Natural or Internal Selection? The Case of Canalization in Complex Evolutionary Systems

Alexander Riegler*
Vrije Universiteit Brussel

Keywords
Canalization, cognition, complexity, epigenesis, evolution, progress, selection

Abstract Using biological examples and theoretical arguments, the case is presented for extending the notion of natural selection to include internal selection in order to account for the evolution of complex systems. It is suggested that we take into consideration internal factors that arise from the hierarchical dynamics of complex systems. In addition to environmental selection, it is argued, decisive constraints are created by the system itself. Canalization is shown to be an indispensable ingredient for evolutionary processes in both biological and artificial complex systems. In artificial life systems canalization is not only an instrument for controlling complexity, it also increases the speed and stability of evolutionary processes.

1 Introduction

> Our Darwinian mission is, after all, to explain the diversity of life—the myriad fascinating changes in shape, size, physiology, behavior, and ecology. [24, p. 199]

The current synthetic theory of evolution features essentially two main factors in evolution: variation due to *genetic* mutation, and elimination of *phenotypic* variants by environmental selection. This paradigm has been shaped over several decades. Despite its many layers, the core of evolutionary theory, in which genetic variation and phenotypic selection oppose each other, has remained simple. This is thought to be the basic engine that drives evolution.

However, this account of evolution has become the subject of criticism because it says little about *how* variations occur (e.g., [21, 23, 24, 38, 41]). All it says is that once they have emerged, their respective fitness will be judged by selection ("Nature selects for outcomes" [32]); it remains silent with regard to how variations are created ("the origin of species—Darwin's problem—remains unsolved" [22]).

Let us pick the analogy of André Ariew ([3], after [49]) to pinpoint what is missing. The analogy asks us to imagine that entrance to a school requires that individuals be able to read at a third grade level. Based on this (fitness) criterion, some students are admitted while others do not pass and so are excluded. The specification of such a selection process explains why the class contains students capable of reading at the third grade level. However, it cannot explain how the students managed to get there. Some students may have been taught reading at an early age by their parents, others may

---

* Leo Apostel Center for Interdisciplinary Studies, Vrije Universiteit Brussel, Krijgskundestraat 33, B-1160 Brussels, Belgium. E-mail: ariegler@vub.ac.be

have taken some pills, and still others may have developed their reading faculty despite unfavorable circumstances in their parents' home. In other words, we have a static description of a certain state of affairs, but no clue as to the dynamic aspects by which these results have been achieved.

The standard assumption in evolutionary theory is that variation comes about through mutations. But how can the book of nature be written by trial-and-error processes alone? Since the synthetic theory is based on the population-genetic approach, it views evolution as change in the genetic composition in a population and is therefore concerned with microevolution, that is, with diversity within a species that gives rise to varieties and races [21]. By extrapolation it is assumed that the origin of genuinely new species, that is, macroevolution, can also be adequately explained by accumulating the tiny steps of microevolutionary change.

The overall picture, of course, is tempting and compares with that of a *universal library*, that is, a collection of books written by random chance that, somewhere, includes the classical works of Shakespeare and Goethe, the intellectual insights of Plato and Kant, and so on. Similar thoughts must have had a dedicated professor in Jonathan Swift's *Gulliver's travels* ("A Voyage to Laputa") [51]. The savant has been working all his life to construct a machine by which "the most ignorant person at a reasonable charge, and with a little bodily labor, may write books in philosophy, poetry, politics, law, mathematics, and theology, without the least assistance from genius or study." It turns out that the scholar "had emptied the whole vocabulary into his frame, and made the strictest computation of the general proportion there is in books between the numbers of particles, nouns, and verbs, and other parts of speech," so that the contrivance could make through mechanical combination of all words "a complete body of all arts and sciences." A great many pages can be left unprinted by taking the relative frequency of characters in a particular language into consideration and, furthermore, the frequency of combinations of *n* letters—the "general proportion" the professor had built into his appliance. Still, nobody would start letting monkeys type on a typewriter to write all the pages of Laputa's universal book, let alone perform the drudgery of picking out the meaningful sentences. Analogously, nature's duty would be to select the comparably few phenotypes that arise from the myriads of possible genetic combinations.

How else does nature find these few phenotypes? The straightforward Lamarckian way—letting the successful phenotype directly inform the genotype of which adaptive changes would be most favorable—is not possible, due to the central dogma of molecular genetics.[1] Evolution is a blind process, albeit not a random one, as Donald Campbell [5] claims. Although targeting "inductive achievements" in general, such as creative thought and other knowledge processes, his notion of "blind variation and selective retention" applies to general evolution as well. Campbell writes: "An essential connotation of blind is that the variations emitted be independent of the environmental conditions of the occasion of their occurrence" [5, p. 381], that is, the organism itself is in charge of creating variations. This is in no contradiction to Darwin's theory. However, Darwin developed his theory *On the Origin of Species by Means of Natural Selection* long before the mechanisms of inheritance were discovered. Therefore, in addition to assuming external factors, it seems appropriate to extend the notion of *natural* selection to also include *internal* selection that prepares for the *arrival* of the fittest. Also in the economic world, from which Darwin took many ideas, "it would be disastrous for a company [...] to have to rely only upon its customers to find out whether the engine was properly put into a car or whether the cylinders are equal in size" [40, p. 362].

To sum up, the starting point of this article is the observation that despite its general success, the weakness of standard evolutionary theory is that it does not reveal anything about *how* variations occur. All it says is that once they have emerged, their respective fitness will be judged by selection. We do not learn anything about evolutionary *kinematics*, that is, about system-internal factors that create variations [16]. This becomes evident if we consider the many phenomena (discussed in Section 2.1) which are the unsettling "epicycles" of current synthetic theory of evolution, especially those examples showing that the "fittest" in the course of evolution are far from any optimal

---

[1] Weismann's doctrine, or the central dogma of molecular biology, claims that nucleic acids act as templates for the synthesis of proteins, but never the reverse [9].

solution (e.g., [23, 59]). For many this casts doubt on the assumption that evolution can bring forth the complex systems we observe in nature.

In this article I will first examine the question of whether there are directional trends towards complexity and what their mechanisms are. Based on the observation that there are simply too many complex structures that have emerged in the course of evolution without having any immediate selective advantage, I will claim that evolution could be described in terms of "garbage collecting." In order to explain observable evolutionary trends that defy external selection, I will focus on concepts such as canalization, functional interdependence, and hierarchy. As we shall see, there are factors in evolution that suggest extending the definition of evolution as a variation-and-selection process, and that give rise to directional evolutionary trends. Furthermore, I will stress that these factors not only accelerate evolution but also give evolution a strong directional bias in order to find the comparably few viable complex structures in the high-dimensional problem space. Finally I discuss the applicability of the insights gained to artificial life and to the animat approach.

2 Directional Trends in Complex Evolutionary Systems

2.1 Examples of Preserved Complex Structures without Selective Advantage

Let your fingers run over your outer ear. In most cases you will feel a small hump, the Darwin hump. It is a remnant of our mammal ancestors that still had pointed ears. Why does the pride of creation run around with such *atavisms*? Or pay a visit to the zoo, look at the giraffes, admire their long neck and how clumsy they are when bending to drink water from the ground. Their cervical vertebrae are up to 30 cm long because they have only seven of them—like almost all mammals (except for sloths and manatees), including the dolphin, whose seven vertebrae are tightly compressed because it no longer needs an elegantly moving neck. Would an engineer ever build an artificial giraffe possessing seven neck bones and call it optimized? Even a duck has more (16), let alone a swan (up to 25), or, at the extreme end of the spectrum, the extinct *Elasmosaurus* (72).

In the nineteenth century Ernst Haeckel noticed that embryos of various species display similarities during their early stages. Consequently Haeckel's (biogenetic) law [39] asserts that during the ontogenesis of individuals, phylogenetically old patterns are repeated. For example, during early embryological periods, mammals develop a complete gill circulation, although gills are completely useless for the adult in its environment. These days, it is absurd to claim that such early embryonic stages are a recapitulation of the evolutionary development within a clade. However, the impression remains very strong that animals, chosen to be the fittest by external selection, waste a considerable period of their development displaying morphological structures that they will not possess in their adulthood.

Today's horses usually walk on two toes. But there are mutations with three toes. Interestingly, the ancestor of recent horses, the fossil Eohippus, had three toes. So, while the third toe is no longer expressed in the phenotype, the information for setting up a leg of the Eohippus is still in the genotype of today's horses [41] and becomes visible in rare mutations. The same applies to cases of spectacularly strong growth of hair in humans, and other instances of *spontaneous atavisms*. Further examples of atavisms are the existence of reduced forms of nipples on human males and the coccygeal bone as the last tail vertebra.

At the beginning of the twentieth century, D'Arcy Wentworth Thompson [52] discovered that the transformation from the human skull to the skull of a chimpanzee as well as harmonious changes in the skull of horses over 60 million years in the phylogenetic tree can be described by appropriate *Cartesian transformations* (see Figure 1). Thompson noticed that by drawing a grid over a bone outline then deforming it in a particular way it was possible to map it onto another bone outline, for example, that of an ancestral form. This means that new morphological features do not appear at arbitrary positions. Rather, these transformations clearly hint at trends in the way proportions are modified over time.

The *antennapedia* mutation of *Drosophila* can be artificially triggered through a mutation of a distinctive gene so that the whole complex subsystem of its legs is developed where its antennae usually

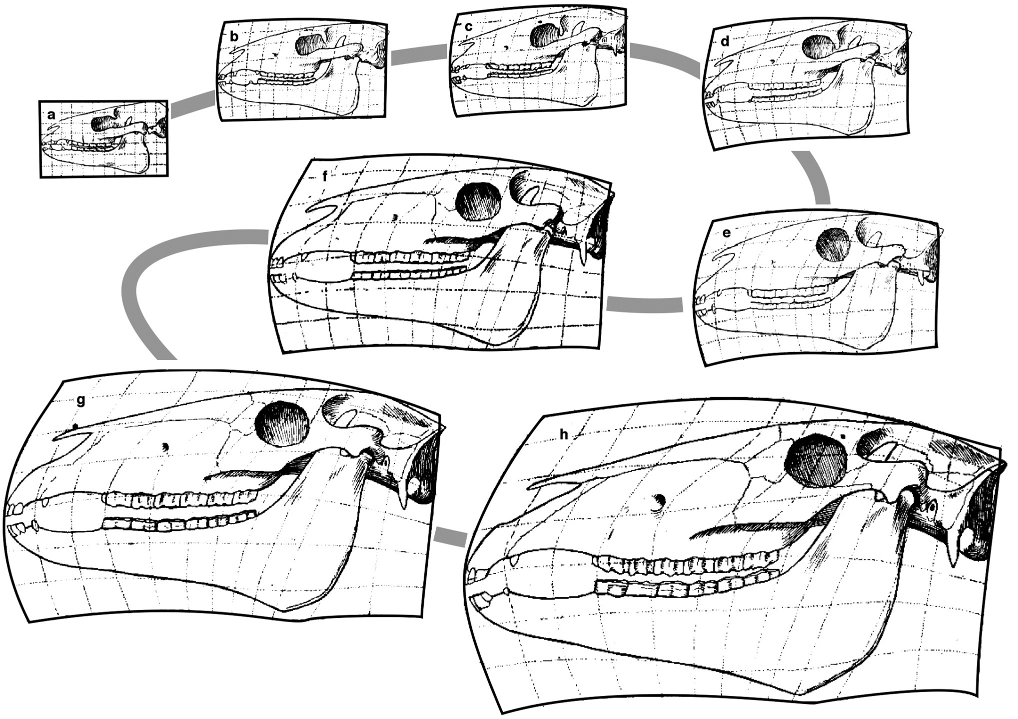

Figure 1. Cartesian transformation in evolution illustrated by the skulls of fossil (a–g) and recent horses (h). (Adapted from [52].)

are (Figure 2). To build complex substructures such as antennae and legs, an enormous number of structural genes is necessary. The *synchronous* exchange of the genes responsible for antennae with those building legs is impossible from a probability perspective. The condition causing the mutation would need to cause all involved genes to change in the same direction. How can several loci be altered to make the successful step from antenna to leg?

While some of these examples do not seem to be disadvantageous, none of them has an advantage with regard to external selection. However, external selection as a process of eliminating inviable structures is not disputed. Rather, the point is that atavisms and similar structures seem to build on other, older structures. This can be assumed to be the result of the fact that evolutionary complexification works with modular entities. So we cannot help but assume that in complex biological

Figure 2. Left: the head of a *Drosophila*. Right: the mutant *Drosophila antennapedia*. (Retrieved from http://www.biozentrum.unibas.ch/pictures/Gehring/Fly640.jpg)

systems, archaic morphological character sets and modules are stubbornly preserved in organisms and defy external selection. Under certain conditions these characters become visible, for example, as retroactively established atavisms.

Why does the ontogeny of animals take such big detours? And what can an engineering discipline such as artificial life learn from it?

2.2 Evolution as Garbage Collector

We can best explain such phenomena by assuming some kind of *historicity* in the phylogenetic tree. Rupert Riedl [40] insists that no organic state exists without tribute to its ancestry, so that all building states are subsequent series of coordinations. However, note that an animal species with degenerated organs is not necessarily simpler than its ancestral forms. As Sean Carroll [7] points out, a greater number of genes does not necessarily result in a greater number of cell types or a more complex morphology. His example is that of the worm *C. elegans*, which shares a common ancestor with the fruit fly but has lost morphological features together with *Hox* genes[2] that were present in that ancestor.

Obviously evolution is tinkering [26]; it is a clumsy and unskillful business. It heaps layers of development above each other without removing redundant older layers. If evolution were a human engineer it would carefully reconsider whether it is indeed necessary to keep the old garbage in a new emerging species or whether to shorten the ontogenetic/developmental pathways instead. Like a person trying to find his or her way in the dark, evolution seems to rely on the availability of a "memorized" sequential order of developmental components. Animal development does not seem to bother with finding new shortcuts. So, due to the historicity of the evolutionary pathways it repeatedly runs over, we cannot help but consider it canalized. Riedl [40] points out that such a *tradition principle* can be interpreted as the effect of interdependencies among building blocks (e.g., genes), which result in system-internal *canalizations*. Due to the interdependencies and hierarchical structures among genes, the freedom of variability is enormously restricted compared to the standard neo-Darwinist model of evolution. Old subsystems like the notochord (chorda dorsalis), the axial skeleton, and the innervation of the limbs, among others, are irreplaceable and carry a high functional burden (cf. also Figure 3). Therefore, it can be found in virtually all succeeding life forms. The chances of successful substitutions by (random) mutations are very low. Haeckel's law demonstrates precisely this. As old patterns serve as constituents for new ones, they must, to some extent, be repeated during ontogenesis.

Such a system of functional interdependencies among components can be extended so that it affects the genetic makeup of the entire organism. Most phenotypic features are bound to a variable number of other features. Only a few are free to develop epigenetically in any direction. Examples of such *burden-free* features are the ornaments of birds (e.g., the magnificent feathers of peacocks) and the horns of antelopes, goats, and other horn-bearing animals (*Bovidae*), which come with an extensive variation of shapes [41]. However, most other components are simply stuck in polygenic and pleiotropic dependencies.[3]

On a more abstract level, Brian Arthur [4] argues in favor of a "general law" behind the relationship between dispensable and indispensable components. He writes that "complexity tends to increase as functions and modifications are added to a system to break through limitations, handle exceptional circumstances, or adapt to a world itself more complex." Jean Carlson and John Doyle are in support of Arthur's observation. For them, the increased complexity of a system is tantamount to robustness. They argue that, for example, high-tech airplanes are not necessarily faster than more primitive airplanes and do not always have a larger payload. However, such low-tech versions "would be much less robust to component variations, failures, or fluctuations such as payload size and distribution or atmospheric conditions" [6, p. 2539]. In this sense, they claim, "robustness drives

---

[2] *Hox* genes provide the identity of particular body regions, that is, they determine where limbs and other body segments will grow.

[3] Polygeny and pleiotropy refer to the fact that many genes determine a feature and one gene determines many features, respectively. Similarly, "epistasis," refers to the dependence of the effect of a genetic substitution on the state of other loci in the genotype [25].

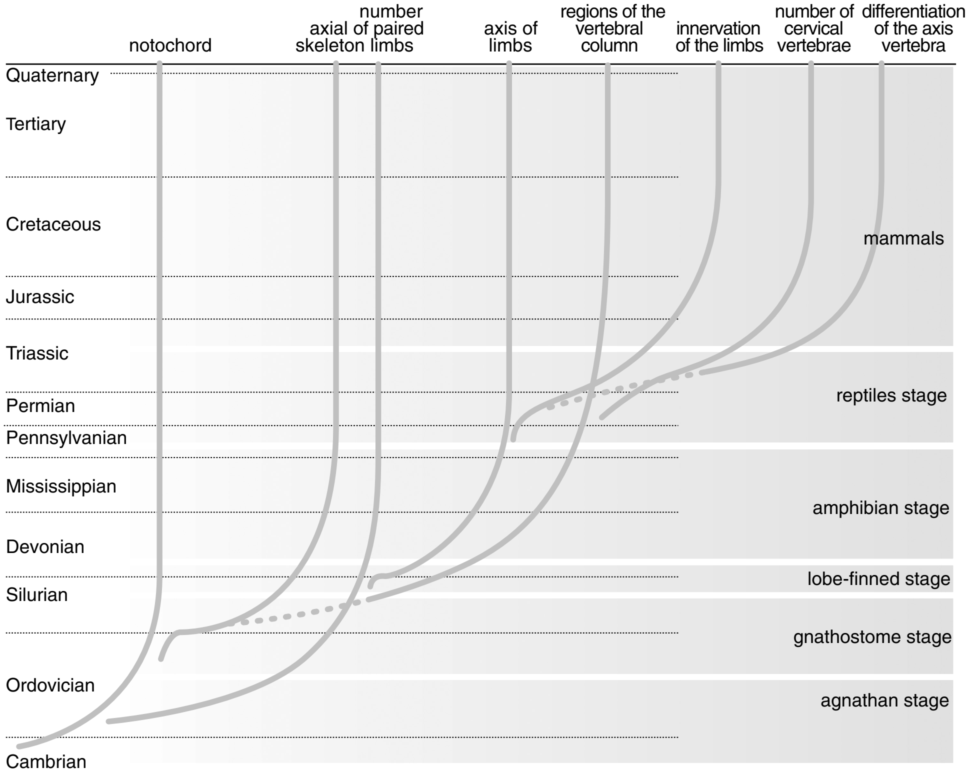

Figure 3. On evolutionary time scales, the building up of typogenetic features relies upon typostatic ones, as shown by certain characteristics of the axial skeleton and limbs in mammals and their ancestors. On the left side the earth epochs are shown, on the right the sequence of systematic groups. (After [41].)

internal complexity"—and robustness comes with increasing the number of standardized interchangeable components. We can compare this with a gigantic jigsaw puzzle in which each piece has found a place where it locks in with its neighbors. By doing so, it also expands the puzzle's border, which in turn enables the addition of further pieces. Therefore the greater the number of interlocking pieces, the larger the puzzle becomes and the more pieces can be attached.

Compounds that have been approved by their evolutionary success are treated as elementary components by compounds at higher levels. The earlier a compound appears in the history of a system, the more likely it is that many other structures are dependent on it. Ultimately, such historically grown systems arrive at a point where it is impossible to remove an older layer. Here, like a card house from which a fundamental card has been removed, the entire system would collapse.[4]

Similar considerations have been made by Peter Saunders and Mae-Wan Ho [46]. For them, while there is always a theoretical chance that a component can be replaced by another component fulfilling an analogous role, it is more likely that components are successfully added than removed. They argue that the more complex a system, the more organization it needs to survive. Consequently, it is in general much easier to add a component, which is not likely to do much harm, than to take away a component that is likely to disturb a complex network of interdependencies. However, in reply to Saunders and Ho, Carlos Castrodeza pointed out that a "random addition may *interfere* with any well connected function, making it non-operational" [8, p. 470].

---

[4] In a similar manner William Wimsatt [58, p. 198] defined his notion of "generative entrenchment": "features that arise early in development have a higher probability of being required for features that appear later [. . .] and tend to have a larger number of downstream traits depending on them."

So which perspective is right? This is exactly where *internal selection* comes into play: Systems with such interfering components are lethal mutants. They go no further than an early embryonic stage and will therefore never found a new species.

It seems that Wynne McCoy's characterization of evolution as a "process of divergence and wandering" that "*permits* the emergence of new complexity, but does not in any particular case necessitate it" [36, p. 458] is the proper way to depict the working of evolution. As long as it collects new items and stores them on top of already established features, it goes on wandering. However, removing an older item disrupts its course.

Nevertheless, reversions of development *can* occur. Looking at species with atrophic organs or senses, such as cavefish or certain newts, we cannot help but notice that the course of degeneration is the reverse of the sequence of ontogenetic formation. The reduction of eyes in cave vertebrates first dismantles the cornea. Then, the lenses are removed, and thereafter the nervous part of the optic vesicle. So the way in which the eye has been decomposed over time is the exact reverse of the evolutionary process that formed the previously fully featured eye of the animal's predecessor. The fact that the decomposition of structures is the exact reverse of their construction leads to the assumption that there are *modules*, which appear or disappear in their entirety. Without modules that build historically on each other, the vestigialization process could take any arbitrary direction rather than following a canalized sequence of ontogenetic formation—the genetic pathway [41].

To sum up, *canalization* refers to restriction of freedom when choosing a future state. A non-canalized system can at any given moment change to any other state. A highly canalized system will eventually arrive in one of several attractor states (a fixed state or a cyclic sequence of states). Internal canalization is imposed by the properties of the system itself. Since the robustness of subcomponents and modules in the construction process of a complex system drives the system's internal complexity, and canalization (as used in this article) is a measure of how much a system has become restricted in its freedom to develop in an arbitrary direction, we can conclude that canalization is a measure of its complexity.[5] In addition, since modules necessarily keep building on older structures, it appears impossible that canalization could lead the system into less complexity.

The examples and theoretical considerations make it clear that there is still a gap between observable evolutionary trends that defy advantageous selection and their genetic reasons. In the following I will describe two possible solutions for bridging this gap. The first builds on *statistical observations* regarding the mapping from genotypes onto phenotypes, the second uses the concepts of *constraints* and *canalization*.

2.3 The Statistical Explanation

Fontana and Schuster's [17, 15] statistical approach is based on insights from RNA folding. Typically there are a huge number of possibilities in folding a given sequence of RNA molecules (the genotype) into a three-dimensional shape (the phenotype). However, due to energetic tradeoffs, only one or a few of these potentialities are actualized, so that a number of sequences yield the same structure (many-to-one mapping). Fontana calls a transformation between any two sequences that does not change its shape a *neutral mutation*. This connects to the work of Motoo Kimura [27], who, in the 1960s and 1970s, developed a *neutral theory of evolution*, which conforms to the synthetic theory in most respects. The crucial exception is that changes at the molecular level are determined by mutations that are neutral with regard to selection. Small mutations and genetic recombinations, even if they are not beneficial, are stored in the genome as long as they are not disadvantageous. The changes are sufficiently small not to disturb the overall organization of the organism.

Moreover, Kimura emphasizes the pressure of mutations and genetic drift. Both lead to the emergence of neutral variants in evolution. Such molecular polymorphisms cause preadaptation. In other words, at the molecular level, framing conditions are defined permitting changes that are neutral with respect to selection. The result of a drifting genotype under an invariant phenotype is

---

[5] Although not a topic of this article, multicellularism can be considered another example in which heavy restrictions on single cells lead to an enormous step forward towards higher complexity.

that at any moment an additional mutation can suddenly change the phenotype in a discontinuous manner. This may appear to the biologist as jumping from one state of equilibrium to another.[6] Fontana argues that such abrupt changes are asymmetrical and appear directed, although selective pressure must be excluded as a possible driving cause. Selection works only at the phenotype level, it cannot possibly "know" which genotypic switches bring about a desired change. The directedness has rather *endogenous* reasons. If mutations occur randomly, then the size of the subspace occupied by neutral mutations that map to the same phenotype must be of crucial importance. The size correlates inversely with the probability that a random step will take the system to an adjacent subspace encoding a different phenotype. As a result, switching between two subspaces of different sizes is an asymmetric event. These variations in the connectivity between any two phenotypes are responsible for the phenomenon of directed evolution; therefore it does not require the presence of external selection, making it "less dependent on external contingencies than hitherto assumed" [17, p. 1454].

What Fontana and Schuster's model hides from us is how the mapping from genotype to phenotype is actually performed. The RNA model they use is probably the simplest biological example available. Mapping in (higher) organisms, however, is much more complex than RNA folding. So in order to allow for a more comprehensive perspective, we need a different approach. This second approach will recognize that the translation from the genotype to the phenotype itself is a highly complex procedure, which runs in several steps, each of which is subject to contextual influences.

2.4 Constraints and Canalization

The second solution is based on the work of Conrad Waddington in the early twentieth century. Waddington, having profound experience in embryology, was interested in unifying embryology and genetics, which he considered two sides of the same coin [20]. His interest was fueled by a landmark experiment conducted in the 1920s by Hans Spemann and Hilde Mangold. They discovered a region of the early gastrula stage amphibian embryo that, when grafted to the ventral side, directs that part of the embryo to develop as if it were dorsal. This results in an amphibian embryo with two heads and two spinal cords. In other words, this region, the *Spemann organizer*, directs the development of other parts of the embryo. In general terms, this is referred to as *induction*: an interaction between two cell groups such that one group influences the developmental fate of the other.

While most contemporaries attempted to track down possible chemical substances that could give rise to the organizer phenomenon, Waddington focused on the developmental action of genes to understand the organizer effect. As a result of his research, he introduced the concept of the *epigenetic landscape*, in which the actions and effects of genes are illustrated through the downward rolling of a ball in an inclined and slightly undulating landscape. The ball follows a path through a continuously ramifying system of valleys. These valleys, or *chreods*,[7] are synonymous with the *potential* developmental paths of the embryo. Genes and their (polygenic and pleiotropic) interactions control the shape of the slope crossings [54]. Thus, the embryonic development is canalized with respect to certain attractors: Environmental perturbations or mutations may force the ball uphill from the bottom of the valley, but as long as it does not cross the ridge to the neighboring valley, it will roll back downhill to the bottom. In other words, genetic heritage alone does not determine what the final phenotype will look like. Rather, the phenotype depends on the complex dynamics of overlapping activities of gene expression, which are referred to as the *epigenetic system*.[8]

In recent years Waddington's concept has exerted increasing influence. Susan Oyama, for example, emphasizes that chromosomal form is but one of the components, or *developmental interactants*, that participate in epigenesis together with many other interacting influences. "It is in this ontogenetic

---

[6] Cf. also the theory of punctuated equilibrium of Niels Eldridge and Stephen Gould [12], according to whom evolution consists mostly of stasis with brief periods of explosive speciation.

[7] In the more modern terminology of complexity theory the chreods are the *basins of attraction*, and the landscape would be called *basin portrait* [29].

[8] It should be noted that Waddington's landscape portrays the ontology of an individual organism as a succession of potentialities (rather than genetic determinism) where the course of time is represented by the inclination of the landscape. The analogy does not depict evolutionary dynamics on the level of populations.

crucible that form appears and is transformed, not because it is immanent in some interactants and nourished by others but because any form is created by the precise activity of the system." [38, p. 39]

The epigenetic system is considered hierarchical and highly recurrently organized. At the lowest level we find structural genes upon which layers of regulator genes have been added in the course of evolution. For example, the phenomenon of spontaneous atavism mentioned above can be accounted for as the reemergence of phylogenetically old features that do not normally become visible. In such cases, the chain of epigenetic instructions has been disturbed so that evolutionarily younger phenotypic features do not overlie the older ones [41]. Consequently, the epigenetic system must be considered a complex dynamic system in which *internal selection* emerges from the functional-systemic conditions in the organization of organisms. In this view, complex organisms are self-regulating and self-organizing systems composed of dynamic elements that define themselves through reciprocal dependencies. These dependencies significantly reduce degrees of freedom and, consequently, randomness in evolution. They introduce canalizations as the driving force behind evolutionary novelty. As a result, the efficiency of mutation and selection mechanisms in complex organisms is not given trivially (as assumed in the discussion of Saunders, Ho, McCoy, and Castrodeza): Morphological patterns and organs cannot be genetically changed independently of each other. Canalization, as the generator of evolutionary processes, must fit the overall complex *body plan* of the organism. This is the missing link in Ariew's analogy, the factor that explains *why* the students were able to join the third grade.

From this perspective, interdependencies among structural components can be held responsible for the phenomena I mentioned above. Spemann's organizer is also, as Waddington recognized several decades ago, the result of a canalizing epigenetic system. By inducing the proper trigger to "competent" tissue, regulatory genes are put to work that orchestrate the necessary structural genes in order to develop the second head. The "competence" of the tissue was Waddington's term to describe the fact that each cell carries a full set of DNA, which has the potential to develop any arbitrary body part.

2.5 Summary and Consequences

Let us summarize the arguments. What happens in evolution? External natural selection is primarily responsible for the elimination of unfit structures that are not sufficiently viable to compensate for environmental distortions; it says nothing about the creation of new structures. With regard to rudimentation, it could be misleading to make normal selection pressure responsible for the organ's elimination by assuming that the organs used limited resources that can be better spent elsewhere. Darwin [10] himself had already questioned the role of selection in eye loss in cave fishes: "As it is difficult to imagine that eyes, although useless, could be in any way injurious to animals living in darkness, I attribute their loss wholly to disuse." As Tamara Franz-Odendaal and Brian Hall [18] point out, the limited-resources explanation does not apply, for the organ's modules are intimately connected at the developmental and genetic levels.

The standard assumption of random mutations cannot account for the extremely improbable construction of organisms and their complex body parts (the "Gulliver argument"). Therefore, trends such as the development of morphological, behavioral, and cognitive competencies over millions of years must be explained in a different, internalist way. As has been shown in various examples, canalization appears to be a promising candidate. It results from the functional interdependency of subcomponents. Due to the canalization of developmental pathways, in the long term changes will only take place in a certain privileged direction, leaving the largest amount of lethal epigenetic combinations by the wayside: A great many potential but irrelevant pathways are removed. Evidently, this resembles a ratchet [44], that is, a mechanism that consists of a wheel with asymmetrically skewed teeth and a spring-loaded pawl.[9] Accumulation of developmental components lets the wheel

---

[9] The concept of ratchets has attracted great interest, largely theoretical, from diverse areas of science and technology. In evolutionary biology, Herman Muller's ratchet [37] explains that small populations are doomed to accumulate deleterious mutations. Without sexual recombination, lines would eventually go extinct because this genetic load would deteriorate the quality of the gene pool. In physics, Richard Feynman used the idea of a ratchet as a simple example of a thermal engine in order to illustrate implications of the second law of thermodynamics [14].

preferentially turn in one direction—an asymmetric, though not strictly irreversible mode. Given this perspective, evolution should be considered to be an asymmetric process and therefore a trend, rather than being equated to the highly problematic notion of progress.

The fact that almost all mammals have seven cervical vertebrae is a consequence of the synchronization of axial specification and cell division, both under control of the *Hox* gene. Such a pleiotropy of the *Hox* gene in mammals prevents evolution from changing the number of vertebrae without a simultaneous and lethal change in cell proliferation [19]. Since such couplings have not occurred in other animal species, they are free to evolve alternative numbers of cervical vertebrae. Couplings also explain why we should not believe in pigs with wings. As with other body parts, the structural information for growing wings is under the control of regulatory genes. This makes it comparably easy to grow an additional pair of wings on *Drosophila*—one mutation suffices to orchestrate an army of subordinate structural genes. However, in the case of pigs, no such wing regulation gene exists. Evolution would first need to connect them to the existing highly complex *developmental* network of tissue, bones, nerve fibers, and blood vessels. Therefore, a tremendously high number of parallel mutations would be necessary (a) to establish the structural information—this is still manageable—and (b) to ensure that the new complex structure does not interfere with the existing body plan, and that there are no pleiotropic effects similar to those of the *Hox* gene in mammals.

As it becomes more difficult to add or take away structural details, the deeper features are entrenched in the epigenetic program and evolution becomes *directed* because it has to build new structures on old ones. The resulting evolutionary ratchet received its last major modification during the Cambrian explosion of life forms some 600 million years ago. Since then, the ratchet's wheel has hardly turned at all in the opposite direction. So the dispute of Ho, Saunders, Castrodeza, et al. can only be decided if one takes into consideration at which level components can be removed from or added to the system without disturbing its overall ability to function.

The effect of this asymmetry can be shown on evolutionary time scales, where processes seem to take place in two phases: In the beginning the morphological distance quickly increments, while later the evolutionary development converges so that only a few changes occur in a species (Figure 3). The transition between the two phases marks the cessation of all changes within evolutionary development [47, 41]. Certain characters become more important because increasingly more new characters are functionally or developmentally dependent on them. In some cases such morphological patterns, which have become fixed in their phylogenetic development, receive freedom again. But this new freedom only consists of features that are based on those old patterns. Any removal or other modifications of the old features will be lethal. Therefore, only those organisms survive that embody the old structures and carry them as a burden irrespective of external influences.

The canalization view provides us with a crucial advantage over the standard perspective of evolutionary processes: Canalizations make evolution of complex structures possible in the first place. This argument is even more important for the evolution of artificial creatures. While evolutionary theory seems to be quite successful in explaining the evolution of biological systems, it can be argued that for artificial systems the time scale is too large: One cannot possibly wait four billion years to breed complex digital organisms.

One could also feel tempted to assume that by increasing the interdependency of modules the appearance of complex organisms is made less likely, simply because it reduces the number of possible pathways. This argument is based on a severe underestimation of the problem space. Complex systems are not abundant, but rather hide like the famous needle in the haystack: How many complex works of science and literature are in the universal library of Gulliver's professor? So we do not need a tool that carefully turns each straw of the haystack. Rather, we want to find the needle quickly.

The amount of acceleration becomes clear in Herbert Simon's well-known metaphor of the two watchmakers Tempus and Hora [48]. They have to build clocks consisting of 1000 parts. Unfortunately, they are interrupted in their work at random moments, causing an unfinished clock to fall apart (this corresponds to external selection). In order to cope with the annoying interruptions, Hora divides the design of a watch into subassemblies of 10 parts each so that in the worst case only 10 components fall apart. Simple calculation shows that Hora's strategy yields a tremendous advantage, with regard to the number of completed watches, compared to Tempus' linear style of working. For example, assuming a probability of $p = 10^{-2}$ results in Hora producing watches about 4000 times faster than his colleague. Simon concluded that "hierarchic systems will evolve far more quickly than nonhierarchical systems of comparable size." Furthermore, Hora's technique also introduces a direction. As Simon maintains, we don't need to assume any explicit teleological mechanism, no *causa finalis* in the sense of Aristotle, in order to account for directedness, as direction "is provided [. . .] by the stability of the complex forms, once these come into existence."

3 Application to Artificial Life

Having identified the nature and mechanisms for evolutionary processes in terms of canalized systems, we will now turn to discussing their application to artificial life. Basically, we can pinpoint two major domains of application: biologically oriented artificial life systems, and the animat approach, that is, the evolutionary (rather than designed) development of cognition [57].

3.1 Biology

To assess the usefulness of canalization for artificial life let us consider Figure 4. It depicts an artificial creature whose survival depends on the fact that it can put food into its mouth with its hand. If we assume that the organism is subject to evolutionary development (e.g., growth), it runs the risk that a mutation in a descendant's genotype could change the size r of its hand so that it is no longer able to use it to feed itself (see Figure 1b). The organism could, alternatively, grow taller while the size of its hand remained the same (Figure 1d). It is obvious that the two phenotypic features r and s should develop synchronously (Figure 1c). Such evolutionary synchronization can be achieved in a genotype that features not only structural genes (responsible for building the hand and determining the body size, respectively), but also regulatory genes that—on a higher level—combine such structural genes, creating a dynamic interplay among various levels of nested subcomponents.

Such regulatory elements are not only advantageous but also indispensable for computational settings. If p is the probability for a feature to be changed by mutation in a reproduction, then the probability of changing n features at the same time so that they stay synchronized will reduce to p^n. The more structural features have to keep in step, the more exponentially unlikely this event becomes. However, as soon as the expression of structural components is dependent on a coordinating component, the probability of changing all these components is equal to the probability for mutating the coordinator. In other words, introducing canalization into the game will be beneficial for those who want to maintain synchronization between hand and mouth. Moreover, only those systems that managed to evolve canalization were able to progress in a period that is considerably shorter than the age of our planet—a time scale that is out of the question for evolutionary algorithms in artificial life.

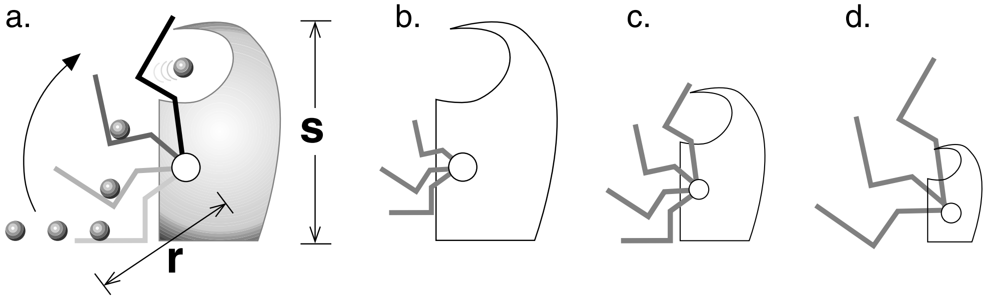

Figure 4. Interdependencies in the evolutionary development of artificial life systems.

Therefore they must not forgo the advantages of evolutionary acceleration offered by canalization. In the following these theoretical considerations are discussed on the basis of an existing ALife model.

In a series of articles, Pete Angeline and Jordan Pollack [1, 2] suggested an addition to the genetic programming paradigm [31], which can be considered as a first step in implementing epigenetic hierarchies. Angeline and Pollack introduced the *module acquisition approach* in order to organize genetic programming code segments in a hierarchical manner. Within an individual, the genetic library builder (GLiB) compresses a portion of the genotype at random time intervals, which results in the creation of a module (Figure 5). Modules are assigned a unique number and are stored in the genetic module library.

In detail, the GLiB uses the following operators:

1. The *freezing* operator freezes the values of compressed representational components such that genetic operators (e.g., mutation and crossover) cannot modify them.
2. *Atomization* or *compression* "...selects a portion of the representation, freezes it and then treats the entire compressed module as a new component of the representation." Depth compression "...extracts the subtree beginning at the randomly selected position of the program and clips off any branch exceeding a maximal depth.... When one or more subtree branches exceed the max depth...GLiB then defines the new module with the variables defined as parameters to the module."
3. *Expansion*: Since compression leads to a loss of genetic material, there is also an expansion of modules so that genetic operators can again be applied to the compressed genotype portion.

The advantage of atomization is that each compressed structure becomes a new atomic element of the representational language. Also, atomization enables an evolved abstract module to be copied and used for multiple aspects of a problem (cf. Section 3.2). So the module acquisition approach increases the expressiveness of the genetic program on the one hand and decreases its length on the other. The modules in GLiB are sequences of *structural* genes. These canalized parts of the genotype are *regulated* by the arguments in the Lisp program, which decide whether or not to execute the respective sequence in its entirety.

Despite the ingenious design of the system, two questions arise:

1. Why do the authors not apply evolution operators to compressed modules? Any change in a particular module would also modify the behavior in all those individuals that use this module.
2. Can the content of the library be considered as a kind of gene material shared by members of a population?

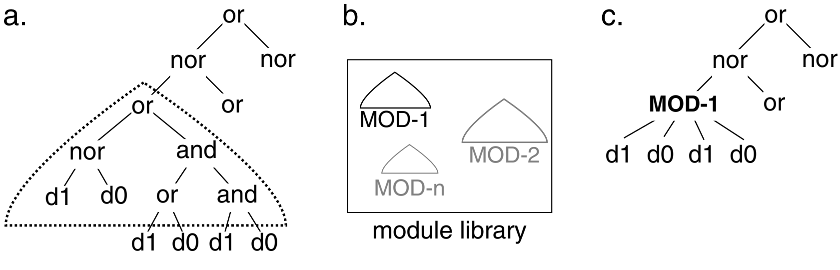

Figure 5. An example of module compression. (a) The original, uncompressed tree of a genetic Lisp program. The part covered by the triangle of a specified depth becomes compressed so that it forms the new entry MOD-1 in the module library (b) through the process of module acquisition. (c) The program and further individuals can now use MOD-1 as a new function of the genetic language. (After [28].)

Both issues concern the phylogenetic part of an individual's knowledge, or the innate knowledge from a biological point of view. If the knowledge of an individual is built with such phylogenetically inherited genotype fragments, this will perfectly implement the idea of functional burdens outlined above. Answers to these questions will be attempted below.

3.2 Animats

The animat approach is defined as the research methodology for understanding cognition and intelligence through simulation of artificial animals [57]. Building on the assumption that this approach is a viable methodology, one can expect an analogous application of what has been said so far about biological-evolutionary structures to cognition and cognitive behavior in natural and artificial systems.

By analogy to the complexity of the epigenetic system, here, too, we face an enormous combinatorial complexity, as is known from the action-selection problem [53]. Calculating the combinatorial possibilities of choosing one of n reactions in each of k situations, we end up with the unpleasant exponential number n^k of possible action sequences. From the psychological literature, however, we know that human problem solvers behave in a rather ignorant and conservative fashion, as the experiments of Karl Duncker [11] and Abraham Luchins [34] show. According to their insights, thoughts are *mechanized* and thinking is functionally fixed, that is, *canalized*, in the sense that when solving a problem, the previous experience and present stage of the solving process canalize the way solutions are sought.

To clarify the link between cognition and canalization, suppose we equip an artificial creature with a knowledge system that is composed of sets of connected production rules. Such rules consist of distinctions (A, B). The distinctions are connected in the form of elementary production rules ("if A, then B"). Both sides may consist of chains of subordinated distinctions. Learning takes place by modifying the elements of the rules, namely, by adding, dropping, and rearranging components on either side. This produces a potentially vast number of combinations. By introducing interdependencies and hierarchical arrangements, however, the evolution of these knowledge systems can be canalized in order to escape combinatorial explosion without becoming arbitrary [42].

Suppose our artificial cognitive agent acts as a predator that has to hunt down its prey. It may use visual, olfactory, and tactile senses. These three modalities combined constitute the attributes of an invariant entity, say, a mouse. However, an artificial agent does not necessarily need to integrate different senses into a coherent picture, since many successful predators in the (natural) animal kingdom do not do this either. A snake, for example, employs them sequentially: First spot the prey, then smell in which direction to strike, and finally find the attacked mouse by touch [50]. This means that if a mouse vanishes into a mouse hole, it no longer exists for a snake—which relies solely on visual impressions before striking—while a cat, for instance, remains in front of the hole and waits for the mouse to reappear. Under normal circumstances, the snake need not know the concept "mouse." It only perceives the mouse in slices of modalities. One could represent its hunting behavior in three rules:

R1: If see mouse then come closer.

R2: If close to mouse then strike.

R3: If struck then start eating.

For a snake these are merely three consecutive *rules*; for us humans (as for most mammals) they form the *concept* of a mouse. In this perspective, we can say that knowledge is a hierarchical scaffolding of rules in which rules at a higher level (i.e., concepts) are dependent on lower-level rules [42].

Now evolution made a snake a good hunter. That is, R1–R3 were *approved* by a sufficiently high rate of successful hunting each time the creature felt hungry. Thus there were good reasons for keeping this set of rules (i.e., this concept) rather than any other set of rules—they became *stable forms* [48]. The advantage is evident. From now on, the new concept can be used as an elementary component in higher-order concepts. Not only mice, but also other small animals, are potential prey for snakes. A cognitive system could find this information useful for the extension of its menu without having to reinvent the same hunting strategy for different animals.

In greater detail, the behavioral component of the artificial system should look separately at conditions and actions. Conditions are interpreted as the recognition capabilities of the system (i.e., distinctions in the above sense), whereas the "then" part specifies possible actions. In this way it is easy to assign an action strategy to different perceivable objects. Mutations do not need to change many details in parallel at the lower level in order to make such modifications—one regulatory mutation is sufficient. However, a single mutation on a lower-level component has far-reaching consequences for all rules that refer to this component and endangers the error-free execution of the regulatory program.[10]

This is a crucial observation and can be directly exploited to improve Angeline and Pollack's approach:

1. Compressed modules are treated as units that can be switched on and off with a single mutation. Furthermore, reusing compressed units as components in other functions, which become in turn compressed, leads directly to a nested hierarchy of functions, each of which can be regulated at the next, higher level. As we have stated before, systems in general build on the availability of standard parts. Thus some of these functions become ubiquitous elements, which encode entire sequences such as the creation of a whole body part in animals. While in natural systems a frequently used subcomponent has to appear in large numbers, a technical system can save memory space by adding a frequency tag to such components. The artificial counterpart of wing creations would therefore feature a high frequency count; the creation sequence of ornaments and horns, a rather low one. The higher its frequency measure, the more likely it is that a component will remain in the system, serving other components.
2. Our artificial system may distinguish between *ontogenetic* and *phylogenetic* sets of rules. Compound rules may contain components from both sets.

In this way, it becomes possible to build individual experience upon knowledge inherited from previous generations [42, 43, 45].

3.3 Summary

As Günter Wagner points out, "phenotypic stability of core characters rather than their variability is a prerequisite for the evolvability of complex organisms" [55: 117]. The first steps that any developmental system makes are based on highly conserved and canalized components. Haeckel's "law" is a case in point.

Clearly, this "starting small" strategy [13] suggests two important issues. Firstly, complex systems consist of a phylogenetic component that is determined by canalized design, and an ontogenetic component of individual fine tuning. Secondly, through the process of epigenesis—or, in more recent cognitive terms, *embodiment*—the constrained phylogenetic design becomes adapted to the actual situation. From a functional point of view, however, such phylogenetic-ontogenetic arrangements present themselves as hierarchies. Old structures are the foundation for new ones such that the latter can be used and understood only when referring to the former, or, as Richard Lenski et al. put it, "complex features generally evolve by modifying existing structures and functions" [33: 143]. These hierarchies are not predefined, but emerge from a continuous interplay that modifies components on all levels in a strictly canalized way: As we have seen above, the enlargement and atrophy of dynamical-hierarchical structures are linear rather than random. The modification of new structures must always take the canalizing effect of entrenched components into consideration.

---

[10] Compare this also with the decision of John Koza [31] to use Lisp in his early genetic programming experiments because its syntax corresponds tightly with its hierarchical decomposition, so that mutations on a Lisp string usually lead to interpretable code.

However, no innovation would be possible in systems that are not able to de-canalize certain trends, to overcome the ancestral developmental constraints [56]. Compressing a subsystem, in the sense that it is not affected by mutations, means on the one hand leapfrogging development, but on the other hand disabling minute modifications. Whenever the design of wings is subject to modifications, it again becomes necessary to make this structural information accessible to further mutation. This justifies Angeline and Pollack's expansion operator. On the genetic level, Marc Kirschner and John Gerhart [30] propose several ways to relax canalization in biological systems, such as flexible protein interaction in gene expression, exploratory subsystems that do the fine tuning of keeping the system together, and compartmentation, which buffers against developmental inaccuracy and the consequences of mutational modification of pleiotropic genes. Sometimes it is even necessary to alternately constrain and relax a system several times, as the robot experiments of Max Lungarella and Luc Berthouze [35] demonstrate.

4 Conclusion

Complexity has become the subject of many research efforts, and new insights have been gained. Developmental and evolutionary biology focus on paradigmatic cases of complex systems. Assemblies capable of a vast number of combinatorial arrangements—our genes—are at the root of an allegedly vast number of phenotypic expressions. To get a grip on the mapping between the two has seemed impossible ever since the simple equation "one gene = one protein" was abandoned. Not only is our morphological appearance of course the result of some mapping processing, but so are our behavior and our cognitive faculty. This makes biological and cognitive entities complex systems *par excellence*.

The evolutionary and ontogenetic development of a complex entity such as a biological organism is a sequence of decisions that have to orchestrate a huge number of details such as the structural compositions of constituent (body) parts. It is clear that this can only be managed in a hierarchical manner. Consequently, if at the highest levels of this organizational hierarchy an error occurs, the body plan of the organism suffers spectacular deviations.

In evolution, compounds of structural genes (e.g., the genes necessary to build the antennae of a *Drosophila*) that have been approved by their evolutionary success are treated as elementary components by regulator genes at higher levels. The earlier a regulator gene appears in the phylogeny of the system, the more likely it is that many other structures will become dependent on it. Heaping layer on layer makes it ultimately impossible to remove an older layer. Hence in the biological context, attempts of mutations to do that result in the collapse of the entire system.

Internal selection is therefore to be interpreted as the result of interdependencies and the hierarchical structures among building blocks, which lead to canalization, that is, to restriction of freedom when choosing a future state. Evolution takes advantage of such "positive choices." With hierarchical canalization, the development of the organism will not necessarily be faced with alternatives at the lower level anymore. Evolution can, therefore, ignore large portions of the search space by applying canalization to structural parts. This improves evolutionary speed and progress by magnitudes and makes the macroevolution of complex forms possible in the first place.

In this view, complex organisms are self-regulating and self-organizing systems composed of dynamic elements that define themselves through reciprocal dependencies. These dependencies significantly reduce degrees of freedom and, consequently, randomness in evolution. They introduce canalizations as the driving force behind evolutionary novelty. As a result, the efficiency of mutation and selection mechanisms in complex organisms is not given trivially (as assumed in the argumentation of Saunders and Ho): The phenotype of an organism cannot be genetically changed independently of each other. Evolutionary processes must both survive the challenges of external selection in the environment and fit the overall body plan of the organism.

In artificial life systems canalization can be used to ensure that functional relationships within complex systems are maintained. It is suggested that a distinction be made between a canalized phylogenetic component and an ontogenetic component open to individual fine-tuning such that old structures are the foundation for new ones. New functionalities can be added by experimentally decanalizing certain compounds. This is a luxury natural systems do not have, but that can be used in artificial systems to accelerate the development toward complexity by means of an extended understanding of "natural" selection.

References

1. Angeline, P. J. (1994). Genetic programming and the emergence of intelligence. In K. E. Kinnear, Jr. (Ed.), *Advances in genetic programming* (pp. 75–91). Cambridge, MA: MIT Press.
2. Angeline, P. J., & Pollack, J. B. (1994). Coevolving high-level representations. In C. Langton (Ed.), *Artificial Life III* (pp. 55–71). Reading, MA: Addison-Wesley.
3. Ariew, A. (1999). Innateness is canalization: In defense of a developmental account of innateness. In V. Hardcastle (Ed.), *Biology meets psychology: Conjectures, connections, constraints* (pp. 117–138). Cambridge, MA: MIT Press.
4. Arthur, W. B. (1993). Why do things become more complex? *Scientific American*, *May*, 92.
5. Campbell, D. T. (1960). Blind variation and selective retention in creative thought as in other knowledge processes. *Psychological Review*, *67*(6), 380–400.
6. Carlson, J. M., & Doyle, J. (2002). Complexity and robustness. *Proceedings of the National Academy of Sciences of the USA*, *99*(Suppl. 1), 2538–2545.
7. Carroll, S. B. (2001). Chance and necessity: The evolution of morphological complexity and diversity. *Nature*, *409*, 1102–1109.
8. Castrodeza, C. (1978). Evolution, complexity, and fitness. *Journal of Theoretical Biology*, *71*, 469–471.
9. Crick, F. (1970). Central dogma of molecular biology. *Nature*, *227*, 561–563.
10. Darwin, C. (1859). *On the origin of species by means of natural selection*. London: John Murray.
11. Duncker, K. (1935). *Zur Psychologie des produktiven Denkens*. Berlin: Springer. Translated (1945): On problem solving. *Psychological Monographs*, *58*(270), 1–112.
12. Eldridge, N., & Gould, S. J. (1972). Punctuated equilibria: An alternative to phyletic gradualism. In T. M. Schopf (Ed.), *Models in paleobiology* (pp. 82–115). San Francisco: Freeman, Cooper.
13. Elman, J. L. (1993). Learning and development in neural networks: The importance of starting small. *Cognition*, *48*, 71–99.
14. Feynman, R. P., Leighton, R. B., & Sands, M. (1966). *Lectures in physics*. Reading, MA: Addison-Wesley.
15. Fontana, W. (2002). Modelling 'evo-devo' with RNA. *BioEssays*, *24*, 1164–1177.
16. Fontana, W. (2003). The topology of the possible. Unpublished manuscript. Retrieved from http://www.santafe.edu/~walter/Papers/top.pdf.
17. Fontana, W., & Schuster, P. (1998). Continuity in evolution: On the nature of transitions. *Science*, *280*, 1451–1455.
18. Franz-Odendaal, T. A., & Hall, B. K. (2006). Modularity and sense organs in the blind cavefish, *Astyanax mexicanus*. *Evolution & Development*, *8*(1), 94–100.
19. Galis, F. (1999). Why do almost all mammals have seven cervical vertebrae? *Journal of Experimental Zoology*, *285*, 19–26.
20. Gilbert, S. F. (1991). Induction and the origins of developmental genetics. In S. F. Gilbert (Ed.), *A conceptual history of modern embryology* (pp. 181–206). New York: Plenum Press.
21. Gilbert, S. F., Opitz, J., & Raff, R. A. (1996). Resynthesizing evolutionary and developmental biology. *Developmental Biology*, *173*, 357–372.
22. Goodwin, B. (1994). *How the leopard changed its spots*. New York: Touchstone.
23. Gould, S. J. (1996). *Full house: The spread of excellence from Plato to Darwin*. New York: Harmony Books.
24. Griffiths, P. E., & Gray, R. D. (2001). Darwinism and developmental systems. In S. Oyama, P. E. Griffiths, & R. D. Gray (Eds.), *Cycles of contingency: Developmental systems and evolution* (pp. 195–218). Cambridge, MA: MIT Press.

25. Hansen, T. F., & Wagner, G. P. (2001). Epistasis and the mutation load: A measurement-theoretical approach. *Genetics*, *158*, 477–485.

26. Jacob, F. (1977). Evolution and tinkering. *Science*, *196*, 1161–1166.

27. Kimura, M. (1983). *The neutral theory of molecular evolution*. Cambridge, UK: Cambridge University Press.

28. Kinnear, K., Jr. (1994). Alternatives in automatic function definition: A comparison of performance. In K. E. Kinnear, Jr. (Ed.), *Advances in genetic programming* (pp. 119–141). Cambridge, MA: MIT Press.

29. Kauffman, S. A. (1993). *The origins of order. Self-organisation and selection in evolution*. New York: Oxford University Press.

30. Kirschner, M., & Gerhart, J. (1998). Evolvability. *Proceedings of National Academy of Sciences of the USA*, *95*, 8420–8427.

31. Koza, J. R. (1992). *Genetic programming: On the programming of computers by means of natural selection*. Cambridge, MA: MIT Press.

32. Lehrman, D. S. (1970). Semantic and conceptual issues in the nature-nurture problem. In L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), *Development and evolution of behavior* (pp. 17–52). San Francisco: Freeman.

33. Lenski, R. E., Ofria, C., Pennock, R. T., & Adami, C. (2003). The evolutionary origin of complex features. *Nature*, *423*, 139–144.

34. Luchins, A. S. (1942). Mechanization in problem solving. In *Psychological Monographs*, 54/248.

35. Lungarella, M., & Berthouze, L. (2002). Adaptivity through physical immaturity. In *Proceedings of the 2nd International Workshop on Epigenetic Robotics (EPIROB'02)* (pp. 79–86). Infanoid Project.

36. McCoy, J. W. (1977). Complexity in organic evolution. *Journal of Theoretical Biology*, *68*, 457–458.

37. Muller, H. J. (1932). Some genetic aspects of sex. *American Naturalist*, *66*, 118–138.

38. Oyama, S. (2000). *The ontogeny of information*. Durham, NC: Duke University Press.

39. Richardson, M. K., & Keuck, G. (2002). Haeckel's ABC of evolution and development. *Biological Reviews of the Cambridge Philosophical Society (London)*, *77*, 495–528.

40. Riedl, R. (1977). A systems-analytical approach to macro-evolutionary phenomena. *Quarterly Review of Biology*, *52*, 351–370.

41. Riedl, R. (1978). *Order in living systems: A systems analysis of evolution*. New York: Wiley.

42. Riegler, A. (1994). *Constructivist artificial life*. Unpublished doctoral thesis, Vienna University of Technology.

43. Riegler, A. (1994). Constructivist artificial life: The constructivist–anticipatory principle and functional coupling. In J. Hopf (Ed.), *Proceedings of the Workshop on Genetic Algorithms within the Framework of Evolutionary Computation* (pp. 73–83). Max-Planck-Institut Report MPI-I-94-241.

44. Riegler, A. (2001). The cognitive ratchet. The ratchet effect as a fundamental principle in evolution and cognition. *Cybernetics and Systems*, *32*(3–4), 411–427.

45. Riegler, A. (2006). The goose, the fly, and the submarine navigator: The case for interdisciplinarity in artificial cognition research. In A. Loula, R. Gudwin, & J. Queiroz (Eds.), *Artificial cognition systems* (pp. 1–26). Hershey, PA: Idea Group Publishing.

46. Saunders, P. T., & Ho, M.-W. (1976). On the increase in complexity in evolution. *Journal of Theoretical Biology*, *63*, 375–384.

47. Schindewolf, O. H. (1993). *Basic questions in paleontology: Geologic time, organic evolution, and biological systematics*. The University of Chicago Press: Chicago. German original published in 1950.

48. Simon, H. A. (1969). The architecture of complexity. In H. A. Simon, *The sciences of the artificial* (pp. 192–229). Cambridge, MA: MIT Press.

49. Sober, E. (1984). *The nature of selection*. Cambridge, MA: MIT Press.

50. Sjölander, S. (1995). Some cognitive breakthroughs in the evolution of cognition and consciousness, and their impact on the biology of language. *Evolution and Cognition*, *1*, 3–11.

51. Swift, J. (1961). *Gulliver's travels. An annotated text with critical essays*. New York: W. W. Norton. Originally published in 1726.

52. Thompson, D'Arcy W. (1917). *On growth and form*. Cambridge, UK: Cambridge University Press.

53. Tyrrell, T. (1992). Defining the action selection problem. In *Proceedings of the Fourteenth Annual Conference of the Cognitive Science Society* (pp. 1152–1157). Hillsdale, NJ: Lawrence Erlbaum.

54. Waddington, C. (1957). *The strategy of the genes*. London: Allen and Unwin.

55. Wagner, G. P. (1999). Is Hsp90 a regulator of evolvability? *Journal of Experimental Zoology*, *285*, 116–118.

56. Wagner, G. P. (2001). What is the promise of developmental evolution? Part II: Causal explanation of evolutionary innovations may be possible. *Journal of Experimental Zoology*, *291*, 305–309.

57. Wilson, S. W. (1991). The animat path to AI. In J.-A. Meyer & S. W. Wilson (Eds.), *From animals to animats: Proceedings of the First International Conference on Simulation of Adaptive Behavior* (pp. 15–21). Cambridge MA: MIT Press/Bradford.

58. Wimsatt, W. C. (1986). Developmental constraints, generative entrenchment, and the innate-acquired distinction. In W. Bechtel (Ed.), *Integrating scientific disciplines. Case studies from the life sciences* (pp. 185–208). Dordrecht, The Netherlands: Martinus Nijhoff.

59. Wuketits, F. (1997). The philosophy of evolution and the myth of progress. *Ludus Vitalis*, *5*(9), 5–17.