Chapter 4
Semiotic Explanation in the Biological Sciences

Ulrich Krohs

Abstract Many biological explanations are given in terms of transduced signals and of stored and transferred information. In the following, I call such information-theoretical explanations "semiotic explanations." Semiotic explanation was hardly ever discussed as a distinct type of explanation. Instead, philosophers looked at information transfer as a somewhat unusual subject of mechanistic explanation and consequently attempted to frame biological information as being observable within physicochemical mechanisms. However, information-theoretical terms never occur in isolation or as a plug-in in mechanistic models but always in the context of information-theoretical models like the semiotic model of protein biosynthesis. This chapter proposes that "information" enters the game as a theoretical term of semiotic models rather than as an observable and that semiotic models have explanatory value by explaining molecular mechanisms in functional rather than in mechanistic terms.

Keywords Biological information • Conserved quantity • Model structure • Nonconservative model • Signal

4.1 Introduction

Biology uses several different kinds of explanation. Among those are causal-mechanistic, constitutive, evolutionary, and deductive-nomological explanations, all of which are well studied in philosophy of science. Giving a causal-mechanistic account is the right way to explain glycolysis or fatty acid synthesis. Constitutive accounts are used in explaining the locomotion system of vertebrates as being made up of bones, muscles, and tendons or in explaining

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cell respiration as being constituted by the respiratory chain, the NADPH/NADP$^+$ system, the TCA cycle, etc. To explain the presence of particular organismic traits in an organism, evolutionary explanations, which refer to an iterated sequence of variation and selection events, seem to be the adequate kind of explanation to give. Deductive-nomological explanations, finally, though they might be less often applied in biology than in physics, are used whenever a phenomenon is found to be governed by a general law.

Some other types of biological explanation, however, are less well understood and raise severe philosophical concerns. Those are functional explanation, which is regarded as teleology laden and was discussed continuously for half a century in philosophy of science (and by Kant anyway), and explanation in terms of transduced signals and of stored and transduced information. This chapter concentrates on the latter.[1] In the following, I shall call such information-theoretical models "semiotic explanations."

A common account of protein biosynthesis may serve as an example for a semiotic explanation. It represents one of two different ways in which molecular biologists describe the DNA-dependent biosynthesis of nucleic acids and of proteins. This first account explains protein biosynthesis in terms of information transfer and decoding, where the protein sequence is regarded as being coded in the base sequence of DNA. Protein biosynthesis is, thus, explained as a sign process or semiotic process. There is of course also an explanation of another kind that explains protein biosynthesis. It is given in terms of the structures of the molecules involved, the chemical reactions the molecules undergo, and the kinetics and thermodynamics of reactions and biosynthetic pathways. Both models explain the very same process but frame it differently. The first model is a *semiotic model* that gives a semiotic explanation in the sense introduced above; the second one is a *physicalistic model* that explains the same process of protein biosynthesis on the basis of the biochemical processes involved, without referring to any coding function of the involved biochemical components.

While the physicalistic model is generally accepted as giving a proper scientific explanation, the intriguing semiotic model is often challenged because it applies seemingly intentionalist concepts in the non-intentional realm of molecules. It refers to information coded in the DNA and describes the different ways in which information is processed within the cell. It states that information is being copied when a structurally identical molecule of DNA is synthesized, that it is transcribed to RNA, that RNA may be further processed, and that the information of some particular kind of RNA is translated into the sequence of a protein. The whole model is based on semiotic – or sign-theoretical – terminology, using not only the terms "information," "coding," "copying," "transcribing," and "translating" but also "proofreading," "correcting," "recognizing," and many other terms from the field of text processing (see, e.g., Alberts et al. 2002). A vivid discussion was going on among philosophers of biology about whether the term "information" is

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[1] In Krohs (2009a, 2011), I deal with the first kind of explanation.

used merely metaphorically in this context (Kay 2000; Griffiths 2001), whether it should be regarded as completely discredited (Sarkar 1998, 2005; Moss 2003), or whether the concept can be naturalized – and if so, in which way this might be done (Sterelny et al. 1996; Godfrey-Smith 1999, 2000; Maynard Smith 2000; Griffiths 2001; Jablonka 2002; Stegmann 2005).[2]

The philosophically less problematic physicalistic model is rather detailed and can be sketched here only superficially. The following account shall merely give an idea of the way this model refers to the processes in question: The structure of the DNA is a sequence of the four bases thymine, adenine, guanine, and cytosine; the molecule is replicated by polymerization of deoxyribonucleotides, the process being catalyzed by the DNA-dependent DNA polymerase and by a strand of DNA; this reaction is thermodynamically driven by the hydrolysis of a pyrophosphate bond in the nucleotides. The description will, of course, add more steps and more details. In the analogous case of RNA biosynthesis, the DNA-dependent RNA polymerase is involved as a catalyst instead, and ribonucleotides are the reactants instead of deoxyribonucleotides. The model also includes the kinetic data of the reactions (Alberts et al. 2002). Overall, the model describes the mechanism of DNA replication, of RNA biosynthesis, and of protein biosynthesis in terms of the components involved and of their interactions. It can therefore be regarded as a mechanistic explanation in the sense of Machamer et al. (2000), Craver (2001), and Bechtel and Abrahamsen (2005).[3] Protein biosynthesis was even made a paradigm case of biological mechanistic explanation (Darden and Craver 2002).

The semiotic and the physicalistic model are, of course, related to each other. Biologists and many philosophers therefore claim that the semiotic model is only a shorthand version of the physicalistic model to which it may be reduced. However, the reducibility claim runs into problems because information is being regarded as multiply realizable. That the very same piece of information may occur in different realizations during processes of information transduction forms a major obstacle to reduction, because identity through different realizations cannot be captured in physicochemical terms, which refer to the realizations only. I shall therefore treat semiotic and physicalistic models separate and inquire into their respective explanatory values.

There is little doubt about the explanatory value of the physicalistic model: it explains the physicochemical processes going on in protein biosynthesis, i.e., it states the mechanism of protein biosynthesis. The case of the semiotic model is not so clear and demands further philosophical analysis. As will become clear in Sect. 4.4, I do not attribute the explanatory success of semiotic models to the concept of information, though it is obviously crucial to these models. No concept has explanatory power in itself. The basic unit of scientific explanation, as Morgan and Morrison (1999) and Giere (2004) plausibly argue, is the model

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[2] For a detailed outline of the debate, see Godfrey-Smith (2007).

[3] Glennan's (1996, 2002) approach is similar, except not counting the interactions among the constituents of a mechanism.

rather than a concept or an isolated general statement that makes use of the concept. Consequently, in trying to understand the explanatory role of semiotic models, I do not start from the very concept of information but from the semiotic model as a whole.

In the following, I first introduce a general distinction between two different kinds of models (Sect. 4.2). Using this distinction as a tool for discerning the epistemic virtues of different models, I then discuss the question of whether or not the semiotic model may be reduced to the physicalistic model (Sect. 4.3). Next, the epistemic role of the semiotic model is discussed (Sect. 4.4). Finally (Sect. 4.5), I propose an altered view on the very concept of genetic information.

4.2 Conservative and Nonconservative Models

Models making use of semiotic terms are in fact of a special kind, different from the kind of models used in physics – and different as well from the physicalistic models that are used in biology. In order to conceptualize this difference, I am introducing a distinction between *conservative* and *nonconservative* models. The distinction is such that it singles out physicalistic models as one of the two kinds. It will be shown that semiotic models belong to the other kind.

In order to find a criterion that singles out physicalistic models from other models in biology, we must use physics as our reference. However, any criterion that is supposedly valid may be falsified by the further development of science. There is neither a stable content of physical theories through the centuries nor a stable language of physics (e.g., Hempel 1980). Therefore, we should not look for an a priori valid criterion but for a demarcation criterion that holds with respect to present-day physics. Causality might count as the first candidate for such a criterion. However, although it may be regarded as one of the central notions of physics, there are also noncausal processes or at least processes that cannot be described as causal ones, such as radioactive decay. Causality also fails to hold in the realm of (relativistic) quantum mechanics. So it does not seem to demarcate physical theories properly. Instead, nowadays the minimal requirement for any physical theory or model seems to be that certain variables obey conservation laws: the laws of the conservation of energy (including mass), of net charge, of momentum, and of angular momentum. This holds for the whole range of accepted physical theories, from the classical harmonic oscillator to quantum electrodynamics (Tipler and Mosca 2007).[4] It holds also for the theory of dissipative structures. A dissipative system loses energy through time, but the energy is not annihilated. Any adequate physical model of such a system must postulate a reservoir outside the considered system that takes up dissipated energy. Constancy of energy of the higher system,

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[4] We must abstain here from phenomena such as symmetry breaking at the level of elementary particles that are not yet understood satisfactorily.

then, which is made up of the system under investigation plus its environment, is presupposed. This is indeed generalizable: each model in any field of contemporary physics must observe the conservation laws.

Conservativity therefore may be used as a criterion to demarcate physicalistic models, i.e., models of the physical and physicochemical perspective on a phenomenon, in present-day science.[5] Physicalistic models are conservative models. An example is the physicalistic model of cell biology, which describes the reaction pathway from DNA to protein by reference to molecules, reaction kinetics, binding energies, etc. Though it may not usually be spelled out fully in terms of energy conservation but is given as a partial model only, scientific research aims at describing every single step in accordance to the requirements of physical theories, in particular to the conservation of masses and energies (cf. the references given by Alberts et al. 2002 and by Darden and Craver 2002). A premise of stating the model is that the full model meets the requirements of the conservation laws, so that all calculations performed on the basis of this model rely on those laws.

Models which focus on quantities that are not derivable from conserved quantities I call nonconservative models. The nonconserved variables of such models do not represent physical quantities. Examples of nonconservative quantities are cellular signals that are related to hormone action or to external stimuli. A signal in the sense of biological information transduction can simply disappear, without being transformed into anything else. There is no law of signal conservation, nor can signals be deduced from conserved quantities – the same amount of energy and the same configuration of masses may or may not be a signal, and in case of being a signal, it may signal completely different things.

Nonconservative quantities can also be found in the realm of technology (Krohs 2009b), where truth-values in models of logic circuits and other symbolic variables[6] may serve as examples. Besides semiotic or symbolic variables, other functions and functional variables are nonconservative as well. This, again, holds for the biological as well as for the technical realm.[7]

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[5] Dowe (1992) and Salmon (1994) correctly identified conservation laws as being at the core of modern physics. The link that these authors draw between conservativity and causality, however, can hardly be justified. In contrast to their proposal, conservativity may neither count as a necessary, nor as a sufficient condition for causality: neither is each conservative process causal (e.g., radioactive decay, tunneling, quantum transitions), nor are all causal processes conservative (e.g., semiotic processes; see Sect. 4.3).

[6] Herbert Simon calls any technical information processing system a physical symbol system (Simon 1996, p. 21, pp. 187–188).

[7] Here the concept of function is taken in the sense of a causal role function (Cummins 1975), which nevertheless allows for judgment about malfunction. To allow for this normativity of the concept, a modification needs to be introduced into Cummins's account, e.g., by reference to fixed types of function bearers (Krohs 2009a, 2011).

4.3 Semiotic Models as Nonconservative Models and the Question of Reduction

To further work out the difference between semiotic and physicalistic models, the distinction between information and its carrier is crucial. The carrier of information may be an electric potential or electric current, be it in a computer or in a nerve cell; it may be the ink on a piece of paper or compressional waves in the air; or it may be, according to semiotic models of molecular biology, the structure of a nucleic acid molecule. The carriers are physical entities, and all transformations they undergo obey the conservation laws. Consequently, they and their relations and interactions may be described by an appropriate physicalistic model.

The case is different with the information that they carry. As already mentioned, information may disappear without residue. It may also appear without being governed or restricted by conservation conditions. For the first case, consider a technical device for information processing like a logical gate, say, the NOR gate. Its output is "one" if and only if both inputs are "zero." In all three other cases of defined input, the output will be "zero." If the output is stored and the gate is then switched off, the stored information is "one" or "zero." In case it is "zero," the information about the input channels, namely, which one of them was "one," is lost. The lost information is neither transformed nor dissipated; it is annihilated. Information is not conserved, and from two bits of information, only one is left. A similar case of information loss can be found in any degenerate code, like the DNA code, where in most cases more than one base triplet codes for an amino acid. The informational content of the third base is lost during translation into a protein sequence. Nonconservativity of information is, however, not restricted to cases of redundancy. Imagine a breakdown of a computer occurring before a freshly composed text or the data obtained in a series of measurements were saved. The energy balance of the breakdown may depend on the number of bits stored in the computer, i.e., on the size of its memory. But it does not depend, at least not in a systematic manner, on the symbolic content of the memory. The information is not transformed but lost when the system breaks down. Similarly, on the hydrolysis of a piece of DNA, genetic information is lost, although binding energy and molecular material of the carrier of information are conserved.

Nonconservativity holds as well for information increase. New information may be generated when a random sequence of DNA is synthesized, when a point mutation gives rise to an altered sequence, or when the insertion of a base or of some pseudogene occurs in a living cell. Thus, on the transformation of some molecule, we see an increase, alteration, or decrease of information. (This, of course, is the image drawn by the semiotic model, not by a physicalistic account, which does not support talking about information.) Information does not obey conservation laws; only the underlying molecular processes do. Semiotic models are nonconservative ones.[8]

These considerations entail several reasons why semiotic models cannot be reduced to physicalistic ones.[9] First, the semiotic model allows to discern between informational processes running properly and processes going wrong. It allows identifying several kinds of copying errors, correction functions, etc. This means that the semiotic model is a functional model that discerns function from malfunction; it is a normative model. Function in the normative sense is and must be absent from physicalistic models Therefore, they cannot fully account for what the semiotic model explains. Next, also concerning the aspect of functionality, physicalistic models can neither account for nor explain multiple realizability of semiotic entities, i.e., for the fact that the same piece of information can have various carriers. Third, it is all but clear how the identity of a piece of information or of a signal through various realizations could be described by merely referring to its various heterogeneous carriers. And finally, though perhaps only of pragmatic relevance, the task of reduction would be much larger than envisaged by accounts concentrating on the concept of information itself: a whole set of semiotic concepts is involved, many if not all of them referring in their original context to intentional text processing. All of those needed to be reduced to physicalistic descriptions.

So the semiotic model is not only an incomplete version of a physicalistic one. It makes use of classifications, such as being a signal or coding for some component, that are alien to physicalistic models. There are two mutually nonexclusive ways to explain protein biosynthesis: by a conservative, physicalistic model and by a nonconservative, semiotic one. Neither of them alone covers all that can be known about the process that is to be explained.

4.4 The Epistemic Role of Semiotic Models in Biology

As already mentioned, the physicalistic model of protein biosynthesis explains what is going on physicochemically during this process. Its epistemic role is to give a mechanistic account of the process. A mechanism in this sense consists of the set of the entities involved and the relations that hold between them. But being conceived as a mechanism, it is also conceived as the mechanism *of something*, namely, as an instantiation of a cellular capacity which is individuated functionally and which consists of a set of functional roles. Darden and Craver (2002) describe

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[8] A further question is whether nonconservativity of functional models holds in general. This seems to be the case (Krohs 2004). The function of a screw (or of any other mechanical device) of being a stop for a lever can simply be lost under certain circumstances, e.g., if the lever is bent. There is no necessity of the function being transformed into anything else according to any conservation law.

[9] Only theory reduction is at stake here. Ontological reducibility may be presupposed, be the semiotic model reducible to the physicalistic one or not.

many of the role functions in protein biosynthesis in terms of information flow. So the mechanistic explanation is also related to the semiotic model, which is given exactly in these functional terms. Inquiring the epistemic role of the semiotic model, one must consider, then, how it relates to what Darden and Craver call a mechanistic schema. The semiotic model is clearly not identical with the schema, since the latter does not refer to actual components of a mechanism but provides placeholders instead: "Mechanism schemata are abstract frameworks for mechanisms. They contain place-holders for the components of the mechanism (both entities and activities) and indicate, with variable degrees of abstraction, how the components are organized" (Darden and Craver 2002, p. 4). The semiotic model, in contrast, does refer to molecular components of the cell, namely to the same ones as the physicalistic account does, so the places are already filled. In contrast to a schema, the semiotic model has an ontology, even more or less the same ontology as the physicalistic one, with the notable exception of semiotic terms. The latter do not have correlates in the physicalistic model. In particular, they are not placeholders for physical entities. So the semiotic model is itself an instantiation of a schema rather than an un-instantiated schema. Darden and Craver conceive the schema as the schema of the mechanism, which is described by the physicalistic model (in my terminology). It now turns out to be the schema of both the physicalistic and the semiotic model.[10]

If the semiotic model is not reducible to the physicalistic one and a fortiori not simply a shorthand or laboratory slang version of the latter, it remains to clarify what precisely the epistemic role of the semiotic model is. The answer is to be found in the biologists' aim to explain both, the physicochemical processes of living entities, and their functional organization. The question about functionality, while absent from physics and chemistry, forms the very basis of physiology. A functional model, e.g., the model of the blood circuit as a distributor system, the model of the liver as a detoxifier, or the model of a mitochondrion as the power station of the cell, helps to understand a biological entity as an organized system. It embeds a particular capacity into the hierarchical structure of capacities of the organism. Such a particular capacity may contribute to the overall capacities (i.e., function) or fail to contribute properly (i.e., malfunction). The semiotic model that serves as an example throughout this chapter places the pathways involved in information processing into a hierarchy of contributions to growth, self-maintenance, and proliferation of the cell; to the regulation of cell metabolism and integration of the organism; and to degradation of cellular components and to cell aging. It does so by simplifying the physicalistic description and at the same time introducing functional

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[10] Darden and Craver (2002, p. 5) ascribe work on information flow to molecular biologists and work on the flow of matter and energy to biochemists. While this might be considered a somewhat artificial attribution of different research topics to disciplines, it clearly emphasizes that physicochemical and semiotic analyses are categorically different and thus should indeed give rise to models of different kind.

entities which are absent from physicalistic models: firstly, diverse processes are unified in regarding physicochemically different steps as the processing of one identical signal or piece of information; secondly, the physical requirements of particular realizations of this organization are disregarded. Most, if not all, functions could be realized in many different ways (Carrier 2000), and each realization would underlie different physical constraints. So building nonconservative models is not sloppiness in constructing a model in order to get rid of too much detail. It is rather the prerequisite for an integrated view on biological organization. The semiotic model, while being silent on the physicochemical mechanism, gives quite accurate an explanation of the functional structure of protein biosynthesis and allows for precise and successful predictions of the behavior of the system's processing of different pieces of DNA. It also allows for judging whether or not, in a particular case, the processes are running properly.

The problem seems to remain that information talk, known from settings with intentional senders and receivers, seems to be inadequate when applied on the molecular level. What, then, justifies the use of semiotic models and their transfer into a new area of application? When we are asking for the justification of the use of a model, two candidates are available for what may be regarded as explanatory: the structure of a model or its conceptual content. With regard to the content, the semiotic model is all about information and its processing. This content does not seem to be justified by the phenomenon to be described, as the critique mentioned in Sect. 4.1 has shown. In particular we do not want to assume or presuppose intentionality on the molecular level, which makes explanation of protein biosynthesis in terms of semiotic processes somewhat dubious. I therefore propose to search for explanatory power in the structure rather than in the conceptual content of semiotic models. Structurally, the semiotic model appears to fit well to the phenomena as described by the physicalistic model. This is not affected by the somehow odd reference of the model to molecular information. In particular, features like the degeneracy of the code – i.e., the finding that different base triplets give rise to the incorporation of the same amino acid into a protein – or the different steps of transcription are captured in a straightforward way by an account that allows for multiple realizability. In the case of signal transduction, one and the same signal, i.e., a nonconserved quantity, is described as being a conformation change of a small molecule, of an enzyme, of an ion channel, etc. This is reflected by the structure of the relevant semiotic model. Its structure, consequently, must be regarded as carrying or contributing to the explanatory power of the semiotic model. The features of the system that are captured by this structure are, in contrast, not grasped by the physicalistic model – neither by its structure nor by its conceptual content. This is why biologists cannot refrain from using nonconservative, semiotic models.

Conceptual content and structure can both matter for the explanatory power of a model. This is usually taken for granted for the content side and spelled out for the structural side by structural realism.[11] Since, in the present case, we find that the conceptual content can hardly explain the epistemic value which the semiotic model obviously has, structure alone seems to be responsible for the epistemic success of semiotic models. We may still blame the model for its misleading content, but as long as the structure of the model is required for epistemic reasons and cannot be had without this very content, the somewhat dubious content alone does not seem to be a sufficient reason for eliminating the model. So, if structural explanation is a part of scientific explanation, the semiotic model has its merits exactly in this realm. Since the conceptual content seems to be ontologically inadequate, a nonconservative model does not, or should not, even aim at a realistic description of the inventory of the physical world – otherwise, it needed to be conservative.[12] Models of both kinds have a different status. Consequently, it would be consistent to allow for metaphorical content of nonconservative models and nevertheless demand ontological adequacy for the conceptual content of conservative models.[13] (Theoretical terms, nevertheless, are notoriously posing a problem in this respect.)

4.5 How to Deal with the Concept of Genetic Information

My account of the explanatory power of semiotic models does not interpret the conceptual content of these models and therefore does not explicate the concept of information. It remains puzzling why semiotic terminology seems to be crucial for the models in question. For now, I can just present a guess why biologists describe the functional organization of protein biosynthesis in semiotic terms. The guess is that simply no other functional model could yet be found that has a comparable structure, i.e., that describes various sequential conformation changes as realizations of the same function or, more generally, of the same nonconservative quantity. No such model was found that uses a terminology that avoids semiotic concepts and nevertheless manages to hook up with our understanding of some processes we are familiar with so that it can be integrated into our system of knowledge. The use of the concept of information seems to be the price biologists have to pay for gaining a structurally adequate nonconservative model of the functionality of protein biosynthesis.

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[11] Nevertheless, one needs not subscribe to structural realism, neither in its epistemic (Maxwell 1970; Worrall 1989, 1994) nor in its ontic variant (Ladyman 1998; French and Ladyman 2003), to accept the explanatory power of the structure of a model.

[12] In so far, the realist interpretation of semiotic terms in molecular biology by some biosemioticians is misguided.

[13] Since the physicalistic model carries the realist burden, the correlated semiotic model even must not be interpreted in a realist way. I see no reason for going as far as postulating an informational ontology (Floridi 2008, 2009).

Does this mean that the concept of genetic information is used metaphorically? As an isolated concept, it is hard to see how it could work as a metaphor at all. What should be the content carried by the metaphor, in a field, where intentionality and interpretation are absent? However, the model makes use of a whole set of interrelated concepts as listed above. If anything, the conceptual set as a whole should be regarded as the metaphor, transporting the structure or the model rather than the semiotic content into the field of molecular biology.

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