

# Historical Essay

## Technology and the Foundations of Biology

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The use of mathematical language and scientific methodology has accompanied our everyday life since the 17th century. Foremost is the dramatic improvement in knowledge and technological success achieved through physics and chemistry. Such a development led, in turn, to a continuous and overwhelming increase in new insights into physical and chemical processes. Biology, however, appears to have faced a struggle, already described by Erich von Holst:

The scientific method, when applied to the living world, necessarily involves the fact that analysis continually progresses with regard to endless and varied chemical and physical elementary processes. From year to year, the ever-growing flood of facts has buried some researchers, forcing them to abandon synthesis and an organizing overview—often to such an extent that thoughts about inner connections among individual facts are disregarded right away, tossed aside as being “mere speculation” before they are even considered at all. Others are satisfied with general “holistic” or “vital” thought processes; and only a small remainder tries to search for and follow the trail of concrete organizational principles that are the factors within the living creature itself, which are decisive for its rule-following, functional context. Adoration of “pure facts” must prove to be momentous when one is talking about functional systems, whose main achievement is the coordination of various elementary processes, hence, above all, the central nervous system. It is indeed the case that here there is a nightmarish (or oppressive) misunderstanding: the many individual facts that are known stand in opposition to the quite humble and unassuming ideas about their combined context within the living organism. (von Holst 1956: 7–8)

Although technology achieved groundbreaking developments through the analysis of the living world, biology has not benefited similarly from technology. Indeed, current biological research frequently misjudges the complexity of the living world, as well as the explanatory limits of ontological reductionism (Lorenz 1973; Mayr 1982; Rose 1997). This occurs even when it has long been accepted that evolving mechanisms of complex biological systems become, on average, exceedingly elaborate from an engineering perspective, and that natural selection does not operate on their geometrical structure, but, rather, on their ensuing functionality. The misjudgments referred to above, therefore, can be thought of as a corollary of teleology (Mayr 1982), which has long influenced the development of biology. Interestingly, von Holst continued:

Thus it was to be expected that powers from outside would someday flow into this vacuum. This process has now gradually begun, and its powers come out of a technique that had learned (during the construction of continually more perfect machines, self-regulating, computing, conclusion-making and archiving) how to “think biologically.” Thus the technique followed exactly the path that most biologists had given up on. (von Holst 1956: 7–8)

In this early statement, von Holst referred to concepts arising from the then new fields of information theory (Shannon 1948), cybernetics, and bionics (Wiener 1948). A purposeful account of these fields lies beyond the scope of this article, however. Here we focus on the relationship between the overwhelming complexity of the living world and a purposeful, modeling approach to biology. This type of approach has largely been used in biology and proved to be beneficial, but appears to be almost unknown to the new generations of biologists. We also present a few examples aimed at illustrating how the use of such an approach can improve our understanding of phenotypic functions; these examples arise from the work carried out by one of us (J.A.N.) during several decades of research.

## Early Influences of Information Theory and Cybernetics

Atneave (1959) described information as an abstract quantity, “something,” neither matter nor energy, that we gain by reading or listening, or by directly observing the world around us, such that it removes or reduces our current level of uncertainty; this concept was poorly understood before Shannon’s (1948) pioneering work. Cybernetics, described by Wiener (1948) as the science of control and communication, developed in close correlation to this concept (e.g., von Bertalanffy 1968), and provided biologists with a new way of approaching questions about the living world, particularly with respect to processes such as communication and the regulation of goal-seeking behaviors (e.g., Hassenstein 1966). Furthermore, one is tempted to assume that cybernetics helped in rejecting the remaining influences of vitalism (Driesch 1951), still present at the beginning of the 20th century, i.e., underlying the conviction that life was more than mere physics and complex chemistry, causal agencies as “entelechies” and “vital forces” were still used to explain communication and the regulation of goal-seeking behavior (Mayr 1982).

Starting from single cells, the entire living world is made up of complex systems. Simon described these systems as those in which “the whole is more than the sum of the parts, not in an ultimate, metaphysical sense but in the important pragmatic sense that, given the properties of the parts and the laws of their interaction, it is not a trivial matter to infer the properties of the whole” (Simon 1962: 468).

Since the middle of the 20th century it became clear that the seemingly goal-directed processes of the living world are not in conflict with physicochemical explanations (Küpfmüller and Poklekowski 1956), although a distinction was still necessary between simple mechanistic approaches to biology and the study of the structure of complex organisms. This has been clearly stated by Mayr:

The explanatory equipment of the physical sciences is insufficient to explain complex living systems and, in particular, the interplay between historically acquired information and the responses of these genetic programs to the physical world. The phenomena of life have a much broader scope than the relatively simple phenomena dealt with by physics and chemistry. This is why it is just as impossible to include biology in physics as it is to include physics in geometry. (Mayr 1982: 52–53)

Together with information theory and cybernetics, a new applied science developed during the 1950s, usually referred to as bionics or biomimetics (Wiener 1948). It focused on the simulation of technical, adaptive solutions found in nature in order to improve task solving and the optimization of different types of processes within the context of technology. Both cybernetics and bionics then showed that phenomena typically observed in nature, such as goal-seeking behavior and communication, can successfully be simulated by artificial, technical

systems. As a sort of side effect of this successful transfer from biology to technology, biological research, at the time focused almost exclusively upon the geometrical structure of its objects of interest, began to incorporate concepts embedded in these new technical fields into the study of numerous physiological processes (e.g., Lorenz 1978). An analysis of diuresis in insects (Núñez 1956) helps to illustrate an early study based upon technical concepts. In the beetle *Anisotarsus cupripennis*, the volume of haemolymph remains nearly constant, and its artificially induced variations are rapidly compensated. However, when larvae lacking their protocerebrum were exposed to water-saturated air, their haemolymph volume and body weight increased significantly, due to water that was absorbed (but not excreted) through the animals’ body surface. This finding pointed toward a regulatory mechanism controlling the insects’ excretory system, i.e., their nervous system must have computed a measure somehow related to the hemolymph volume, and evaluated it against a reference value via one or more feedback mechanisms. Indeed, it turned out that sensory information from abdominal stretch receptors actually constitutes the input of a feedback mechanism regulating water balance in this and other species of insects (Núñez 1956). This work also gave us the first evidence for a diuretic hormone in insects, the source of which depends upon cells of the dorsal protocerebrum (Núñez 1956). We now know that both excretion and water balance are controlled by diuretic and anti-diuretic hormones produced, stored, and released in the insect nervous system (Coast 2001). Eventually, the application of concepts from the theory of control also shed light on various fields of biological research. And the lesson was this: the identification of organizing principles and regulatory mechanisms in complex living systems is possible only by evaluating the functioning of the system as a whole. Still, scientists from vast and rather different areas of biology frequently seem to not be aware of the potential explanatory reductionism within which their own views may be embedded. Dissecting constituent parts from the functional whole may easily lead us away from the study of organized complexity (e.g., Dubos 1965; Lorenz 1973; Beckner 1974).

## Evolution Strategy

Evolution strategy (Rechenberg [1965] 1998, 1971), or ES, was developed in the 1960s within the general context of bionics, and, specifically, the field of biologically inspired engineering algorithms. This field also gave rise to genetic algorithms (Holland 1975), or GAs, computational models of evolution extensively used in research on artificial-life systems (Holland 1995). GAs can be thought of as an abstraction of the genetic turnover (adaptation) of candidate solutions to a problem (genes) that arises through genetic operators (crossover and mutation) and selection (Holland 1975). Beyer and Schwefel (2002: 4–5) have recently defined ES as “a set of rules for

the automatic design and analysis of consecutive experiments with stepwise variable adjustments driving a suitably flexible object/system into its optimal state in spite of environmental noise". The term "evolution strategy," as related to engineering algorithms (Rechenberg 1973), refers to the ES' two original rules, thereby resembling mutation—though not necessarily in the sense of a random trial—and selection, as derived from the Darwin-Wallace theory of biological evolution. In his pioneering studies, Rechenberg ([1965] 1998, 1971, 1973, 1978) simultaneously changed all the variables of his system of interest, and discarded each new set of variables if it diminished the ensuing goodness of the system, thus simulating the basic strategy of biological evolution. At the time, ES appeared to some skeptics to be too coarse to be seriously considered in the context of engineering, based on the impressive number of possible configurations and iterations that might be required to optimize the goodness of an inanimate system. Nevertheless, against all predictions, ES proved to successfully achieve its goal after a surprisingly low number of "mutational steps" (Rechenberg 1994). This success lies in the fact that complex systems involve numerous components and their corresponding nonlinear interactions. The task of optimizing the outcome of a system comprising a single-digit number of components can successfully rely on mathematics (Rechenberg 1994). (The same might be true when the number of components increases but one possesses substantial knowledge of the functioning of the whole system.) On the contrary, while addressing complex systems one must cope with random complexity and indeterminacy (Rechenberg 1994). In these cases, it is precisely the inherent indeterminacy of the systems that explains the adequacy of ES for task optimization.

In its simple form (Rechenberg 1973; Beyer and Schwefel 2002), ES presents two options (mutants) per iteration, and the rate of progress in the optimization process depends upon the mutation strength (MS), i.e., the standard deviation of each component as related to the normally distributed mutation vector. Optimal MS values, in addition, are independent of the dimension of the search space. This means that the rate of progress improves throughout successive iterations when MS is adjusted to the proper order of magnitude, indicating, in turn, that ES presupposes no more than the soundness of strong causality, i.e., only small changes in the system's components can predict the ensuing slight variations in performance. According to Rechenberg (1994: 36), "Strong causality is the guide for practical acts of man, and strong causality is also the soil of Evolution. Strong causality means prediction of local values, and evolution occurs in the range of validity of strong causality." Intriguingly, the adjustment of the mutation strength also allowed ES to optimize the optimization process itself (Rechenberg 1994), thereby referring to evolutionary mechanisms that promote heritable variability within populations (e.g., genetic control of mutability, sexual reproduction, crossover and recombination, etc.). But how could one explain

that, within evolutionary processes, a mutation mean step-size is targeted at a given "evolution window"? Rechenberg (1994) thinks it does not happen via phenotypic characteristics, but by changes in the strategy of some specific population parameters; optimization now operates on its own efficiency and the population is the "biological invention" for the task at hand. Similarly, evolutionary biologists stress the fact that evolution can be thought of as the genetic turnover of the individuals of every population from generation to generation (Mayr and Provine 1980), although it involves not only changes in genetic frequencies but also in adaptation and diversity with respect to the technical solutions that enable organisms to deal with a variable environment. Technically speaking, therefore, ES-rules allow optimizing the functioning of a complex system, and the same basic principles might partially explain the diversity and specificity of the technical solutions found in nature after  $3 \times 10^9$  years of biological evolution.

### Function and Form

Living systems are undoubtedly complex; unlike inanimate objects, they exhibit random complexity and organization, chemical uniqueness, variability, genetic programs and historical nature, properties semantically crystallized through the concepts of pleiotropy and polygeny (for a detailed account of these properties see Mayr 1982). These concepts point toward the fact that there is no linear relationship between single genes and traits in naturally evolved systems (Dobzhansky 1970), which implies, in turn, that temporal predictions in biology are only probabilistic (Scriven 1959). Hence, most aspects of living organisms are not readily comprehensible and cannot be mathematically described, which is probably the reason why natural selection operates on the functionality of any given system, and not on its underlying structures. Here the lesson is this: the complete spectrum of functions and behavioral flexibility of an organism's subsystem (e.g., an insect's excretory system, as in the example described above) cannot be inferred by pure structural analyses, or such that focus on isolated constituents. Take the case, for example, of the complex structures involved in the beetles' defensive mechanisms (Schildknecht 1970). Coleoptera comprise the largest group of organisms at the order level, and have evolved a rather sophisticated defensive chemistry, well suited to their various living environments. Their defensive strategy is based on exocrine glands, called pygidial glands, which have been extensively studied in the context of biochemistry and chemosystematics. These glands are paired, complex structures comprising secretory lobes, gathering tubes, reservoirs, discharging tubes, and closing valves. The defensive substances produced by the lobes are collected by the gathering tubes, stored in the reservoir and released when the closing valve opens. While the functions of the lobes, reservoirs, discharging tubes, and valves appeared to be self-evident, the variable length and fine structure of the

gathering tubes lacked explanation. Núñez (1961) found that the glandular vesicles of the secretory cells undergo dilatation when the reservoir is full, and collapse when the valve is removed, meaning that the reservoir's internal pressure is transmitted into the glandular vesicles, and that the regulation of the glands' activity depends upon the mechanical properties of the gathering tubes. For this kind of regulation to occur, the structure of the tubes must allow them to experience rapid variations in their internal pressure without undergoing dilatation, thereby ensuring the faithful transmission of pressure from the inner reservoir toward the lobes and eventually to the secretory cells. It turned out that this is indeed the case (Núñez 1961). To the best of our knowledge, this technical analysis was the first description of mechanically regulated gland activity.

The complex relationship between form and function in evolutionary terms lies far beyond the horizon of a single organism. It involves, for example, the interplay between completely different, still related species. Consider the coevolution of flowers and insect pollinators (Núñez 1975). Insect-mediated spore dispersal has probably existed since Devonian time (Kevan and Baker 1983), and modern flowers can be thought of as structures evolved to maximize attraction and minimize energy expenditure. Floral attraction appears to have initially been exerted through pollen, but became enhanced by the simultaneous presentation of sugars secreted by specialized glands, called nectaries, which in its early stages probably helped spore germination (Kevan and Baker 1983). Proteins are pollen's basic components, equivalent to sugars with respect to their gross energy value (~4 Kcal/g), but their synthesis, relative to that of sugars, demands additional (~34%) energy. Flowers, therefore, improve their economy by substituting fractions of their pollen loads with sugar, which might explain, in turn, the drop in the number of stamens observed in flowers offering both pollen and nectar (Percival 1965). Moreover, reducing the level of uncertainty of the prospective pollinators also enhances attraction. Scents associated with pollen and nectar, as well as floral shapes and colors, certainly constitute a guiding code for insect pollinators (von Frisch 1967; Heinrich 1975; Menzel 1985). They thus improve their energy gain by reducing their searches and handling times. In the course of evolution, flowers might have reduced the quantity and diversity of ambiguous structures—initially adapted for ensuring pollination—by means of signals whose functions became highly specific. *Ophrys* orchids nicely illustrate the concept of “informational simulation” (Kullenberg and Bergström 1973). They produce scents that closely match the pheromones of sexually receptive females of *Gorytes* hymenoptera, and their petals resemble the insects' antennae, eyes, and wings. The overall result of this mimicry is that they become highly attractive to the males of this species, which efficiently serve pollination in their efforts to copulate with the flower. The plant thus produces nothing but information for

the insect pollinator. Interestingly, optimization seems to have molded not only the floral components that may directly modulate the foraging choices of pollinating insects (like colors, scents and flower morphology), but also the temporal programming of both nectar secretion and pollen presentation, which are well-coordinated with physically relevant environmental factors as well as the pollinators' foraging rhythms (Rathcke and Lacey 1985). Complex organizational structures in mutual interaction arise by incorporating the pollinator side into this scenario: While plants tend to optimize pollination by reducing their energy expenditure, pollinators enhance food gain by optimizing the mechanisms underlying their foraging decisions (Núñez 1966). Functions are critical in this context, and it is reasonable to expect a true network of opposing control systems, energetically adapted to one another and to their corresponding physical environments. Most important is this: in this and many other biological examples, neither the structure of the subsystems involved nor the semi-autonomous functions they serve predict the efficiency of the system as a whole. Perhaps the most prominent examples of the nonlinear relationship between form and function arise from the study of the human brain (Rose 2005).

### Are There “Functional” Fractals?

Holland (1995) states that all complex adaptive systems can be described in terms of common properties (i.e., aggregation, nonlinearity, flows, and diversity) and mechanisms (i.e., tagging and internal models). Increasing complexity in addition leads to threshold-point phenomena, although the properties and mechanisms of these complex adaptive systems appear to not depend—at least not necessarily—on the number of aggregating agents (Holland 1995). It follows, therefore, that the single agents of a multi-agent aggregate might also be subject to selection. Since natural selection operates on phenotypic efficiency, we ask whether the single, interacting subsystems of a complex living system may also be selected on the basis of their individual, semi-autonomous efficiency. Here we refer to “functional” entities primarily defined on the basis of their information processing capacities, and their role within the system's inherent hierarchical organization, either exclusive or inclusive, irrespective of their geometrical limits. We do not conceive these entities as the ultimate units of selection, however. Rather, we ask whether their individual efficiency may vary autonomously, and whether they may fulfill, at least theoretically, the necessary requirements to be conceived as parallel, albeit second-order, units of selection. In fact, no matter what one designates as a possible unit of selection, it will only exist as long as it is functionally embedded in a complex adaptive system. This by no means implies that natural selection will not operate on the efficiency of the system as a whole, but it does mean that any suitable approach

aimed at explaining the functioning of a complex living system will strongly depend upon the study of these integrated, self-regulated functional subsystems, which will in turn exhibit self-similarity and independent abilities for handling information. They therefore cannot be isolated elements, like cells or molecules, but are still expected to be methodologically accessible without suffering from ontological damage (Lorenz 1973; Ayala 1974). Remarkably, research on animal behavior and physiology already had given us precise descriptions of complex functional entities, which are relatively independent and exhibit self-similarity and successful information processing (see, e.g., Barlow 1961; Reichardt and MacGinitie 1962; Lorenz 1978). Note that this concept is reminiscent of Ashby's (1956) account of black boxes, originally coined in the context of engineering. Black boxes, however, are defined on the basis of geometrical arrangements, and their possible functions are constrained a priori, since their otherwise unknown contents can only be inferred via specific input-output relationships. In contrast, we focus on entities that become evident only through their function, irrespective of their geometry. It follows, then, that they are intangible in the absence of the entire operating system, due to the fact that the performances they serve are part and parcel of the system at its higher organization level.

Mandelbrot (1975) coined the term "fractal" while referring to structures that show self-similarity, scale invariance, and Hausdorff-Besicovitch dimension. His landmark work eventually led to full-fledged theories of the geometry of complex structures, which helped in describing irregular and fragmented geometrical patterns found in nature (Mandelbrot 1982). In principle, therefore, fractals account for shapes, without reference to functions. Nevertheless, when conceived as functional entities based on their abstract, distinctive properties, fractals may also be embedded into structures (living systems) of hierarchically organized, functional units for information processing (subsystems), and account for the technical capacities of the living systems at their higher organization level. (One might still argue about how to designate these units, but it seems that their most salient features become evident even in highly complex human endeavors; e.g., Warnecke 1992.) Theoretical accounts on the evolution of replicating systems postulate that systems of a given order might have emerged via the combination of the functional properties of simpler precursor systems (Mereschkowsky 1920; Taylor 1974; Margulis 1993; Knoll 2003; Cheng et al. 2004). Here we hypothesize that it is a multidimensional topology of functional fractals that allows living systems to handle large amounts of information and respond to the technical challenges imposed by the environment. These functional entities might be distinguished according to both the type of information they handle and their information-processing abilities, and will determine the functioning of the entire organism on the basis of their self-organizing capacities.

## Conclusion

Early in the 20th century, biology still focused almost exclusively on the geometry of nature, thereby describing complex structures across phyla. It was within this context that a growing understanding of regulatory mechanisms and different forms of communication underlying the functioning of artificial, complex systems gave rise to new perspectives about the relationship between form and function (e.g., von Holst 1956). Cybernetics (Wiener 1948) nurtured biology with universal principles. The power of mutation and selection, in addition, became empirically evident by simulating the fundamentals of evolution strategy (Rechenberg 1994). Furthermore, these simulations demonstrated that the process of optimization does not depend linearly upon the number of mutational steps, and that it only presupposes the soundness of strong causality. All these achievements led, in turn, to a more accurate comprehension of the interplay between natural selection and the behavior of evolving organisms, which was nicely illustrated by the development of ethology in the previous century (Lorenz 1978). Hence, it is fair to postulate that, since the 1950s, new vistas based on technical aspects of the living systems have strongly influenced the development of current biological thought.

Natural selection operates upon the efficiency of complex adaptive systems. It follows that only systems or subsystems that exhibit their own dynamics, but not their isolated, constitutive elements, can be thought of as the subject matter of selection. Fractals (Mandelbrot 1975), conceived as technological units serving specific functions, i.e., without reference to their geometrical boundaries but only to their self-similarity and scale invariance, appear to be suitable entities to consider in the study of the functional capacities of the living world. These functional entities, however, cannot be identified or characterized by molecular or morphological, single-character classifications.

More than two decades ago, Mayr stated that a new philosophy of biology was needed, and wrote: "This will include and combine the cybernetic-functional-organizational ideas of functional biology with the population-historical program-uniqueness-adaptedness concepts of evolutionary biology" (Mayr 1982: 73). Here we claim that current biology needs to become less vulnerable to explanatory reductionism. For this to be accomplished, however, emphasis is necessary on the analysis of the technical organization of living systems. This might allow new generations of biologists to strengthen the course that biology took after the enunciation of the Darwin-Wallace theory of natural selection.

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