

The epistemology of biomimetics: the role of models and of morphogenetic principles

Forthcoming in *Perspectives on Science*; scheduled for Vol. 30, Issue 1, 2022.

Ulrich Krohs

Department of Philosophy, Westfälische Wilhelms-Universität Münster,
Domplatz 23, 48143 Münster, Germany

ulrich.krohs@uni-muenster.de

Abstract – Form follows function, but it does not follow from function. Form is not derivable from the latter. To realize a desired technical function, a form must first be found that is able to realize it at all. Secondly, the question arises as to whether an envisaged form realizes the function in an appropriate way. Functions are multiply realizable—various different forms can bear the very same function. One needs to find a form of a technical artifact that realizes an envisaged function sufficiently efficient, robust, or whatever criteria might be imposed. This paper scrutinizes biomimetics as one way to find a good solution to the realization problem. Drawing on an approach from the philosophy of simulations, it reconstructs the biomimetic relation as being mediated by a theoretical model. It is shown that the robustness of the functioning system is usually reached in different ways in biological and in technological systems, which explains differences in morphogenetic mechanisms or principles found in these fields. This reconstruction helps to understand problems with robustness in synthetic biology that occur when technical design principles are implemented in a biological system. The mimetic relation between the biological and the technical realm is found to be asymmetric.

Keywords: Biological Function; Evolution; iGEM; Morphogenesis; Robustness; Simulation; Systems Biology; Technical Function.

1. Introduction

Form does not follow from function. It is therefore not a trivial task to find a form that realizes a desired technical function. “Form” in the wide sense that is used here is not restricted to morphology and geometric properties, but includes

all kinds of structural relations, be they static or dynamic. In this sense, the architecture of a gene regulatory network and its regulatory relevant feed-forward and feedback loops count as form, as do the architecture of a computer program and the reaction network of a chemical oscillator. “Function,” on the other hand, is either the capacity realized by a structure or the contribution of a component of the structure to higher capacities; in the field of biology, often the function contributes to maintaining the integrity of the organism or, more generally, keeping it alive. For the present purpose, this informal, intuitive characterization of the highly disputed concept should of function suffice.¹

Realizations of a large number of technically interesting functions can be found in living nature, from lightweight structural elements via self-cleaning surfaces to strategies and control of locomotion on land, in water, and in air. Biomimetics takes such biotic realizations of functions as antetypes for their technical realization and thus counts on living nature to find solutions to the realization problem.

The aim of my paper is to better understand the epistemology of biomimetics. In following this aim, I first reconstruct the process of copying a biological function as being mediated by an abstract model that holds for the biological as well as for the technical system and thus links them (section 2). Next, I reflect on the sources of robustness in both biological and technical systems in order to spot a major difference between what is sometimes called morphogenetic principles in biology on the one hand, and classical engineering strategies on the other (section 3). I then discuss the prospects of mimicking not only biological structures, which are always the results of evolution and development, but the very mechanisms of evolution and development themselves and provide an example (section 4). Finally, I discuss an example from synthetic biology that exemplifies what I call the mimetic asymmetry: transferability between biological and technological systems is by and large a one-way system. Therefore, one should follow a biomimetic rather than a technological approach even when re-constructing gene regulatory networks for their technical use (section 5).

2. Biomimetics: models bridging biology and technology

Copying a biological function is an indirect process of reconstructing functionally crucial properties (both static and dynamic) of the underlying biological structure in a technical artifact so that the mimetically reconstructed structure can fulfill the desired function in the system in which it is embedded.

¹ For the extended philosophical debate on the concept of function, see (Wouters 2003; Perlman 2004; Krohs 2009a; Garson 2016).

A lotus effect coating, for example, copies elements of the surface structure of the lotus petals, but it serves its function only in an appropriate environment in which water dabbles the surface from time to time.

The transfer from the biological to the technical realm is an epistemic process as well as a constructive one. In order to be able to transfer the function, one needs to understand how the biological structure realizes it (Nachtigall 2010). Uncovering “the general principles behind its functioning” (Vincent et al. 2006, p. 474) is an important step in the transfer process. Thus, biomimetics does not primarily aim at copying a biological structure, but at adopting and adapting those structural features that realize the function. Copying a biological structure—usually with major modifications—is just a means to the end of realizing a function; however, it is a promising means because the biological system to be copied is itself a realization of the function.

Looking for as much similarity as possible between the biological template, the *donor system*, and the technical device, the *receiver system*, would not sufficiently guide the transfer process. If a function is realized biologically by, say, a proteinaceous structure or a polysaccharide structure, it will not usually be helpful to find a chemical realization that is similar to these materials that are often perishable. In contrast, realizations might be based on metal parts, ceramic nanoparticles, or inorganic chemical complexes. The scale might be different, as is often the case in locomotive devices like wings or walking machines, and the energy supply might rely on completely different sources like batteries instead of metabolism, thus resulting in a need for completely different actuation systems, etc. As a result, the technical system that is most similar to the biological one will usually not be the best technical realization of the function, if it realizes it at all. This means that another guideline than just structural similarity needs to guide the mimetic process, namely, as already quoted, an “understanding” of functioning or of its principles. “Understanding” in this context requires a theoretical explanation of how the function is realized or why the structure is able to perform the function. One needed to (i) find out that the lotus effect is a consequence of superhydrophobicity, which is due to the microstructure of the lotus petal’s surface, in order to be able to develop lotus effect surfaces (Barthlott and Ehler 1977, pp. 445–46; Solga et al. 2007); (ii) understand that the flapping flight of many insects, birds, and bats depends on high degrees of torsion of the wings before artificial insects could be constructed (Chin and Lentink 2016; Dickinson and Muijres 2016; Shyy et al. 2016; Karásek et al. 2018); and (iii) know that gecko adhesion is brought about by short-ranged forces between the surface they stick onto and the minime soft branchings of the lamella of the gecko foot, the spatulae, which nestle to the surface on the atomic scale, before adhesives that function similar to gecko’s

feet could be developed (Bhushan 2016; Kroner and Arzt 2016). These cases show that functioning needed to be explained before it could be copied. The explanation usually comes in the form of a model of performing the function that specifies the contributions of all components and the ways in which these contributions in combination bring the function about. Biologists construct models of bird flight, biped locomotion, protein-biosynthesis, echolocation in bats, the lotus effect, and gecko adhesion. These models inform and direct the technical implementation of the functions at stake.

The principles of the donor system's functioning are thus depicted in an explanatory model. The technical structure, as the receiver system, simulates the biological system by functioning according to the same principles. I therefore reconstruct biomimetic copying, or biomimesis, in terms of model-based analog simulation (Krohs 2008). In an initial step, the biological realization of the function is modeled theoretically, meaning that an understanding of the structural means is gained that realize the biological function: how the surface of the lotus flower repels dirt, how the bumblebee flies, etc. In the second step, the insights of this model are transferred to the technical realm; a technical structure is designed that instantiates the theoretical model by realizing the identified crucial structural elements in a system that provides an appropriate context for fulfilling the desired function.

In a coarse-grained description, the process of model-mediated biomimesis consists of four steps:

1. Identification of a biological function or of a desired technical function in the biological realm.
2. Description of how this function is realized; i.e., constructing the model that is instantiated by the biological system and that explains its functioning.
3. Envision of an alternative, technically feasible instantiation of the model.
4. Construction of the technical system and thereby technical realization of the function.

Steps 2 and 3, as well as step 4 most of the time, need to be reiterated before a satisfying result is obtained. It is also possible to further split the steps into smaller ones; however, any more fine-grained scheme would only be valid for a particular case or for a certain class of cases, so I do not include them in the general scheme. Even the four-step scheme is not obligatory. Research and development are fundamentally influenced by certain kinds of epistemic luck (Pritchard 2005), path dependencies (Peacock 2009), the order in which information is gained or retrieved, etc. This might lead to variation in the reiteration of steps and even to skipping a step: it is epistemically possible that

somebody happens to envisage a technical realization of a biological function without having an explicit model of the functional system. The four-step scheme could thus best be regarded as a rational reconstruction or as an in-principle-reconstruction of the process of the development of biomimetic technology. It is certainly not the only possible reconstruction, but, as is shown below, it is one that helps to understand—and consequently to also plan and steer—the process.

Therefore, I strongly disagree with the judgment that only one part of the epistemological framework of biomimetics can be fixed, namely “searching biological literature for functional analogies to implement” (Vincent et al. 2006, p. 747). The central steps of the epistemic process pertain to modeling rather than library work. They involve generation and reapplication of the model of how the biological system realizes the function. A literature search is one way to retrieve the model and is thus often highly important from a pragmatic perspective, but this only means that one relies on model building that was done previously by others and does not change the general epistemic process. Such cases could even be seen as temporally stretched analogues to interdisciplinary cooperation, though the important aspect of bidirectional communication is missing. As Green et al. (2019) point out, biomimicry practitioners, typically engineers, physical scientists, and chemistry and biological engineers, may often profit from direct interaction with those more knowledgeable about the wealth of functions realized by biological traits, like biologists in natural history museums and collections. Certainly, this holds also for cooperations with physiologists and partners from many other biological disciplines. The need for interdisciplinary cooperation can also be read from the four-step scheme given above: step 1 relies on empirical description and research and is thus primarily a task for empirical biologists; step 2 is the application of—formal—modeling techniques often done by theoretical biologists; and steps 3 and 4 demand the core expertise of engineers and perhaps further cooperation with physicists, chemists, or biologists.

3. Robustness in biological and in technical systems

Biological systems are stable enough to resist thermodynamic and mechanical as well as other challenges, and are flexible enough to adjust to changing conditions. The combination of stability and flexibility is a precondition for their persistence. Adjustment to changing conditions involves changes in structure and in the operation of the system. Not the exact form is maintained by the adjustments, but the organizational integrity of the organism and its self-regulatory capacities. A system adjusting in such a way is called a robust

system. “*Robustness* is the ability of a system to maintain its functionality across a wide range of operational conditions” (Hammerstein et al. 2006, p. 90). This definition avoids reference to specifically biological criteria for robustness and thus takes into account that robustness applies to both biological and technical systems. The robustness of technical artifacts, however, differs significantly from the robustness of biological organisms. This difference has important consequences for biomimetics. In order to discuss these, we first need to compare aspects or kinds of robustness in both sorts of entities. In this paper, I am focusing only on aspects of particular importance for the epistemology of biomimetics.

Let us first look at biological organisms, which need to be robust in several respects. Organisms are not very stable in the classical sense, (they can be wounded, poisoned, damaged by heat, etc.) so they need repair mechanisms. Since many organisms feed on different sources, they also need mechanisms for switching their metabolism. Moreover, since challenges vary during the day and during the year, they need to follow these external rhythms and respond differently to the very same kind of stimulus at different times. In addition, the environment challenges not only the fully developed organism, but also its development. Thus, development itself needs to be robust and lead to the same, or at least similar, results, independently of deteriorations.

Besides such external challenges, there are also internal ones: the genetic material is subject to mutations, so developmental pathways need to be robust with respect to mutations. This is achieved in part by a degenerated code that allows for many mutations being silent, but also by the structure of the gene regulatory networks that govern development and metabolism. These networks provide redundant functionality and regulation mechanisms so that blocking or altering a node or link in the network by mutation does not typically affect its overall action.

Robustness also applies to lineages on an evolutionary scale. Lineages remain stable despite changing environments and despite being subjected to evolutionary processes; in fact, they often remain stable *due to* evolutionary processes. Robustness can be achieved by maintaining variants even under selection pressure so that future generations have a chance to adapt quickly. Thus, the fundamental mechanisms that make organisms robust include the following: a) *generational* mechanisms that robustly lead in to a robust result; b) *maintenance* mechanisms, including replacement; and c) *adjustment* mechanisms. Specific accounts of overall robustness are given in the theory of autopoietic systems (Maturana and Varela 1980) and by Rosen’s (M, R)-systems (Rosen 1973, 1991; cf. Letelier et al. 2006).

Robustness in technology is usually achieved by different means. First of all, measures are often taken to reduce the wear and tear of the artifact. This means that robustness in technology is based much more on stability and much less on a regular turnover of components, which is a highly important factor in the biological case. Another aspect of robustness in technical systems is a modular architecture that, in addition to its support of the processes of developing and of constructing the structure, helps to maintain the system by replacing modules. If a component becomes damaged, the damage is often isolated in the module it occurs in so that no major problem occurs until this module can be replaced. In contrast, modularity in biology might often be less relevant for (self-)maintenance of the system than for development and evolution. Moreover, modules of gene regulatory networks are usually much more interlinked and even overlapping, and the delineation of modules is often more of an epistemically valuable constructive step rather than a neutral depiction of a complex network (Krohs 2009b).

While biotic systems gain robustness through adaptive fluidity, technical systems are often robust because of their stability, elasticity, or rigidity; in other words, their ability to return to the previous state after deterioration. Before investigating the consequences of this difference in section 5, I will first look at the prospects of transferring morphogenetic strategies from biology to the technical realm.

4. Biomimetic approaches to morphogenesis

The highly complex biological structures are brought into being by processes of evolution and development. Therefore, it seems advisable to take advantage of the capacities of these biological processes and include them in the biomimetic approach. Consequently, definitions or characterizations of biomimetics quite often include the idea of mimetic construction in addition to mimetic structure and function, though often without providing examples. Copying synthetic pathways is sometimes even considered on par with copying structure and function: “biomimetics is the study of biological structures, their function, and their synthetic pathways, in order to stimulate and develop these ideas into synthetic systems similar to those found in biological systems.” (Sarıkaya and Aksay 1995, p. xi). It might be useful to discern different levels of technical biomimesis. According to Borsari (2017), the first level is copying biological structures in order to realize a function technically: examples of this would be the lotus effect or gecko adhesion. The second level refers to the mimicking complex strategies from nature, where fault tolerance in the brain by

redundancy is mentioned as possibly providing a helpful model in electronics. The third level, then, is mimicking evolution.

While Borsari's first level includes mimicking not only structures, but also their involvement in processes, which might already be quite complex, his second level requires mimicking complex *strategies*. His example makes clear that this does not primarily refer to developmental processes, which also could be described as strategies to bring about the very same structure under a broad range of conditions, but rather to complex mechanisms in the fully developed biological entity that make it robust. The line between developmental robustness and robustness of developed entities by means of complex strategies might be fuzzy and even vanish under a certain perspective, but for systematic reasons, I nevertheless want to keep this distinction. The biomimetics of levels one and two then mimic evolved and developed biological features: level one is the mimicking of structures and their dynamics to implement a function, and level two is mimicking complex strategies rather than mere processes. The difference between a strategy and a process might best be seen as follows: while a process is a regular way that leads from state *a* to state *b*, a strategy is the way how the system finds, under varying condition, a way that leads from *a* to *b*. With this distinction in mind, fault tolerance mechanisms in electronics, as well as locomotion of artificial worms (Menciassi et al. 2004; Boxerbaum et al. 2012) and the goal-finding behavior of vehicles (Braitenberg 1984) are examples of the second level of biomimetics— they are mimicking strategies. In contrast, the processes involved in the self-cleaning of lotus effect-surfaces and the reversible adhesion of gecko pads remain on level one.

Level three differs from the first two levels by focusing on the generation of form rather than on the given form and the processes in which it is involved. Level three literally deals with biomimetic approaches to morphogenesis. Borsari (2017) mentions evolution as the morphogenetic process to be mimicked, which is what we find in the literature about technical mimicking of biological morphogenesis. Evolutionary strategies were already propagated in an early phase of biomimetics (Rechenberg 1973). Examples from these early beginnings until today include the evolutionary way to shape a two-phase nozzle (Schwefel 1968), the evolution of neuronal networks as controllers of autonomous robots (Hülse et al. 2004), the directed evolution of proteins (Kan et al. 2016; Arnold 2019), and the evolution of artificial cells (McCaskill 2009). As the examples show, we are often, but not always, still dealing with systems close to biological ones when evolutionary strategies are at stake. Evolutionary strategies are also quite often applied in certain fields of applied mathematics and programming, but I will not consider these examples because they deal with abstract entities that have symbolic content: including

this other realm would demand starting another debate. I confine my treatment of level three biomimetics to cases of concrete entities. Results can then be transferred to the abstract case afterwards.

Let me start with some general considerations. A system's realizing functions do not emerge from a simple mixture of components; they need to be put together in an ordered way. In the biological realm, this seems to restrict possible outcomes since the systems and *a fortiori* their functions can only be results of developmental processes, which are themselves only the results of evolutionary processes. We can thus expect to find a nested path dependence that constrains the outcomes. On the other hand, nature obviously found ways to come up with results on complicated paths that we would judge as extremely clever if found in technology, so restrictions might not be an issue in the long run.

Biomimetic artifacts, on the other hand, are not usually built in a biomimetic way. Their construction follows technical paradigms rather than morphogenetic principles learned from biology. As it turns out, it is nevertheless valuable to look at such principles and consider the third level of biomimetics: morphogenesis. Since biological morphogenesis includes not only phylogenetic but also ontogenetic processes, my take of this level is wider than in Borsari's approach and includes both evolution and development (Krohs 2021). This widening appears to be necessary because even one of the most intriguing examples of biomimetic evolution, the previously mentioned evolutionary optimization of a two-phase nozzle (Schwefel 1968), combines evolutionary and developmental mechanisms. The nozzle, with its initial taper in diameter, was cut into sections so that the opening in each section had a different diameter. Sections were then put together in an arbitrary order, resulting in an irregular shape of the nozzle, and efficiency measured. This structure was optimized following a scheme of variation and selection. Two arbitrarily chosen segments of the nozzle were exchanged with each other and efficiency was measured again. The better structure was chosen for further changes. This trial and error process of optimizing efficiency lead to a nozzle with an irregular shape that would hardly have been rationally constructed (Schwefel 1968). Since technical morphogenesis was driven by an evolutionary paradigm taken from biology, the optimization is to be taken as level three biomimetics.

However, despite implementing variation and selection, this process of technical development is in important respects not an evolutionary process. With this caveat, I am not referring to the fact that trial and error procedures belong to the methodological spectrum of engineering so that the distinction between a rational engineering methodology and the trial-and-error process of

evolution is overstated (cf., Morange 2013). Rather, what is at stake is that the engineering process, while taking up one aspect of evolution, namely variation and selection, realizes variation in a way highly different from variation in evolution. There, variation is between different individuals. In the engineering case the very same individual is varied again and again, which might not make a difference in the outcome, but is much more resource efficient than an overproduction strategy. Similar changes of the shape of an individual through rearrangement are apparent from biological development. Together with growth processes, such changes might even be considered the kernel of a developmental process, so the “evolution” of the nozzle crosses the line between evolution and development. However, also the developmental metaphor would not be fully adequate for the case of the optimization of the nozzle. Biological development usually follows either a definite order of steps or leads, via regulation, to a predefined result, neither of which seems to hold in our case. However, the spectrum of developmental mechanisms is much broader. The shape of a tree is prefixed only to a certain degree, leaving open a wide range of options. Branches can be ordered in this or another way, as do leaves or roots. Interaction with the environment (e.g., with wind or with stones in the soil) has a huge impact on the precise morphology of the tree. Changes of position can also occur: cells migrate to their “destination” in the embryo, morphogenetic factors spread by diffusion, the differentiation of tissues is induced by another tissue that it comes into contact with due to the growth of some third part of the embryo, etc. (Gilbert 2010). Though it is quite obvious that Schwefel’s experiments with the nozzle were inspired by evolution rather than by biological development, we can hardly classify it as a clear-cut case of an evolutionary procedure.

Fortunately, nothing depends on such a classification. The only reason why I insist on distinguishing aspects of evolution and development in biological morphogenesis is that the pool of morphogenetic mechanisms is obviously much larger than the trial-and-error mechanism that biomimetics adopted from evolution. Biomimetics of level three could draw not only on this single aspect but on a wide spectrum of mechanisms, many of which have evolutionary as well as developmental roots. Evolution and development are intertwined: developmental mechanisms are themselves subjected to—and outcome of—evolutionary processes; evolutionary mechanisms do not bring about isolated and fully developed traits, but rather developmental processes that might contribute to more than one trait. Realizable development is a precondition of evolution, at least of eukaryotes. Since development is susceptible to environmental influence, the environment may have an impact on the variants of phenotypes available for selection and even give rise to new

phenotypes (Gilbert 2010), and since the action of organisms may modify the environment in a systematic way in processes of niche-construction, these actions may in turn have an impact on evolution. These interdependencies are accounted for in the so-called extended synthetic theory of evolution (cf. Sultan 2015; Huneman and Walsh 2017).

I do not mean to propose that biomimetics should try to mimic this entanglement of evolution and development. I simply want to point out that there is much to discover in evolution and development that might be worth mimicking in level three biomimetics. An example might be the development of bones; when a bone grows, its microstructure develops in direct response to the mechanical stress it is subjected to, in a way that allows for maximum stability with respect to the forces that are actually imposed on it via minimal weight. This is mimicked in the construction of bone repair materials (Zhang et al. 2014; Chahal et al. 2019) within a field of biomimetics that re-engineer biological systems.

5. The mimetic asymmetry

Having reconstructed the biomimetic relation that holds between biological and technical systems as mediated by a model, it looks as if transfer could occur in both directions so that a biological—or rather, biotechnological—system designed by a technomimetic approach would be as easy to conceive as biomimetic classical technology. It must be taken into account, however, that technical morphogenetic principles differ from biotic ones in several respects. *Ontogenetic* biological morphogenesis is based on developmental processes. The structures brought about by such process are constrained by the following requirements: that mechanisms that bring such a process about are available, that any intermediate state of the process is viable, and that the processes is robust. Technical construction, while not being restricted by developmental pathways, underlies its own constraints of technical feasibility, budgeting, etc. *Phylogenetic* morphogenesis in the realm of biology again underlies constraints resulting from path dependence and other historical contingencies, while analogous processes in technical development can easily bring together disparate paths. Moreover, the stability requirements for the resulting structures are different in the biological and in the technical realm.

Despite these differences, considerations about the symmetry of the transfer between biology and technology are at the basis of several projects in synthetic biology. Synthetic biology is a heterogeneous field, including top-down modification of existing organisms, bottom-up approaches to the de novo synthesis of new life forms from nonliving materials, and rational engineering

approaches as well as evolutionary ones (Krohs and Bedau 2013). I shall be dealing only with rational engineering in the modification of existing organisms, focusing on the approach that led to the idea of programming cells by arranging bio-bricks, which are short pieces of DNA with particular functions, in a way similar to writing a computer program (Endy 2005). The idea is to generate a particular behavior of the cell, be it a recurrent sequence of states (e.g., in an oscillator like a circadian clock) or an artificial biosynthetic pathway. This approach is often considered to be as appealing as its success is poor. The annual student International Genetically Engineered Machine competition (iGEM), which is based on such an approach, succeeds for other reasons than the development of stable biotic machines (cf. Betten et al. 2018), and rightly so.

Endy and others state the technomimetic aspect of this approach explicitly and design the bioengineering-process accordingly. A flow chart is translated into a modular gene sequence in order to generate a simple gene regulatory network. The program is kept as linear as possible, following a strategy from modular programming in computer science. It links linear sequences with decision points, loops, and plugged-in subroutines. As in rational engineering, components are standardized and modules as decoupled from each other as much as possible. However, it usually turns out that the result, even when it works initially as supposed, is unstable. Elements are expelled from the program since the chassis cell does not copy the program—the engineered DNA—as expected. How and why does this happen? The “how” is obvious: the engineered cells need to divide and multiply in order to generate a measurable and significant output. As soon as cell division comes into play, all kinds of modifications of the genetic material may happen, including gene loss. Measures might be taken to minimize this, like coupling the new material to antibiotic resistance genes, but in the end multiplication of engineered cells happens always in a way that allows for evolutionary change.

It can thus be observed that the genetic material of the engineered cells is evolutionary unstable, as was already the case in the repressilator, a forerunner and still best-known example of this approach (Elowitz and Leibler 2000). Evolutionary instability corrupts the technomimetic bio-brick approach. But why does this happen, despite the success of the rational engineering approach in many other fields of application? The answer I want to propose refers to the conditions for robustness of biological and of technological devices, respectively, as reconstructed in section 3. There, we saw that robustness in biological systems is based on ongoing morphogenesis and a deep entanglement of all processes: structures are not stable, but are permanently rebuilt and adjusted by trial and error and/or by regulated replacement of all

components, and processes are interdependent by involving shared components. In technical systems, on the other hand, robustness is based on low rates of wear and tear, in decoupling and other mechanisms limiting the impact of errors, and in easy maintenance. Though there are certainly exceptions, robustness of biological systems generally lies in the interdependence of all their components, while robustness of technical systems is based on the separation of effects even though functions are brought about only by coupling and interaction. In other words, messy, holistic interactions lead to robustness in biological systems, while sterile, analytic interactions lead to robustness in technical systems.

This observation suggests a plausible answer for why a rationally planned and modified organism lacks robustness: the implanted modules are not deeply embedded in the system of the organism, but are instead added in a sterile way. But the modified organism cannot be maintained like a technical artifact, which would allow for the robustness of such a delicate system with only few interconnections. It maintains itself by expelling every implant that is not deeply embedded in the functioning of the cell. To put this in evolutionary terms: rationally planned top-down synthetic biology tries to get the implanted genetic programs selected, and the strategy is to couple them superficially to other genes that are under selection pressure. The setting *selects for* these other genes, and this is supposed to result in the *selection of* (Sober 1984) the implanted program that is coupled to the primarily selected genes. This, at least, is the rationale of the process. In reality, *selection of* the implanted program is not sufficient since the coupling to the genes *selected for* is easily dissolved in a few evolutionary steps. The technomimetic biological system still underlies biological (evolutionary) criteria of robustness and expels hitchhikers that do not themselves contribute to the stability of the system. Seen this way, expelling the implanted material is a result of the robustness of the cell rather than an indicator of lacking robustness.

In principle, applying a biomimetic third-level approach could solve this situation by taking advantage of evolutionary and developmental mechanisms in stabilizing the genetically engineered system. This would require deeply embedding the added components rather than implanting them in a decoupled way. The goal would be that *selection for* these components occurs rather than the mere *selection of* them. This would require their involvement in pathways that are required for survival of the cells, in addition to their respective roles in the constructed pathways: the components needed to perform roles in fundamental processes within the cell. I do not dare speculate how this would be possible, as strategies would be required to embed the additional genes or their products deeply into metabolism or cell regulation. Such strategies might

best be copied from biological processes. Such biomimetic copying of genetic robustness will almost certainly require a far more sophisticated approach than plugging together bio-bricks.

The following picture of a biological cell with its gene regulatory network may illustrate my claim: look at the cell and its metabolism as if it were a bowl filled with pebbles. The pebbles build up a fairly stable structure since they are supporting each other and are restricted by the bowl. Implanting additional genes would be like adding marbles on top of the pebbles; this will work for a few added marbles, especially if you arrange them in a single layer or in the shape of a pyramid. Now try to build a delicate sculpture, say with the proportions of a Giacometti figure, from the added marbles with as few links to the pebbles as possible with the aid of only some viscous grease. It is highly unlikely that your structure will survive for a long time or remain intact when moving or shaking the bowl. A much better way to stabilize the marble structure would be to embed it within the pebbles. It might not be easy and you will not be able to see the submersed structure, but it is there, stabilized by numerous interactions with the pebbles. If the delicate sculpture represents the sophisticated program constructed out of bio-bricks, and moving and shaking of the bowl stands for selection pressure, this picture provides an apt understanding of the lack of robustness of the genetically engineered “machine” cell and the problems of stabilizing it, which hold on as long as the add-ons are not deeply embedded in the fundamental processes of the cell.

We can now describe the biomimetic relation between biological and technical system in a more detailed manner than in section 2. Instead of the biological and the technical system being considered just as two instantiations of a model of the desired *function*, which lead to a symmetrical relation that did not hold in the example from synthetic biology, the picture needs to account as well for the *robustness of the realization*, which is not represented by the model of the mere function. A biomimetic device needs to be a *robust* instantiation of the model, where robustness is to be achieved in a way that is adequate for the receiver system rather than for the donor system. If the receiver system is a purely technical one, then the criteria for technical robustness hold. If it is a biological system, then biological robustness needs to be implemented. This means that the mimetic relation is doomed to fail when robustness of the receiver system is constructed according to robustness mechanisms of the donor system. I have demonstrated this idea in regard to the technomimetic reconstruction of a biological system, where the receiver system is a biological cell and the donor system a (envisaged technical implementation of a) computer program, but it will hold also in the other direction, which simply does not attract attention because it is routinely observed: a biomimetic artifact that is

not itself a biological system needs to be robust in terms of artifact robustness, and engineers know how to achieve this. Biological robustness is not at stake in such a case. Where it would be at stake in the bio-brick approach of synthetic biology, one does not know how to implement it. Therefore, the mimetic relation is at present asymmetric and leads not on the same way from biological to technical systems as the other way around.

6. Conclusion

Biomimetics is a relevant and very successful approach for implementing technical functions. The reconstruction of the epistemology of biomimetics demonstrates that the approach is based on models of the function that link biological and technical systems. At first glance, the relation between biological and technical systems is symmetrical. Since the strategies to make the systems robust differ between biology and technology, the transfer is limited by needs for robustness. In this regard, it is the receiver system and not the donor system that determines the criteria of a successful implementation of the function, which breaks the symmetry of the relation between donor system, model, and receiver system. This helps to understand why the bio-brick approach in synthetic biology ultimately failed. It tried to transfer not only the technical design principles for implementing a function from the technical to the biological realm, which worked nicely, but also the means to achieve robustness, which failed. In a biological system, even if it is technomimetically re-engineered, robustness needs to be biological.

Acknowledgments:

I wish to thank all discussants at the summer school ‘Varieties of Experiment and Measurement in Technoscience – The case of Synthestic Biology’ and at my lecture within the series ‘Morpho-Genesen – Formgeschichten aus Biologie, Architektur, Mathematik und Design’, in particular Alfred Nordmann and Marco Tamborini who organized both events at the Technical University of Darmstadt in 2018, for their helpful feedback on my presentation of topics from this paper. Treatment of evolutionary questions was inspired by the DFG-funded Collaborative Research Centre TRR 212 ‘A Novel Synthesis of Individualisation across Behaviour, Ecology and Evolution: Niche Choice, Niche Conformance, Niche Construction’ (NC³).

References:

Arnold, Frances H. 2019. “Innovation by Evolution: Bringing New Chemistry to Life (Nobel Lecture).” *Angewandte Chemie International Edition* 58:14420–14426.

- Barthlott, Wilhelm, and NESTA Ehler. 1977. "Rasterelektronenmikroskopie der Epidermisoberflächen von Spermatophyten." Pp. 367–467 in *Tropische und subtropische Pflanzenwelt*. Vol. 19. Mainz: Akademie der Wissenschaften und der Literatur. Wiesbaden: Franz Steiner Verlag.
- Betten, Afke Wieke, Virgil Rerimassie, Jaqueline E. W. Broerse, Dirk Stemerding, and Frank Kupper. 2018. "Constructing future scenarios as a tool to foster responsible research and innovation among future synthetic biologists." *Life Sci Soc Policy* 14:21.
- Bhushan, Bharat. 2009. "Biomimetics: Lessons from Nature – an Overview." *Philosophical Transactions of the Royal Society A* 367:1445–1486.
- Bhushan, Bharat. 2016. "Gecko Effect." Pp. 1319–1328 in *Encyclopedia of Nanotechnology*. Edited by Bharat Bhushan. Dordrecht: Springer.
- Borsari, Andrea. 2017. "Human Mimicry and Imitation: The Case of Biomimetics." *Aisthesis. Pratiche, Linguaggi E Saperi dell'estetico* 10:51–61.
- Boxerbaum, Alexander S., Kendrick M. Shaw, Hillel J. Chiel, and Roger D. Quinn. 2012. "Continuous Wave Peristaltic Motion in a Robot." *The International Journal of Robotics Research* 31:302–318.
- Braitenberg, Valentino. 1984. *Vehicles: Experiments in Synthetic Psychology*. Cambridge: MIT Press.
- Chahal, Sugandha, Anuj Kumar, and Fathima S. J. Hussian. 2019. "Development of Biomimetic Electrospun Polymeric Biomaterials for Bone Tissue Engineering. A Review." *Journal of Biomaterials Science, Polymer Edition* 30:1308–1355.
- Chin, Diana D., and David Lentink. 2016. "Flapping Wing Aerodynamics: From Insects to Vertebrates." *The Journal of Experimental Biology* 219:920–932.
- Dickinson, Michael H., and Florian T. Muijres. 2016. "The Aerodynamics and Control of Free Flight Manoeuvres in *Drosophila*." *Philosophical Transactions of the Royal Society B* 371:20150388 <http://dx.doi.org/10.1098/rstb.2015.0388>.
- Elowitz, Michael B., and Stanislas Leibler. 2000. "A Synthetic Oscillatory Network of Transcriptional Regulators." *Nature* 403:335–338.
- Endy, Drew. 2005. "Foundations for Engineering Biology." *Nature* 438:449–453.
- Garson, Justin. 2016. *A Critical Overview of Biological Functions*. Dordrecht: Springer.
- Gilbert, Scott F. 2010. *Developmental Biology*, 9th ed.. Sunderland: Sinauer Associates.

- Green, David W., Jolanta A. Watson, Han-Sung Jung, and Gregory S. Watson. 2019. "Natural History Collections as Inspiration for Technology." *BioEssays* 41:1700238. DOI: 10.1002/bies.201700238.
- Hammerstein, Peter, Edward H. Hagen, Andreas V. M. Herz, and Hanspeter Herzel. 2006. "Robustness: A Key to Evolutionary Design." *Biological Theory* 1:90–93.
- Huneman, Philippe, and Denis M. Walsh (eds.). 2017. *Challenging the Modern Synthesis: Adaptation, Development, and Inheritance*. Oxford: Oxford University Press.
- Hülse, Martin, Steffen Wischmann, and Frank Pasemann. 2004. "Structure and Function of Evolved Neuro-Controllers for Autonomous Robots." *Connection Science* 16:249–266.
- Kan, S. B. Jennifer, Russell D. Lewis, Kai Chen, and Frances H. Arnold. 2016. "Directed Evolution of Cytochrome C for Carbon–Silicon Bond Formation: Bringing Silicon to Life." *Science* 354:1048–1051.
- Karásek, Matěj, Florian T. Muijres, Christophe De Wagter, Bart D. W. Remes, and Guido C. H. E. de Croon. 2018. "A Tailless Aerial Robotic Flapper Reveals that Flies Use Torque Coupling in Rapid Banked Turns." *Science* 361:1089–1094.
- Krohs, Ulrich. 2008. "How Digital Computer Simulations Explain Real-World Processes." *International Studies in the Philosophy of Science* 22:277–292.
- Krohs, Ulrich. 2009a. "Functions as Based on a Concept of General Design." *Synthese* 166:69–89.
- Krohs, Ulrich. 2009b. "The Cost of Modularity." Pp. 259–267 in *Functions in Biological and Artificial Worlds: Comparative Philosophical Perspectives*. Edited by Ulrich Krohs and Peter Kroes. Cambridge: MIT Press.
- Krohs, Ulrich. 2021. "Evolution und Entwicklung – universelle Konzepte?" Pp. 77–90 in *Biologische Transformation – Interdisziplinäre Grundlagen für die angewandte Forschung*. Edited by Tomas Marzi, Hans-Werner Ingensiep, and Heike Baranzke. Oberhausen: Laufen.
- Krohs, Ulrich, and Mark A. Bedau. 2013. "Interdisciplinary Interconnections in Synthetic Biology." *Biological Theory* 8:313–317.
- Kroner, Elmar, and Eduard Arzt. 2016. "Gecko Adhesion." Pp. 1308–1319 in *Encyclopedia of Nanotechnology*. Edited by Bharat Bhushan. Dordrecht: Springer.
- Letelier, Juan-Carlos, Jorge Soto-Andrade, Flavio Guíñez Abarzúa, Athel Cornish-Bowden, and María Luz Cárdenas. 2006. "Organizational Invariance and Metabolic Closure: Analysis in Terms of (M, R) Systems." *Journal of Theoretical Biology* 238:949–961.

- Maturana, Humberto R., and Francisco J. Varela. 1980. *Autopoiesis and Cognition: The Realization of the Living*. Dordrecht: Reidel.
- McCaskill, John S. 2009. *PACE Report: Programmable Artificial Cell Evolution*. http://www.biomip.org/pacereport/the_pace_report/index.html Accessed March 17, 2021.
- Menciassi, Arianna, Samuele Gorini, Giuseppe Pernorio, Liu Weiting, Francesco Valvo, and Paolo Dario. 2004. "Design, Fabrication and Performances of a Biomimetic Robotic Earthworm." Paper presented at the 2004 IEEE International Conference on Robotics and Biomimetics, August 22–26.
- Morange, Michel. 2013. "Comparison Between the Work of Synthetic Biologists and the Action of Evolution: Engineering Versus Tinkering." *Biological Theory* 8:318–323.
- Nachtigall, Werner. 2010. *Bionik als Wissenschaft. Erkennen – Abstrahieren – Umsetzen*. Berlin: Springer.
- Peacock, Mark S. 2009. "Path Dependence in the Production of Scientific Knowledge." *Social Epistemology* 23:105–124.
- Perlman, Mark. 2004. "The Modern Philosophical Resurrection of Teleology." *The Monist* 87:3–51.
- Pritchard, Duncan. 2005. *Epistemic Luck*. Oxford: Oxford University Press.
- Rechenberg, Ingo. 1973. *Evolutionsstrategie – Optimierung technischer Systeme nach Prinzipien der biologischen Evolution*. Stuttgart: Frommann Holzboog.
- Rosen, Robert. 1973. "On the Dynamical Realization of (M, R)-Systems." *Bulletin of Mathematical Biology* 35:1–9.
- Rosen, Robert. 1991. *Life Itself: A Comprehensive Inquiry Into the Nature, Origin, and Fabrication of Life*. New York: Columbia University Press.
- Sarikaya, Mehmet, and Ilhan A. Aksay (eds.). 1995. *Biomimetics: Design and Processing of Materials*. Woodbury: AIP Press.
- Schwefel, Hans-Paul. 1968. "Experimentelle Optimierung einer Zweiphasendüse." Report HE/F 35-B from AEG Forschungsinstitut Berlin.
- Shyy, Wei, Chang-kwon Kang, Pakpong Chirarattananon, Sridhar Ravi, and Hao Liu. 2016. "Aerodynamics, Sensing and Control of Insect-Scale Flapping-Wing Flight." *Proceedings of the Royal Society A* 472:20150712. <http://dx.doi.org/10.1098/rspa.2015.0712>.
- Sober, Elliott. 1984. *The Nature of Selection: Evolutionary Theory in Philosophical Focus*. Cambridge: Bradford/MIT Press.
- Solga, Andreas, Zdenek Cerman, Boris F. Striffler, Manuel Spaeth, and Wilhelm Barthlott. 2007. "The Dream of Staying Clean: Lotus and Biomimetic Surfaces." *Bioinspiration & Biomimetics* 2:126–134.

- Sultan, Sonia E. 2015. *Organism and Environment: Ecological Development, Niche Construction, and Adaptation*. Oxford: Oxford University Press.
- Vincent, Julian F. V., Olga A. Bogatyreva, Nikolaj R. Bogatyrev, Adrian Bowyer, and Anja-Karina Pahl. 2006. "Biomimetics: Its Practice and Theory." *Journal of the Royal Society Interface* 3:471–482.
- Wouters, Arno G. 2003. "Four Notions of Biological Function." *Studies in History and Philosophy of Biology and Biomedical Science* 34:633–668.
- Zhang, Xuesong, Ming Lu, Yan Wang, Xiaojing Su, and Xuelian Zhang. 2014. "The Development of Biomimetic Spherical Hydroxyapatite/Polyamide 66 Biocomposites as Bone Repair Materials." *International Journal of Polymer Science* 2014:579252. <http://dx.doi.org/10.1155/2014/579252>.