e., initiate, facilitate or inhibit, other system processes such as replication of nucleic acids, immune response in antibodies, signal transduction in receptors, or regulation of enzymes. The semiotic character of the process, then, lies in the fact that unlike non-living processes, the categorization of substances through processes of molecular recognition, as exhibited e.g. at the level of bacterial chemotaxis, already realizes the split between objects and properties. In many cases, several different compounds may serve exactly the same functional end implying that the process is fallible (while it makes little sense, by contrast, to conceive of pre-living processes as fallible) - in the sense that certain other compounds recognized and “approved” by the bacteria may nevertheless fail to support survival. *E. coli* is able to swim upstream in a sugar gradient due to its ability to recognize a range of carbohydrates (objects) from the partial shape of the perimeter of the molecules (properties) and, for the same reason, they will be deceived by artificial sweeteners with the same partial shape property, just like human beings will be so deceived. Molecular recognition may *fail*, leading the organism to accept irrelevant or even poisonous substances, a failure which is objectively measured through its consequences for survival. Thus, it is basic Darwinian selection pressure that makes organisms depend upon signs being able to inform truthfully about the environment. The implicit recognition of this fact is evident in the reliance of biological research upon more or less spontaneous sign concepts (code, information, signal, cue, etc.) omnipresent in all sub-disciplines of biology.

The Prokaryote-Eukaryote Transformation: Privatization of the Genome

A major step - perhaps the most decisive step of all - in the evolution of semiotic competence was taken by those bacterial species, prokaryotes,[5] that some two thousand million years ago formed narrow association with one - or more likely - several other kinds of prokaryotes under the creation of the so-called eukaryotic cell.[6] To see the great significance of this step it should be noticed that membranes, or proteins topologically linked to interior and exterior surfaces of membranes, control by far most of what goes on in a cell. In the prokaryote, the plasma membrane attends to all vital processes, while in the larger and more advanced eukaryotic cells these same functions are taken over by subcellular organelles—the individually membraned mitochondria, chloroplasts, Golgi apparati, ribosomes, lysosomes, etc. Some of these membranes (perhaps, even all of them) are probably descendants from once free-living prokaryotic organisms, which at one time in the remote past probably were engulfed by some other prokaryotes and which by luck managed to survive, reproduce, and after some time enter into a symbiotic relation with the host organism—what Lynn Margulis called the process of *endosymbiosis* (Margulis 1970; Margulis and Fester 1991).

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[5] Prokaryotes are single-cell organisms without cell nuclei or any pronounced internal architecture.

[6] Eukaryotic organisms are composed from large cells with nuclei and a rich internal structure, such as those found in plants, fungi, and animals, as well as in many single-celled organisms such as yeast and amoeba. The diameter of a eukaryotic cell lies in the range of 10–100 μm, whereas prokaryotic cells have diameters in the range of 0,2 to 2,0 μm. The internal space of a eukaryotic cell may easily contain thousands of prokaryotic cells.

The richness of the collaborative patterns and communicative mechanisms to be found in the bacterial world is only now beginning to be realized (see Ben-Jacob et al. 2004). Microbiologists often chose to study bacteria while they are in the *exponential growth phase,*[7] when they are close to optimally supplied with nutrients. Under natural conditions, however, this artificial laboratory situation is far from typical and it has become clear in recent years that under more poor growth conditions, all kinds of interesting cooperative strategies arise between bacteria. This has inspired some researchers to talk about a *bacterial linguistic communication* and about its networked *social intelligence*. Aside from such high-flown metaphors it remains true that bacterial cooperation across taxonomic barriers - based on the exchange of genetic material (vira or plasmids) - operates as a kind of bacterial world wide web, called a “global organism”, serving to bring around life-sustaining messages (Sonea 1992, 380). The sheer amount and variety of bacterial colonies around the globe make sure that the right piece of DNA-information to help one or another bacterial colony to sustain its life will be present somewhere. Bits of DNA are exchanged randomly between bacterial colonies due to the omnipresence of plasmid vehicles trafficking among individual colonies and delivering their DNA-content by a process known as transduction. Seen from the point of view of a starving or otherwise stressed population of bacteria, this state of affairs represents a “hope” for being rescued. And while, for any single population, the probability of such a “lucky” outcome is, of course, infinitesimal—considering the astronomical numbers of bacteria present everywhere, a successful result is virtually guaranteed to occur *somewhere*. In sum, we may say that prokaryotic life on our planet managed to make use of the law of great numbers to establish a kind of global prokaryote semiosphere—a semiotically based coordination of prokaryotic life into one worldwide swarm.

Compared to the extreme openness toward foreign DNA-messages exhibited all over the prokaryote world, eukaryotic organisms appear to be isolated beings. In eukaryotic cells, DNA-transmission is predominantly *vertical* or *temporal*, limited to the events of cell divisions. The *horizontal* or *spatial* transfer of DNA between species is not completely absent in eukaryotic organisms, but only occurs as an exception, not a rule. The one major exception to this rule is the fusion of genomes taking place in sexual reproduction. A deep difference in semiotic logic between prokaryotic and eukaryotic life is buried here. Rather than depending on the reception of visiting genes through plasmid infection, eukaryotic cells relyed on genetic self-sufficiency. Yet this strategy had the consequence that eukaryotic organisms became genetically segregated from one another, and increasingly more reliant upon *endosemiotic resources* than on *exosemiotic interactions* for both survival and continuation of their line. “But what eukaryotic life forms lost in capacity for horizontal genetic communication, they copiously gained through the development of sophisticated kinds of communication based on a diversity of nondigital biochemical and behavioral signs. For while the evolution of eukaryotic cells implied a strong restriction in the channels suitable for digitized communication, it opened the way to the development of life forms that possessed far more architectonic multiplicity and behavioral degrees of freedom than prokaryotic organisms could ever have obtained. The transition from prokaryotic to eukaryotic life forms thus exemplifies a general principle pertaining to emergent

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[7] Because only in this state reproducible data are easily obtained.

processes—i.e., that *in emergent processes, freedom of possibility will always be constrained at the simpler level in order to allow an altogether new kind of freedom to appear and unfold at a more complex level*. The emergence of multicellular life and of social life are but two more examples of this fundamental dynamic principle" (Hoffmeyer 2008, 258).

Thus, the growth in size, complexity and isolatedness of eukaryotes is possible only due a vastly larger amount of semiotic activities both internally in the organism and relating the organism to its environment. The loss of the relatively free accessibility of DNA in the prokaryote world was compensated in the eukaryote world by a growth of autonomy and semiotic capability.

Division of Labor in Multicellular Organism (Endosemiosis)

The crucial evolutionary step from uni- to multicellular organism involves the differentiation between different, collaborating cell types and hence the semiotic coordination of different behaviors of those cells. Multicellular organisms may have evolved in several different ways (Waggoner 2001), but the importance of communication between cells is clearly demonstrated by the lifespan of the slime mold *Dictyostelium discoideum* that involves unicellular as well as multicellular phases. (cf. e.g. Margulis and Chapman 2009, 136). When nutrition is rich, the mold dissipates into single-celled amoeba, but when nutrition becomes scarce, these cells are able to organize themselves into growing a stalk with a fruiting body at the upper end, allowing for some cells to be taken by the wind to a location more rich in nutrition. Here, a primitive division of labor anticipates the distinction between germ cells and soma cells, as the lower cells in the stalk so to speak "sacrifice" themselves for the survival of the group. Such large-scale coordination between cells presuppose the recognition of conspecifics and a sophisticated chemical-spatial communication between them.

Coordination patterns between cells in multicellular organisms form the prerequisite for simple behavior types such as irritability and phenotypic plasticity.

From Irritability to Phenotypic Plasticity in Plants

Irritability in the sense of a system's physiological response to a stimulus may be taken to occupy a slightly higher position at the semiotic scale. 'Irritability' is semiotically more developed than 'molecular recognition' since it occurs at the level of the organ or whole organism and typically implies the simultaneous activation of several parallel and/or consecutive recognition processes. A typical example of irritability would be plant thigmotaxis, i.e. the movement upon tactile stimulus e.g. touch) that already Darwin discussed with many examples in his book on plant movements (Darwin 1880). This allows for a plant to reorient its leaves under influence of sun, rain, insects, etc.

Godfrey-Smith reckons phenotypic plasticity under a category of *proto-cognitive* capacities exhibited mainly by bacteria and plants. He advocates a broad concept of cognition "as a collection of capacities which, in combination, allow organisms to achieve certain kinds of coordination between their actions and the world" (Godfrey-Smith 1998, 5), and underlines that a central nervous system is only one among many different ways to process information and control behavior. In Godfrey-Smith's understanding, cognition proper shades off into different kinds of proto-cognitive processes that, as a minimum, exhibit some degree of "arbitrariness" in how the cue effects the system. By proto-cognitive capacities he understands "capacities for controlling individual growth, development, metabolism and behavior by means of adaptive response to environmental information" (*ibid*, 8). Although plant plasticity will be the standard case, Godfrey-Smith is keen to stress that even multicellular organisms like ourselves contain "subpersonal" systems with some of the proto-cognitive capacities of simpler whole organisms. The vertebrate endocrine and immune systems are examples of such "subpersonal" systems. Obviously, however, plants in general are more dependent on phenotypic plasticity than are animals, since the relative immobility of plants bids them to either adapt to the environment at the very spot they happen to occupy, or perish.[8]

From a semiotic point of view, all cognition necessarily implies an interpretative act: some system (a cell, a tissue, an organ, an organism, or perhaps a group, herd, hive, or other social system of organisms) must let itself change its own inner state (for instance by enacting a new behavior) as a response to a cue - in a way that is framed by the system's own evolutionary history. The distinction between behavior, on the one hand, and activities such as growth, development or regulation of metabolism, on the other, is therefore gradual rather than discontinuous and cannot be used as a demarcation line sorting out an area of cognition from an area of proto-cognition. We agree with Silvertown and Gordon that movement is not an important criterion for something to constitute a behavior and we thus endorse their extension of the term 'behavior' to generally include "what a plant or animal does, in the course of the individual's lifetime, in response to some event or change in its environment" (Silvertown and Gordon 1989: 350).

Phenotypic plasticity is an umbrella under which many diverse semiotic control systems are assembled. A standard case might be the regulation of the length of new shoots. Jones and Harper found that the growth of *Betula pendula* (silver birch) is influenced by the presence of close neighbors. As one would expect, "fewer buds were 'born' and a greater proportion died in the areas of the crown most subject to interference from the branches of neighboring trees and this was reflected in smaller mean branch size in these areas" (Jones and Harper 1987, 1).

Silvertown and Gordon emphasize that "many of the things that plants cannot do, but most animals can, happen quickly, e.g. reflexes, escape, arousal, attack, and recognition" (Silvertown and Gordon 1989,362). And, of course, plants do not have an organ for central processing of information and tend rather to control their behavior by locally mediated, comparatively slower responses.

Sense Perception

"Take away perception... and you are left with a vegetable" writes Fred Dretske (Dretske 1995, 118). Dretske's concern was not so much sense perception per se (nor vegetables) as it was sense perception as cognitive experience. "It is not what you see

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[8] Aspen trees, however, are known to form clones of trees where thousands of shoots (ramets) are linked together to form one individual covering tens of hectars. Not only are these forests probably the largest "individuals" on Earth, they may also be among the oldest, some as old as 1.000 years. The strong emphasis in gene centered evolutionary theory on reproduction seems somewhat misplaced in such cases.

that is important in the struggle for survival, it is what you know about what you see" (*ibid*). If we accept Dretske's view it remains to be clarified what should be meant by 'knowing'. Does 'knowing' require the possession of mental states with explicit propositional stance or should we broaden the concept to encompass 'bodily knowing', like forms of perception that serve to guide 'brainless' animals such as cnidarians (jellyfish, sea anemones, corals, and freshwater hydra)? Although such animals may not have any explicit knowledge of what they perceive, in the mental sense of the word, their 'perception' nevertheless is fully involved with interpretations that help them escape and survive. So we tend to take a broader view of perception as semiotic processes informing the organism, supported by specific signaling systems such as nervous systems.

Cnidarians exhibit radial symmetry along a dorso-ventral (or top-down) axis and well-preserved cnidarian fossils are found as far back as 580 million years ago (the Ediacaran period). Unlike the group of animals from which they diverged, the sponges (see Fig. 1), which lack neurons and therefore respond to stimuli only exceedingly slowly, cnidarians possess a diffusely organized net of nerve cells distributed regularly over their surface and are capable of coordinated body movements and quick responses. Interestingly, cnidarians already posses most of the basic neurophysiological features found in 'advanced' metazoan nervous systems, including multifunctional neurons, action potentials, synapses, and chemical neurotransmission (Prescott 2007, 12). Yet, their diffuse nerve system does not allow for linear nerve propagation and is unfit for fine control of motor movements.[9] At this stage of animal evolution, behavior still seems to be largely reflexive rather than selective.

A primitive form of learning, *habituation*, has been demonstrated in cnidarians, however. Thus polyp clones of sea anemones have been shown to moderate their propensity for attacking foreign clones upon repeated encounters (Ayre and Grosberg 1995). Habituation refers to the ability of an organism to respond with decreasing force to a repeated stimulus (as when the stimulus becomes a 'habit'). The effect depends on the frequency and duration of the stimulus, and if the stimulus is withheld for a long period of time recovery of the response will eventually occur.

We do not imply, of course, that such very simple sensation processes involve any degree of awareness or consciousness. It is an open issue when such mental qualities appear in the course of evolution, and there is even no agreed-upon criteria nor methodology for assessing their existence, but our contention is that they require a more developed central nervous system preoccupied with the integration of different perception modes and with the selection between different elaborated agency possibilities.

Behavioral Choice

Proceeding one step further in the phylogeny of animals (Fig. 1) we come to the platyhelminthes or flatworms such as planarians, flukes, and tapeworms. These animals are so-called bilaterals named for the symmetrical arrangement of body parts around an anterior-posterior axis (allowing for a distinct front area, the head, with eyes). The

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[9] Although they have independent circuits for feeding and movement respectively the latter also serving fast escape behavior.

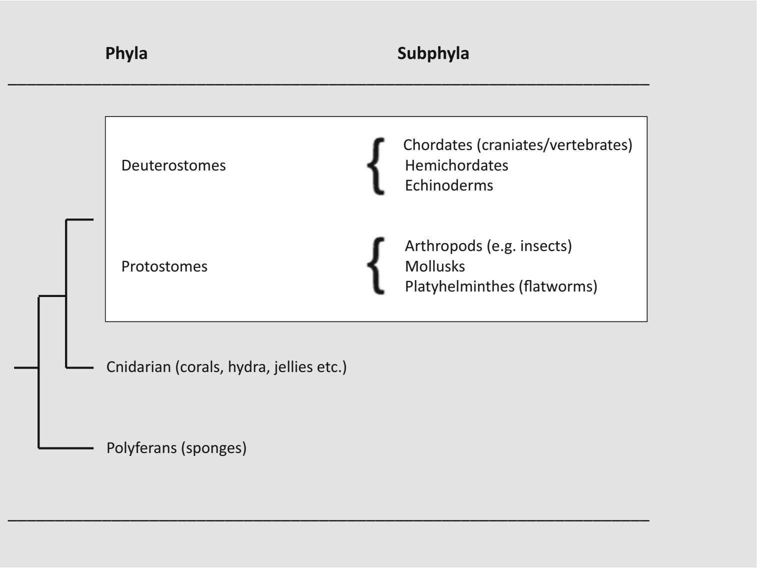

Fig. 1 *A rough sketch of early metazoan phylogeny*

bilaterals go back at least 550 million years, and in this group we find the earliest appearance of a central nervous system organized around a massed concentration of nerve cells in the front called the *cephalic ganglion*, or "archaic brain". Experiments with decerebrated worms have shown that such worms retain an ability for both normal swimming and normal crawling but these two behaviors are now no longer integrated into the normal sequence, and the overall movement patterns become irregular and uncoordinated. Neither do decerebrated worms display the normal retraction response to mechanical stimulation and they fail to show satiety even when their gut is completely full. At this level of evolution of the nervous system, it is obvious to most observers that the animals exhibit genuine 'behavioral choice' or 'action selection'. Expressed in semiotic terms, we might say that the semiotic freedom is here at the brink to passing from the phylogenetic level to the ontogenetic level: choices made by bacteria, fungi, plants, sponges, and cnidarian animals are still mostly if not completely "premeditated" at the level of the lineage (as an evolving unit) to which they belong, whereas even the simplest bilaterian organisms seem to possess some minimal freedom from evolutionary predetermination, in the sense that these animals may interpret important cues (sign vehicles) according to the situated context.

Interestingly, Koopowitz and Keenan suggest that bilateral symmetry as such may have been the prime feature that necessitated the evolution of a brain: "Bilateral symmetry required that the right-hand side knew what was happening on the left, and vice versa. In effect, with the advent of bilateral symmetry, the evolution of the brain was necessary for the coordination of disparate peripherally-based reflexes. This was of prime importance in preventing the two sides from engaging in contradictory activities" (Koopewitz and Keenan 1982, 78).

An illustrative case of contradicting behavior, in the sense which Koopowitz and Keenan are speaking about here, was observed by the German embryologist Nobel laureate Hans Spemann when as a young embryologist he constructed a Siamese twin salamander with two heads, one trunk and one tail. When these animals came to the stage of feeding it was most remarkable to see how once one head and later the other caught a small crustacean, and how then the food moved through the separate foreguts to the joint posterior intestine. Although it was of no importance for the well-being of this strange double creature which head caught the food Spemann nevertheless observed how one head pushed the other away with its forelegs (Spemann 1938).

Normally the “egotism” of animals does not strike us as odd at all. But the case of an animal possessing two opposed “egotisms” immediately shows how much in need of an explanation this property is. By the very failure to serve its ordinary purpose in these poor creatures, we are directed to the question of how agency brings about a holistically functioning “egotism” in normal multicellular organisms (Hoffmeyer 2006). If Koopowitz and Keenan are right, this was exactly the job which the first brains evolved to solve.

Here we may face a very general feature in the evolution of semiotic freedom. Sharply stated, the thing is that there are so many more ways to be intelligent than there are ways to be stupid. With increasing semiotic sophistication also comes increased inventiveness and learning capacity, which again means increased accumulation of individual experiences during ontogeny. Semiotic freedom therefore implies an increased range of potential response patterns available to a species, but also, at the same time, an increased risk of contradictory or mutually counterproductive behavior patterns. The increased richness of possibilities will put stronger selective pressures for evolving solutions to the coordination problem, and such solutions very likely will consist in modifications of brain architecture. A potentially self-amplifying dynamics is involved here: smarter organization of the brain will tend to support the development of richer behavior patterns. The challenge posed by contradictory behavior may thus well have been an important motor behind the progressive evolution of cognitive capacities and semiotic freedom.

Active Information Gathering

From a semiotic point of view the development of brains probably more than anything else demarcates a separation between the animal form of cognition and the protocognitive capacities of plants and fungi. Brains obviously not only helped animal species to coordinate the movements of different body parts, they also gradually evolved to possess the necessary sophistication to be of help in safeguarding a range of other and more complex coordinative tasks. Essential to this new agenda for organismic activity was the internalization of the surroundings of an organism into its internal phenomenal world, or in other words, the appearance of environmental mappings. This constitutes a most important step in semiotic freedom: *the single organism now becomes able to displace itself according to the double determination of its inner needs and its outer sensations.* In an inverted sense, animal cognition forms an enhanced version of plant phenotypic plasticity: here, the very location of the organism is subject to ongoing variation and negotiation with the surroundings. As von Uexküll noted, this step requires an increase in the internal complexity of perception signs:

“As soon as body profiles appear as perception-signs, the picture of the perception-world changes thoroughly, for now relative positions in space begin to play a decisive role. [...] Only when spatial differences appear within the perception-sign itself you may talk about a higher stage of perception-world. The presupposition for the existence of objects in the perception-world of an animal is provided by the ability of the animal to construct its own functional rules for action" (von Uexküll 1928, 189, our translation).

The ability of the organism to orient itself in the surroundings requires integrated perceptions recording spatial differences.

In single-cell animals, the direction of movement is informed by simple signs without any degree of full or more integrated perception of the surroundings; in early organisms equipped with a CNS, evolution makes different aspects of such integrated perception possible:

1) the integration of subsequent perceptions of the same object or event from different viewpoints during the trajectory of the organism;
2) the integration of different sense-modality perceptions (vision, hearing, smell, taste, touch, electro communication, etc. of the same object or event);
3) the evolution of moveable sense organs to facilitate quick perception-action cycles permitting the focusing of attention on selected features of the environment, speeding up information gathering;
4) the integration of maps of the surroundings, more extended than the single situation, making possible the situating of the organism itself in the map;
5) recognition of conspecifics and individuals from biologically relevant species (predator, prey, competitors, etc.);
6) as indicated by Uexküll, this also makes possible the appearance of neutral objects, not immediately relevant for organismic needs, in the surroundings of the animal - objects whose affordances offer a new degree of semiotic freedom because the organism may now ontogenetically learn to deal with them, and in some cases, combine them;
7) the ability to autonomize the anticipation aspect of all cognition into imaginary scenarios of immediate future events, guiding action;

The evolution of such capabilities forms an enormous field from simple cnidarians and bilaterals to the complicated semiotic capabilities of octopuses, insects, and vertebrates, and will probably require subdivision into several specific semiotic steps. Active information gathering, of course, is closely related to the notion of individual ontogenetic learning.

Collaboration and Deception

The bilaterians are divided into two major groups, the *protostomes* and the *deuterostomes* which, as can be seen from Fig. 1, roughly correspond to our everyday separation of animals into invertebrates and vertebrates. The flatworms belong to the protostomes whereas we, the vertebrates, are descendants from the deuterostomes. It is presently not clear how far back we need to go in order to find a common ancestor to these two major groups, but the best bet seems to be a 555 million years old fossil animal known as *Kimberella*. The cognitive capacities of fossilized animals are of course not easy to determine, but Kimberella most likely would not have been any smarter than present day flatworms. Since many invertebrate species - especially arthropods (insects) and cephalopods (e.g. octopus) - are known to have quite well-developed brains, e.g. an octopus may have as many as 168 million neurons in its brain, evolution of complex brains must have occurred independently in the two lines. This is further supported by the fact that while all vertebrate brains share a common underlying form, invertebrate brains deviate so much from the vertebrate pattern that it seems hard to make meaningful comparisons.

The surprisingly sophisticated semiotics of insect life as exemplified by fireflies was analyzed by El-Hani et al. (2010). Fireflies have species-specific flash patterns functioning as mating signals. Typically, the female sits perched in the grass signaling while the flying male responds and approaches her. This general pattern has been exploited, however, by the predatory species *Photuris* which is able to imitate the flash patterns of other firefly species. Thus, when a female *Photuris* sees an approaching male of another species, such as a *Photinus* male, she is able to imitate the mating signal of that species, luring the lovesick male to her location where she devours him. Such deception, of course, functions as a selection pressure on the evolution of new, more refined flashing patterns, and the exhibition of a variety of such patterns may be due to an “arms race” between fireflies species, thus pushing semiotic evolution ahead. Even if the signaling process takes place in the here-and-now of ontogenetic time, the evolution of the signal codes used, however, takes place on a phylogenetic timescale: the learning of new such codes occurs during the trial-and-error process of evolution, not in ontogenetic learning.

A central issue here is the recognition of such coding in phylogenetic time as establishing semiotic habits. There is a widespread tendency to admit the semiotic character of ontogenetically learned patterns but to refuse the same status to phylogenetically established patterns. To us, this is merely a timescale difference (oftentimes a very considerable such difference, that is true), but not a difference in kind. Many semiotic abilities involve the integration of both phylo- and ontogenetic aspects. Thus, von Frisch’s (1967) famous “waggle dance” indicating the direction and distance of nectar-rich flowers to fellow bees in the hive is an innate coding indeed - but nonetheless semiotic and communicative (a high flexibility of the sign, involving individually acquired information about landscape structure and flower positions, is required for its efficiency). Such innate signals are widespread in the insect world with both collaborative and deceptive functions, even across species. As an example may serve the black-and-yellow striping in insects recognized as meaning “danger” across many species, also including non-insects like human beings - and even allowing certain harmless flies to display the pattern deceptively in order to scare away predators. Ontogenetically established semiotic behavior based on individual learning and flexibility, however, is also found in many insects such as honey bees able to navigate in a landscape based on mental maps involving particular local landmarks (Gould 2002).

Even if firefly signaling is coded in evolutionary time, the crucial sign exchange takes place in the brief lifetime of single individuals. It thus forms an example of the important evolution of semiotic capabilities from serving cognitive aims primarily to serving also communicative aims. Importantly, the firefly case involves intraspecies as well as interspecies communication. It is difficult to establish the first occurrence of such communication. As soon as individuals of a species appear as an object in the Umwelt of other individuals, the possibility of evolving that appearance for communicative means is established. This appearance may be shaped in order to communicate stable signs (like the black-and-yellow striping) or more timebound signs (like firefly flashing). The important thing is that the cognitive ability in individual organisms now makes it possible for other individuals to try to influence that cognition. While simple, pre-communicative cognition enables an organism to establish some simple environmental fact (is there sugar around?), the semiotic aspects of such behavior lie hidden in the perception-action cycles of the organism. As soon as communication enters the game, explicit signs make their appearance with all the aspects of attention-directing in a proto-public space of many individual organisms.

While the capacity to influence cognitive functions of other organisms is of course a tremendous tool for deception it may also be a tool for cooperative action as is seen in the sophisticated semiotic interactions controlling colony behavior in social insects.

Learning and Social Intelligence

In order to locate the origin of consiousness, we will probably have to follow further the vertebrate line, the *Chordates*. Vertebrates, however, cannot be linearly ordered in a simple series. Thus mammals diverged from the common reptilian ancestor some 300 million years ago, while birds only parted from dinosaurs 150 million years ago. The traditional ranking of vertebrate groups according to supposed cognitive abilities put fish at the bottom followed by amphibians, reptiles, birds, mammals in that order, and with humans at the top. Although this scheme accords with data on brain complexity it should be taken as a very rough approximation only. Some bird species, e.g. parrots and corvidae, are able to handle complex tasks that may be well out of reach for many mammalian species and, in general, the sheer variety of kinds of cognitive skills exhibited by different species precludes any ranking of major groups after a linear scale.

Fish are by number the most successful of the major vertebrate groups.Traditionally, it has been supposed that fish orientation and migration were to a large extent genetically hardwired. But, as pointed out by Odling-Smee and Braithwaite (2003), in aquatic environments, the physical landscape as well as biological important locations will be subject to varying degrees of change, favoring an ability to learn and they cite evidence from many sources showing that many fish species possess spatial as well as temporal memory and exert a behavioral flexibility reflecting their ability to learn during ontogeny. The cognitive skills of fish are indeed quite impressive, and Bshary et al. even claimed in a recent review that differences among vertebrates (apart from humans) in cognitive skills are mostly differences of degree, not of kind: “We are aware of only one experimentally shown qualitative difference in mechanisms between primates and fish, and this difference is the ability to imitate” (Bshary et al. 2002, 9). If learning is something like *a capacity for modifying one’s responsive predispositions and align them to the challenges posed by the particularities of one’s environment*, and if we suppose that the cognitive capacities of modern fish species have not changed too much since ray-finned fish first appeared, then advanced learning skills have been a part of life on Earth for more than 400 million years.

For illustration, let us here consider Odling-Smee and Braithwaite (2003) of orientation behavior in three-spined sticklebacks showing that sticklebacks originating from a pond tended to adopt a different strategy from sticklebacks of the same species originating in rivers when the task was to find a goal in a maze. Sticklebacks from both sources were trained to locate a goal in one arm of a T-maze either by learning a turn-direction out of the start box, or by using plant landmarks as signposts indicating the rewarded end. Pond fish used both turn directions and plant landmarks, while river fish showed a strong preference for using turn direction only. The obvious explanation is that sticklebacks living in fast-flowing water would have learnt early on not to rely on local features of the microhabitat that might quickly change, and the experiment thus shows that "orientation behavior may be adapted to specific habitat conditions" (Odling-Smee Odling-Smee and Braithwaite 2003, 240).

Many fish species also exhibit behaviors that seem to indicate the presence of social intelligence. The most conspicuous example here is probably observed in species of cleaner fish that get their livelihood by eating and thus removing parasites from other fish called clients. In addition to the parasites the cleaner however also likes to eat the more nutritious body mucus of their clients which, understandably, maddens the client fish which may visibly "jolt" and dart off when cleaners bite them. There then develops a trade-off situation between cleaners and clients in which the clients attempt to avoid cleaners that have previously cheated upon them by eating mucus instead of parasites or - more remarkably perhaps - which have been observed cheating on others (Bshary et al. 2002). Full-time cleaners such as the cleaner wrasse *Labroides dimidiatus* may have about 2.300 interactions per day with clients belonging to over 100 different species (Grutter 1996). Bshary et al. lists a number of behaviors found in cleaners and clients that may be likened to behaviors more usually observed in primates: categorization, cheating, punishment, manipulation through tactile stimulation, and so-called altruism. Thus cleaners can categorize their 100-or-so client species into types that may be cheated and types that are not so prone to cheating. Clients, on the other hand, may 'punish' (inflict expenses upon) individual cleaners, which would seem to imply an amount of individual recognition (probably by scent).

Sentience

When did animals develop sentience? As always when evolution is concerned there is no distinct event where it happened but rather a gradual change towards more and more 'sentience-like' abilities. As in the case of consciousness, the issue is complicated by the fact that we have no assured third-person methodology to establish the presence of sentience with certainty. Since at least some modern ray-fins, as we just saw, exhibit behaviors such as cheating and punishment they must be capable of some individual recognition. Is this possible without there also being a kind of sentience? The answer will depend on how sentience is defined, of course. We shall prefer here to use the term in a more-or-less sense, as a property that has something to do with *mapping of an experience on feelings*, where feelings are understood as "mentally processed emotions" (the evolutionary motive for emotions, supposedly, being the optimization of the connection from perception to action). While keeping open the question of sentience in fish we shall briefly consider the evidence for occurrence of sentience in reptiles.

Cognitive abilities of amphibians or reptiles have not been much studied and most of the earlier studies found little evidence of impressive cognitive skills, but more recent studies have shown that many reptile species are indeed capable of learning things like escape and migration routes, foraging behavior, and recognition of individual conspecifics or keepers (Evans et al. 2008).

Of particular interest in this context is the question of whether reptiles may sometimes engage in playful behavior as seen in mammals and birds. Play behavior is notoriously difficult to define, but we shall use the concept as referring to activities that are voluntary, intrinsically motivated and not connected with any immediate utility or material interests. In addition to these criteria play is also, and importantly, associated with pleasure, but for obvious reasons we cannot with certainty evaluate the presence in an animal of a subjective state like pleasure. Moreover, playful behavior is often associated with individual learning in the practicing of skills not immediately necessitated. In so-called object play, presumably the simplest kind of play, an object such as a basketball is manipulated for no other immediate purpose than the manipulation itself, and even though it is often assumed that play behavior does indeed prepare the player, usually a youngster, for the tasks of adult life, the play behavior presupposes an unpredictable context-framed interaction between the animal and object that cannot possibly occur in the absence of an experiential component, and this experiential component will have to be pleasurable for the animal to pursue the activity or, in other words, the experiential component maps upon feelings.

There are a couple of anecdotal reports on play in reptiles but only few controlled studies. Perhaps the most persuasive example concerns the play behavior observed in an adult, long-term captive Nile soft-shelled turtle, *Trionyx triunguis* (Burghardt et al. 1996). It is a well-known fact that stereotyped and maladapted behavior in captive animals may be avoided by environmental enrichment, and keepers of the Washington D.C. zoo exemplar of this particular turtle had noticed that a changed feeding schedule, implying that the turtle would now have to engage in the highly energetic fishing behavior, had lead to a decline in the severity of self-inflicted injuries. For several years the turtle was provided with objects such as balls, sticks, and hoses in an attempt to reduce self-mutilation behavior, and the turtle spent considerable time with the objects.

According to Gordon Burghardt, the relative absence of play in ectothermic reptiles may be explained by a lack of parental care, efficient metabolism, endothermy, and arousal (*ibid*) – factors that are known to be important determinants for the presence of play in mammals. The fact that vigorous playful behavior in a member of an ancient reptilian lineage may nevertheless occur, as we have just seen, indicates that, in the right circumstances, object play can be performed by reptiles.

One speculative idea that suggests itself when evaluating the implications of the observed “play” is that sentience in reptiles comes by glimpses, to die out again as the stimulus disappears. This might explain the very sporadic character of playfulness in reptiles. Or, one might perhaps even generalize this conception to the effect that sentience is never permanent but is always experienced rather in shorter or longer intervals and with more or less intensity. The fraction of time an organism will spend in a sentient state of mind is one possible among many other dimensions that together define the semiotic freedom of a species. It should be noticed, of course, that we cannot even know for sure that our own sentience is continuously present during waking hours, since it might easily stay away for extended periods without our recognition. How should we possibly know?

Consciousness

Consciousness[10] probably evolved somewhere along the line of CNS-equipped animals, certainly somewhere in the vertebrate line; whether it is also present to some degree in particularly "brainy" species of invertebrates - such as e.g. octopuses - is as yet a matter of speculation. In its human form, consciousness supports a long series of different processes and scaffolds perception, cognition, reasoning, categorization, action, communication, language, and a host of other abilities.

One of us has suggested that consciousness, as an iconic inner experience, works as a holistic marker focusing the enormous diversity of ongoing calculations upon a single path of action (Hoffmeyer 2006). A moving animal in a moving world is confronted with a perpetual need for making split second choices of behavior. Such choices evidently will serve survival the best if they are based on some kind of anticipatory calculation which integrates inner body parameters such as emotional states, fatigue, hunger, memory into a range of external parameters as registered by the sense organs.

As long as the animal has a survival strategy based on simple activity schemes in a predictable space of challenges these behavioral decisions may well be accounted for in terms of instinctive patterns of sensomotoric reflex circles. Such a direct connection between a stimulus and a corresponding behavioral act is perhaps what takes place in the snake so that its Umwelt indeed contains no mice, but only things to be searched for, things to be stroked, and things for swallowing. In animals dealing with more complex patterns of challenges, a direct coupling of stimulus and behavior is no longer sufficiently flexible. Instead, the brained body as a holistic intentional unity must now make decisions based on split-second evaluations of unforeseeable events. Judging from the efficiency of modern computer programming in producing virtual realities, there is probably no a priori reason why brains could not have solved this problem by a sophisticated elaboration of the reflex circuit principle. But while computers are designed to obey strategies decided by the programmer, organisms had to develop designs obeying their own interests; and here the computer analogy may mislead us. Organisms must integrate their life project into their calculations, and the body as flesh and blood, therefore must, from the very beginning, be part of the anticipatory and inventive brain models they produce. This might well be the reason why evolution "invented" the trick of producing an experienced holistic virtual reality, an internal icon more or less isomorphic in its properties with those parts of the real world that the animal could not safely ignore. The exciting (threatening, attractive, etc.) aspects of the outer world in this way became internalized as inner threats, attractions, etc., thereby assuring the necessary immediate emotional bias in all choices of action. The hard problem was not just to calculate the path of action but to make sure that this path of action was the most relevant given the esoteric life project of the individual animal, and this is the point where the emotional apparatus must be brought to play. The iconic inner experience in this scenario works as a holistic marker focusing the enormous diversity of calculations upon a single path of action.

It is our hypothesis that the function of consciousness is basically to enhance the speed, precision, and efficiency of processes otherwise already realized by the nervous,

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[10] Whereby we mean something like "any mental state (x) about which it is meaningful to ask the question "how is it like to experience (x)?"

motor or metabolic systems or by social action on herd level (such as all of the above with the exception of language in its human shape). As consciousness thus serves to support a long series of functions, it is as yet a matter of speculation which such function was the first to call consciousness self-control to its aid during the process of evolution. Most probably, consciousness took its beginning as the support of one such function and subsequently, by exaptation, spread its support to a host of other semiotic and cognitive functions as well. One basic function might be the hypothetical testing in the imagination of an anticipation decoupled from actual action, thus constituting a fictive trial-and-error level in addition to that of ontogenetic learning in higher animals, and that of phylogenetic adaptation in all organisms. As Millikan (2006) says, it is evidently safer to experiment with a dangerous action in imagination than performing that action in reality, and the latter, if chosen, may profit from a preceding imaginary test of some of the action possibilities at hand - giving the possession of consciousness a high selection value.[11]

The Conceptual Framework for Biosemiotic Evolution

Many different ideas have been attempted to account for the increasing sophistication of biosemiotic processes during evolution, and it is indeed our contention that a substantial part of the problem is conceptual. Too many crude conceptual dualisms are in play, resulting in the classic dualist pineal-gland-kind of transition problems. A simple distinction, for instance, between animal signals and full-blown symbol-based conscious communication in humans is often encountered (in different guises such as distinctions between mechanical reaction and mental action, between association and rationality, between prelinguistic and linguistic reasoning, etc.), and often a whole bundle of such characteristics is assumed to appear evolutionarily simultaneously with the transition from the simpler to the more complex side of the dualism (mental representation, logic, semiotics, language, consciousness, etc.). As against such a viewpoint, an evolutionary history with the gradual appearance of semiotic and cognitive capabilities forms an alternative. A tempting idea here is to take large phases of biosemiotic evolution to conform with the Peircean triad of sign types icon-index-symbol so that a simpler iconic phase should precede a more complicated indexical phase to be followed by a human, symbolic phase. Such an idea, however, does not conform to the basic definition of icons, indices, and symbols in Peirce's thinking where pure icons and indices are limit phenomena and semiotic processes typically include both iconic, indexical, and symbolic aspects. As a guideline, we take the observation that even the most simple semiotic phenomenon recorded here, that of molecular recognition, potentially guides the organism towards behaviors related to the actual state of affairs as indicated by the sign used. But this implies that even very simple sign processes always are truth related; that the ability of informing an organism about aspects of environmental states-of-affairs, such as they truly are, forms the most basic *raison-d'ê tre* for signs in the first place.

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[11] We do not address here the further semiotic step distinguishing human semiotic capabilities from those of other primates. One of us has argued a good candidate for that is "hypostatic abstraction", that is, the ability of creating new thought objects on the basis of first-order objects - facilitating increasing self-control of thought and ensuing action (Stjernfelt 2014, ch. 6).

Biologically efficient signs must be able to inform biological systems (tissues, organs, organisms etc.) about true states-of-affairs. A pure icon, taken in isolation, denotes no more than the virtual existence of a large range of merely possible objects similar to it, just like a pure index denotes nothing more than the here-and-now presence of something as yet undescribed: none of these offers, in themselves, sufficient content to inform an organism truthfully. In human beings signs stating truths are those that express propositions - often, but not always, accompanied by conscious consent to the fact claimed, and often, but not always, expressed in linguistically shaped sentences. Lacking human semiotic possibilities, most other organisms are unable to articulate propositions explicitly, but given the central biological task of informing truthfully, biosemiotic signs must be taken to form proto-propositions undertaking that task. Peirce's notion of proposition, "Dicisign", gives the idea of the general structure of proto-propositions. They have a dual Subject-Predicate structure, involving the indication of an object (S) on the one hand and a description (P) of that object on the other. The former has the function of an index, pointing out an object or set of objects; the latter claims a quality or relation holding for those objects. Linguistic examples are simple sentences like "That (S) is blue (P)", but examples seamlessly comprise language-image compounds like pictures with captions or wholly non-linguistic propositions like gesture propositions where both the S and P parts are given by gestural means (like pointing to a person and rotating your index finger while pointing to your head to say "He's crazy").

These examples are all from human semiotics, but as Hurford (2007) argues, higher animals must have the ability to assess proto-propositions - to realize that this and that is the case in their environment. Hurford has a strong argument pointing to the fact that the split between a dorsal and a ventral stream in visual perception of higher animals functionally realizes the S-P analysis of propositions: in visual processing, e.g., the dorsal stream gives a spatiotemporal analysis of the surroundings ("Where"), enabling the organism to perform precise motor behavior related to the location and movement of objects, while the ventral stream provides a categorization of objects and events ("What/How"). The integration of the Where and the What information in perception thus realizes the S-P structure of propositions making it possible for higher animals to realize propositional content in perception (equivalent to "This figure over there is a predator" or "This ball is red") without expressing it verbally or otherwise than in ensuing action.

Our claim now is that this dual S-P structure of propositions forms the basic biosemiotic sign all from the very beginning, the sign's S part constituted by the insistency of its spatio-temporal presence while the P part is constituted by the repeatable quality or relation characterizing the object thus deemed present. As S and P involve indices and icons, respectively, both of these sign types are thus involved from the very beginning of semiosis.[12]

It should be emphasized, that this does not imply any ascription of *mental* representation of a propositional kind to simple organisms. As discussed through this paper, the ability to make explicit mental representations probably only occurs somewhere in

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[12] Our rejection of a purely iconic phase in evolution does not imply, thus, a rejection of hypotheses like Donald's of a mimetic phase or Tomasello's of a gestural phase in human cognition as a prerequisite to language; both mimesis and gestures are able to express proto-propositions.

the vertebrate lineage (with the possible exception of octopuses). But our contention is that semiotically supported cognition forms a central feature of life all from the very beginning. Already in single-cell organisms, behavior aided by molecular recognition displays, in germ form, the S-P duality of proto-propositions. In *E. coli* chasing carbohydrates, the partial surface shape of the molecule is the P meaning "sugar", and the spatio-temporal localization of that shape plays the S role so that the signal interpretation of the organism is equivalent to the proposition "In this direction (S) there is sugar (P)".[13] The ensuing action - swimming upstream in the carbohydrate gradient - then forms the conclusion in a basic belief-desire argument. Thus, the loop of proto-propositions guiding behavior is taken to form the basis of biosemiotic evolution, this evolution then constituting the ongoing sophistication, refinement, subdivision, articulation, and, finally, conscious access and control of such propositions. This loop is initially holophrastic - its different parts and aspects are only analytically accessible, and initially, there is little or no freedom on the part of the organism to select or highlight different such parts. Semiotic evolution then is very much framed through the subdivision, articulation and differentiation into a range of autonomous parts and aspects of the originally holophrastic loop in a step by step process leading to the attainment of higher degrees of semiotic freedom, higher degrees of combinatorial complexity, and higher degrees of selection between articulate semiotic possibilities in cognition, action, and communication.

An important step is that from cognition to communication discussed above: In the former, the dicisign remains confined to the cognitive process guiding organismic behavior in the environment; with the appearance of communication, the propositional structure of the dicisign - its duality of indexically directing attention to an object and iconically describing it - comes out in the open, so to speak, and the two aspects may be separated as different aspects of the sign. In the firefly example discussed earlier, the indexical aspect is thus the flashing light, efficiently calling attention to the precise location of the communicator, while the flash pattern forms the iconical aspect, characterizing the species to which the flashing individual (claims to) belong. Thus, the gradual isolation of indices (the direction of the waggle dance in bees, the flashing in fireflies, the pointing gesture or pronouns in humans) forms one example of this sophistication; the distinction between object types and their different typical iconical predicates (the look, smell, sound, etc. of one and the same predator or prey) forms another. In that sense, the quasi-autonomy of subject indices and predicate icons is a higher-level result of evolution rather than its beginning point. And thus, the gradual articulation of action and communication syntax makes possible an increase in the combinatorics of semiotic possibilities. Therefore, *the evolution of biosemiotic capabilities does not take the form of the ongoing composition of simple signs* (*icons*, *indices*, *signals*, etc.) *into composite wholes. Rather*, *it takes the shape of the increasing subdivision and control of a primitive*, *holophrastic perception-action circuit already committed to proto-propositions guiding action reliably.* Compositionality, then, is not the motor of biosemiotic evolution. There are no simple signs to begin with which may then be composed into more complex signs. Compositionality is rather one of the

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[13] Or: "Swim in this direction (S), there is sugar (P)"; biosemiotic proto-propositions hardly make the distinction between indicative and imperative and are most often both at the same time; they describe a state-of-affairs which immediately initiates action (Millikan 2006)

sophisticated *achievements* of the process of semiotic evolution, enhancing semiotic freedom and reaching its provisional peak in the rich combination possibilities of human thought and language.

In this paper, we have attempted to the initial charting of some of the important steps in that evolutionary process.

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