

Semantic explanation in the biological sciences

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Abstract

Some types of biological explanation are mostly considered respectable, like causal-mechanistic, constitutive, and evolutionary explanation. Other types raise philosophical concerns. Those are (i) 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 (ii) explanation in terms of transduced signals and of stored and transferred information. In the following, I call such information-theoretical models ‘semantic explanations.’

This paper concentrates on semantic explanation, which was hardly ever discussed as a type of explanation. Instead, philosophers either looked at information transfer as a subject of mechanistic explanation, or attempted to explicate the concept of biological information in isolation. As a result, some contested that the term is of any use at all. However, the success of information-theoretical models in molecular biology suggests that they have some explanatory value, despite contested content and regardless the mechanistic explanation of information transfer processes.

Taking the semantic model of protein biosynthesis as an example, I focus on the model as a whole rather than on its isolated terms. This focus reflects the role of information talk in molecular biology, where on the one hand molecular processes are described by semantic models, but where on the other hand no piece of information was ever characterized or identified outside the context of a description by a semantic model. This leads to the view that ‘information’ enters the game as a theoretical term of the semantic model rather than as an observable. I discuss possible ontological commitments and argue in favor of the explanatory value of semantic models. They are not merely summing up what is to be explained by mechanistic models. They rather explain mechanistic models in functional terms.

I finally draw parallels between semantic explanations in biology and certain types of explanation in other sciences.

1 Introduction

Some types of biological explanation are mostly considered respectable, like causal-mechanistic, constitutive, and evolutionary explanation. We do not generally question whether a causal-mechanistic explanation of glycolysis or of fatty acid synthesis is the right kind of explanation to give (though, of course, any particular explanation might turn out to be incomplete, over-simplified or even plainly wrong). We also feel comfortable with constitutive explanations of organismic, organ-related, cellular or sub-cellular capacities: The visual sense is constituted by the system made up from the eyes (including lens and retina), the optical nerve, and visual cortex; cell respiration is constituted by the respiratory chain, the NADPH/NADP⁺ system, the TCA cycle etc. Finally, the explanation of the presence of particular organismic traits is most often explained in terms of an iterated sequence of variation and selection events in evolution.

Some other types of biological explanation, however, raise severe philosophical concerns. Those are (i) 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 (ii) explanation in terms of transduced signals and of stored and transferred information. My paper concentrates on the latter kind. In the following, I call such information-theoretical models ‘semantic explanations.’

As an example for a semantic explanation I chose protein biosynthesis as the explanandum. Molecular biologists describe the DNA-dependent biosynthesis of nucleic acids and proteins in two different ways. The easiest explanation seems to be a model constructed in terms of decoding of a base sequence, i.e., of semantic processes. The other explanation is 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. The first model is a *semantic model* in the sense explained above, the second one is a *physicalistic model* of the very same process.

While the physicalistic model is generally accepted as giving a scientific explanation proper, the semantic model is often challenged because it involves the use of seemingly intentionalistic concepts in the non-intentional realm of molecules. It refers to information coded in the DNA and describes the different ways in which it is processed within the cell. Information is said to be copied when a second, structurally identical molecule of DNA is synthesized. It is also said to be transcribed to RNA, the RNA may be further processed and the information of

some particular kind of RNA translated into the sequence of a protein. The whole model is based on semiotic or semantic terminology, using not only the terms “information”, “coding” “copying”, “transcribing” and “translating” but also “proofreading”, “correcting”, “recognizing” and many other semantic terms from the field of text processing (see, e.g., Alberts et al. [2002]). A vivid discussion was going on among philosophers of biology for a while about whether the term “information” is 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]).¹

The 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. It describes the structure of the DNA as a sequence of the four bases thymine, adenine, guanine and cytosine; it describes the mechanisms of replicating the molecule by a polymerization of deoxynucleotides, catalyzed by the DNA-dependent DNA polymerase and by a strand of DNA as a catalyst; it describes the reaction as thermodynamically driven by the hydrolysis of a pyrophosphate bond in the nucleotides, etc. In RNA biosynthesis, the DNA-dependent RNA-polymerase is the enzyme involved, and nucleotides are the reactants instead of deoxynucleotides. The model also includes the kinetic data of the reactions (Alberts et al. [2002]). It describes the mechanism of DNA replication, of RNA and protein biosynthesis in terms of the components involved and their interactions, and can therefore be regarded as a mechanistic explanation in the sense of Machamer et al. ([2000]), Craver ([2001]) and Bechtel and Abrahamsen ([2005])—though these accounts also refer to the semantic model, as will be shown in Section 4. Protein biosynthesis was even made a paradigm case of biological mechanistic explanation (Darden and Craver [2002]).²

The semantic and the physicalistic models are, of course, related to each other, so biologists often claim that the semantic model is only a shorthand version of the physicalistic model to which it may be reduced. However, reducibility is

¹ For a differentiation among the naturalization approaches, see Section 4. For a detailed outline of the debate, see Godfrey-Smith ([2007]).

² Glennan’s ([1996], [2002]) approach is similar, but does not count the interactions among the constituents of a mechanism.

neither accepted by the critics of the use of semantic concepts in molecular biology, nor tenable from a point of view that regards the structure of the semantic model as more relevant for its explanatory success than the concepts it makes use of, as will be shown below in Section 3. I shall therefore treat the models as separate and inquire their respective explanatory values.

There is little doubt about the explanatory value of the physicalistic model: it explains the physico-chemical processes going on in protein biosynthesis, i.e., it states the mechanism of protein biosynthesis. The case of the semantic model is not so clear and demands further philosophical analysis. Given that the dispute about an adequate explication of the concept of genetic information has not yet yielded a satisfying result, I undertake it in this paper to throw light on the problem from a different angle. At issue is explanation in biology. The basic unit of scientific explanation is the model rather than a concept or isolated general statement that makes use of the concept (see, e.g., Morgan and Morrison [1999]; Giere [2004]). Consequently, I do not start from the very concept of information but from the semantic model as a whole. While this approach can hardly be expected to justify the use of the concept of information, it helps evaluating the epistemic status of the model.

In the following, I will first introduce a distinction between two different kinds of models (Section 2). Using this classification as a tool to discern the epistemic virtues of different models, I will then discuss the question of whether or not the semantic model may be reduced to the physicalistic model and if so, in which sense of “reduction” (Section 3). Next, the epistemic role of the semantic model will be discussed (Section 4). Finally (Section 5), I will propose an altered view at the concept of genetic information. In this section, I will also sketch some ideas about the relation between semantic models in biology and explanation in other sciences and humanities.

2 Conservative and Non-Conservative Models

It first needs to be shown that models making use of semantic 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. For doing this, I am introducing a distinction between *conservative* and *non-conservative* models. The distinction is chosen in a way that it singles out physicalistic models as one of the two kinds. It can then be shown that semantic models belong to the other kind.

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 a first candidate for such a criterion. But although it may be regarded as one of the central notions in physics, there are also non-causal processes, such as radioactive decay. Causality also fails to hold in the realm of quantum mechanics. Instead, nowadays the central aspect of any physical model seems to be that certain variables obey conservation laws: the laws of the conservation of energy (including mass), net charge, momentum, and angular momentum. This holds for the whole range of accepted physical theories, from the classical harmonic oscillator to quantum electrodynamics (Tipler and Mosca [2007]).³ Even though a dissipative system loses energy through time, the energy is not annihilated. Any physical model of such a system must postulate a reservoir outside the considered system that takes up this energy. Satisfaction of the conservation laws must be observed by any physical model, chemical models included.⁴

Conservativity therefore may be used as a criterion to demarcate physicalistic models in present-day science. The physicalistic model of cell biology, which describes the reaction pathway from DNA to protein by reference to molecules, reaction kinetics, binding energies etc., is a conservative model. Though it may not usually be spelled out fully in terms of energy conservation but is given as a partial model only, scientific literature aims at describing every single step in accordance with physicalistic requirements (cf. the references given by Alberts et al. [2002] and by Darden and Craver [2002]). It is presupposed that the full model meets the requirements of conservation laws and that all calculations performed on the basis of this model rely exactly on these laws.

The second kind of models to be characterized is the non-conservative model. In these models, non-conservative variables play central roles. The non-

³ We must abstain here from phenomena such as symmetry breaking at the level of elementary particles that are not yet understood satisfactorily.

⁴ Similar laws can be identified in other disciplines, e.g., in economics in the context of labor theories of value, as developed by Locke and Marx (Vaughn [1978]; Diederich [2000]).

conservative variables of such a model do not represent physical quantities. Examples are cellular signals that are related to hormone action or external stimuli. Signals are transformed several times, e.g., from the excitation of a small molecule into a conformation change of a protein, then into the activated state of an enzyme, to the open state of an ion channel etc. Non-conservative variables can not only be found in biological models but also in the technical realm (Krohs [2009b]). Truth-values in models of logic circuits may serve as an example. In any case, the signal must be strictly distinguished from its carrier. Conservation laws hold for the processes the carrier undergoes. These are described in the physicalistic model. But there is no law of signal conservation. A signal in the sense of semantic information can simply disappear, without any need that it be transformed into anything else. This will be further worked out in the next section. The carrier of the signal is, of course, governed by conservation laws.

Besides these semantic or symbolic⁵ variables other functions and functional variables are non-conservative as well. This holds again for biological and for technical functions.⁶ The function of a screw (or of some 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.

3 Semantic Models as Non-Conservative Models and the Question of Reduction

To further work out the difference between semantic and physicalistic models, the distinction between information and its carrier is crucial. The carrier of information may be an electric potential or electric current, e.g., in a computer or in a nerve cell; it may be ink on a piece of paper or compressional waves in the air; or it may be, according to semantic models of molecular biology, the structure of a nucleic

⁵ Herbert Simon calls any technical information processing system a physical symbol system, (Simon [1996], p. 21, pp. 187-8).

⁶ Here the concept of function is taken in the sense of a causal role function (Cummins [1975]), not as an etiological function (Wright [1973]; Millikan [1984]). To allow for the normativity of the concept that allows discerning function from non-function and from malfunction, a modification needs to be introduced into Cummins's account, e.g., by reference to fixed types of function bearers (Krohs [2009a]).

acid molecule. These 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 may carry.

As already mentioned, information may disappear without residue. It may also appear without satisfying a conservation condition. Consider for the first case a logical gate, for example a NOR-gate, which is a technical device for information processing. Its output is “one” if and only if both inputs are “zero”. In all three other cases of definite input the output will be “zero”. If the output is stored and the gate is then switched off, the saved information is “one” or “zero”. In case it is “zero”, the information whether the first or the second channel or both were “one” is lost. This lost information is not transformed or dissipated, it is annihilated. From two bits of information only one is left, information is not conserved. 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. But non-conservativity of information is not restricted to such cases of redundancy. Imagine a breakdown of a computer occurring before a freshly composed text or the data obtained in a series of measurements was 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. It does, however, not depend, at least not in a systematic manner, on the symbolic content of the memory. On a breakdown, the semantic information is not transformed but lost. Similarly, on the hydrolysis of a piece of DNA the information it carried is lost, although binding energy and matter of the carrier itself is conserved. This non-conservativity is not restricted to cases in which information is lost; it applies to information increase as well. 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 some base or pseudogene happens to occur in a living cell. A sudden increase of information is due to the transformation of some molecules. (This, of course, is the image drawn by the semantic model, not by a physicalistic account.) Only the molecular processes obey conservation laws, but not information as such. Accordingly, semantic models are non-conservative.⁷

⁷ A further question is whether non-conservativity of functional models holds in general. This cannot be discussed here in detail. Non-conservativity seems to hold for any functional model ([Krohs 2004]). The example of the function of a screw in the exposition of the distinction of the two kinds of models may serve as

From these considerations, several reasons can be deduced why semantic models cannot be reduced to physicalistic models.⁸ First of all, the semantic model deals with the functionality of a process, and function, understood normatively so that it is linked to a concept of mal- or dysfunction, is absent from physicalistic models. Next, also concerning the issue of functionality, physicalistic models can neither account for nor explain the multiple realizability of semantic entities. Then, it is all but clear how the unity of a piece of information or of a signal through its various instantiations could be described merely by reference to the various carriers of the information. 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 semantic concepts is involved, many if not all of them also referring in their original context to intentional text processing, and all of those needed to be reduced to physicalistic descriptions.

It is important to notice that a functional 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—only the different carriers of a signal can occur there. So there are two mutually non-exclusive ways to model protein biosynthesis: by a conservative, physicalistic model, and by a non-conservative, functional, semantic model. Neither of them alone covers all that can be known about this process.

4 The Epistemic Role of Semantic Models in Biology

As already mentioned in the introduction, the physicalistic model explains what is going on physicochemically during protein biosynthesis in the sense of a mechanistic explanation. 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 one of the different possible instantiations of a schema, which is often given in terms of functional roles. Darden and Craver ([2002]) describe many of the role functions in

an indication; examples from the biological realm are mentioned below, in Section 4. What is relevant now is only that the non-conservative models in question, i.e., semantic models, are functional models.

⁸ Only theory reduction is at stake here. Ontological reducibility can be presupposed, be the semantic model reducible to the physicalistic one or not.

protein biosynthesis in terms of information flow, which shows immediately that the mechanistic explanation is also related to the semantic model. Inquiring the epistemic role of the semantic model, one must consider, then, how it relates to a mechanistic schema, and whether it may even be identical with it. The latter can clearly be denied, since a schema 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 semantic model, in contrast, refers to molecular components of the cell, namely to the same ones as the physicalistic account does, so the places are already filled in the semantic model. In contrast to a schema, the semantic model has an ontology, even more or less the same ontology as the physicalistic one, with the notable exception of semantic entities, which have no correlate in the physicalistic model. It is an instantiation rather than a schema.

However, the schema as given by Darden and Craver, although it makes use of some relations of the semantic model, is conceived by these authors as the schema of the mechanism which is described by the physicalistic model. In fact, it turns out to be the schema of both models.⁹ This view may solve the following problem that occurs with Darden and Craver’s account of the schema in this special case: The philosophical debate on the concept of biological information shows that this concept is richer than terms for mere Cumminsian role functions would allow for. In any attempt to reconstruct it, reference not only to a system but, for example, to its etiology (e.g. Sterelny et al. [1996]; Maynard Smith [2000]; Jablonka [2002]) or to ontogenetic processes (e.g. Godfrey-Smith [2000]; Krohs [2004]; Stegmann [2005]) is required. Now, in a schema for a physicalistic description of a mechanism there should be no place for functional terms that cannot be reduced to role functions. But there is place as soon as it is accepted that the schema is also the schema of a corresponding semantic model.

So why are biologists using both models in parallel, and what precisely is the epistemic role of the semantic model? The answer is to be found in the aim of biologists to explain both, the physicochemical processes of living entities and their

⁹ Darden and Craver ([2002], p. 5) in a way refer to the different models when ascribing work on information flow to molecular biologists and work on the flow of matter and energy to biochemists (which might be considered a somewhat artificial attribution of different research topics to disciplines).

functional organization. The question about functionality, while it is 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, of the liver as a detoxifier or of a mitochondrion as the power station of the cell, helps understanding a biological entity as an organized system. It embeds a capacity into the hierarchical structure of other capacities. So does the semantic model of protein biosynthesis: it places the pathways involved 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; to degradation of cellular components and—where it applies—also to cell aging. It does so by simplifying the physicalistic description, and at the same time introducing functional 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 non-conservative models is not sloppiness in the formulation of the model. It is the prerequisite for meeting the first condition of an integrated view at biological organization. The semantic model seems to give a quite accurate explanation of the functional structure of protein biosynthesis and allows for precise and successful predictions of the behavior of the system, e.g., when processing different DNA templates.

When we are asking for the justification of the use of a particular model, there is a basic decision about what we regard as explanatory: the structure of a model or its conceptual content. In respect of the content, the semantic model is all about information and its processing. This content seems not justified by the phenomenon to be described, as the critique mentioned in Section 1 has shown. In particular, semantic processes seem to be based on intentionality and we do not want to assume or presuppose intentionality on the molecular level. However, conceptual content is not all what the model has to offer. I propose to also have a look at its structure, which appears to fit well to the phenomena as described by the physicalistic model. This is not affected by the reference of the model to 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 much more straightforward way by an account that allows for multiple realizability than in a physicalistic model: one and the same signal 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 semantic model, but neither by the structure nor by the conceptual content of the physicalistic model. Consequently, the structure of the semantic model must be regarded as contributing to its explanatory power.

Conceptual content and structure can both matter, which is spelled out for the structural side by structural realism. One needs not subscribe to structural realism in either its epistemic (Maxwell [1970]; Worrall [1989], [1994]) or ontic variant (Ladyman [1998]; French and Ladyman [2003]) to accept the explanatory power of the structure of a non-conservative model. Since we find in the present case that the conceptual content can hardly explain the epistemic value which the semantic model obviously has, one should indeed have a look at the contribution of the structure of the model to its epistemic success. 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 can not be had without this very content, the content alone may not be sufficient reason for eliminating the model. So, if structural explanation is a part of scientific explanation, the semantic model has its merits exactly in this realm.

We may not be so easy off with respect to problematic conceptual content of conservative models, but demand ontological adequacy for the conceptual content of those models (theoretical terms, then, are notoriously posing a problem in this respect). A non-conservative model does not even aim at a realistic description of the inventory of the physical world—otherwise it needed to be conservative—while a conservative model does. Both have a different status. Consequently, it seems to be consistent to allow for metaphorical content of non-conservative models without doing so in the case of conservative models.

5 How to Deal with the Concept of Genetic Information

The question of how to interpret the concept of genetic information is still open and even claimed to be unimportant. My account of the explanatory power of semantic models does not interpret the conceptual content of these models and therefore does not explicate the concept of information. My account may, however, be used to reframe the debate. Of the two possible reasons why the semantic model may have explanatory power, its structure is a much better candidate than its content. I can for now just present a guess why biologists describe the functional organization of protein biosynthesis in semantic terms. The guess is that simply no other functional model could be stated until now that has a comparable structure, i.e., that describe various sequential conformation changes as realizations of the same function or the

same non-conservative variable, but that does not rely on semantic concepts. So the use of the concept of information seems to be the price biologists have to pay for gaining a structurally adequate non-conservative model of the functionality of protein biosynthesis.

Does this mean that the concept of genetic information is used metaphorical? As an isolated concept, it is hard to see how it could work as a metaphor at all in a field where intentionality and interpretation are absent. What should be the content carried by the metaphor? However, there is a whole set of interrelated concepts as listed above. They are all linked together in the model. While the isolated concept of genetic information may well be regarded as discredited, the structure of the model is adequate to the structure of the phenomenon. If anything, the model as a whole should be regarded as the metaphor, transporting its structure rather than the semantic content into the context of explanation in molecular biology.

Let us take for granted that there is an acceptable description of semantic models in (molecular) biology, be it mine or another one. If semantic explanation, then, is a philosophically respectable kind of explanation, its application might not be restricted to the biological sciences. And indeed, we do find semantic explanation in a wide variety of academic disciplines. First of all, *oral and written communication* is usually described by semantic models rather than by physicalistic descriptions of sound emission and reception or of the effect of odd-shaped spots of ink on the retina and of cerebral processes – no wonder, this is where the model was borrowed from when applying it to the molecular realm. Second, *signal transduction in technical devices* including *computers* is usually described at the semantic level. Here, in a way, the devices were constructed to fit the model, they were designed to handle symbols as various realizations. There is also a whole range of models that are semantic without the modeled processes being undoubtedly sign processes. I will leave this for the specialists but mention at least some ideas about where explanation may be similar to semantic explanation in biology. This may hold for language of form (“Formensprache”) in architecture and design, for those models of social processes which interpret actions of impersonal agents as meaningful and not merely as having an effect. It may also hold for the interpretation of history in terms either of the meaning that context has for an individual and vice versa (e.g., in “follow the actor”-approaches) or in descriptions of historical processes in terms of institutions reacting on the goals and aims of other institutions (e.g., parliaments, governments, NGOs, enterprises, markets).

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