Holism and reductionism in biology and ecology

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CHAPTER 7
FUNCTIONAL EXPLANATIONS IN BIOLOGY

7.1   Introduction

In this chapter I will deal with the last of the alleged contradistinctions between holism and reductionism in biology, namely the one between functional explanations (holism) and causal explanations (reductionism).

There is an enormous amount of literature in which the status of functional explanations in biology is being discussed.[41] The major reason for this is that functional explanations appear not to meet the standard view of explanations as developed in the tradition of the logical positivist philosophy of science, to wit the structure of causal, deductive-nomological explanations (Nagel 1961/82; Hempel 1965; Salmon 1984). Two different and opposite conclusions are being drawn from this. Adherents of the standard view, whom I have earlier called, with a term of Rosenberg (1985), *provincialists*, conclude that functional explanations are non-scientific pseudo-explanations which must be replaced by causal explanations. Their opponents, whom I have called *autonomists* (Rosenberg 1985), insist that functional explanations are indispensable in biology and that, therefore, biology is an autonomous science. But still a science and not a pseudo-science.

Although there appears to be no one-to-one correspondence between on the one side provincialists and reductionists and on the other side autonomists and holists - there are, for instance, autonomists who do not call themselves holists (Ayala 1968, 1974) - it is true that both parties view functional explanations as obstacles to the reduction of biology to physico-chemistry. Moreover, functional explanations are the prototype of explanations illustrating the holistic claim that one should explain entities of biological levels of organization not only in terms of causal mechanisms on lower levels, but also in terms of their relations to (functions in) the larger whole. For these reasons, I am prepared to say that autonomists are at the same time holists, whether they like it or not. In the rest of this chapter I will therefore keep on using the terms reductionists and holists to characterize the parties involved in the debate.

In this chapter I will argue on the one hand, contra reductionists, that functional explanations in biology are indeed indispensable and, moreover, perfectly legitimate explanations, while on the other hand, contra holists, they provide no obstacles to the reduction of macro-laws or theories in biology. On the contrary, they contribute to such reductions. I will also argue that in the context of functional explanations, too, holistic and reductionistic research programmes co-operate and are mutually dependent.

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[41]The main sources are: Broad 1925; Sommerhoff 1950, 1974; Braithwaite 1953; Dobzhansky 1955, 1973; Mayr 1961, 1963, 1974, 1982; Taylor 1964; Bock and von Wahlert 1965; Nagel 1961/82; 1977; Tinbergen 1963, 1976; Hempel 1965; Williams 1966; Ayala 1968, 1970; Ruse 1973; Hull 1974; Cummins 1975; Bennett 1976; Woodfield 1976; Wright 1976; Brandon 1981; Kitcher 1981; Lewontin 1981, 1983; Rosenberg 1982, 1985; Millikan 1984, 1989; Sober 1984; Futuyama 1986; Kuipers 1986, 1992/3; Woodward 1989; Maynard-Smith 1990; Neander 1991; Wouters 1995.

7.2 Analyses of functional explanations
7.2.1 Functions, goals and intentions

In the literature several types of 'non-standard' explanations are recognized, which are (or are not) being ranked under the names of functional, teleological and intentional explanations. The differences between these types are not immediately clear and the boundaries between them are vague. Thus, an example of a functional explanation is: 'Vertebrate animals carry hemoglobin in their red blood cells because it allows them to bind and release oxygen more quickly'. An example of a teleological explanation (in the strict sense of an explanation of goal-directed behaviour or a goal-directed process) is: 'Woodpeckers peck on the barks of trees in order to find larvae of insects'. And an example of an intentional explanation is: 'Paul went to his favourite pub in order to meet his friends there'. These explanations have in common that at first sight they all seem to appeal to something, a function, effect or goal, that lies in the future. As future things cannot be considered antecedent conditions, these explanations cannot be called causal explanations. Still, there are important differences, not only in the contents but also in the structure of these explanations.

The clearest difference appears with respect to intentional explanations, because, as the name indicates, they pertain to intentions and because intentions are usually ascribed only to humans or at most to some other 'higher' or intelligent animals. Intentional behaviour may be generally described as some action A performed by person P in order to reach a goal G. This goal G may be seen as some future state of affairs which is desired by P. However, it can also be seen as an *internal mental state* of P, which, together with the other internal state of '*wanting* G' and the *belief* that action A will contribute to reaching G, is a *causal determinant* of A. According to Nagel (1977; see also Woodfield 1976), this type of explanation is therefore actually a species of causal explanation: "though the *occurrence* of the action A can be explained teleologically, the explanation is ostensibly a species of *causal* explanation. For, by hypothesis, the action is initiated because the agent *desires* a certain goal and also *believes* that the action will contribute to its production" (Nagel 1977, p. 264). The 'desire' and the 'belief' are antecedent conditions, causal factors, of action A.

According to Nagel (1977), the same applies also to other teleological explanations in the sense of explanations of goal-directed or purposeful behaviour of, or goal-directed processes in, organisms. "Explanations of this sort are often said to be "causal". They resemble in structure, though not in specific content, typical explanations in the physical sciences. As the example just considered [the maintenance of homeostasis in blood temperature; RL] suggests, they are like the latter in accounting for the occurrence of some phenomenon by deriving the statement of its occurrence from assumed laws (or general hypotheses), when these are conjoined with statements of relevant initial conditions. Putting all this briefly, one sort of explanation is in terms of antecedent conditions and causal laws; and goal-directed processes, among other things, can in principle be explained in this way. Explanations of this type are not distinctive of the life sciences, they are found in all branches of inquiry, and there is nothing teleological about them" (Nagel 1977, p. 277; see also Cummins 1975; Rosenberg 1985).

Nagel states, however, that this does not apply to the third type of 'teleological' explanation, viz. functional explanations, because in this type the explanans is a certain *effect* of the property, trait or behavioural pattern to be explained, which can not be seen as an antecedent condition or cause of this property, trait or behavioural pattern (Nagel 1977, pp. 277-301).

Although he nonetheless maintains that functional explanations are legitimate explanations, in a sense he thereby retreats from his earlier position that functional explanations too can be reconstrued as causal, deductive-nomological explanations (Nagel 1961; see below in section 7.2.4).

The distinction upon which Nagel's (1977) analysis is based is the one between 'goal ascriptions' (intentional explanations and teleological explanations *sensu strictu*) and 'function ascriptions'. I have strong doubts about this distinction, however. Nagel provides, among others, the following examples of goal ascriptions: "The goal of the pecking of woodpeckers is to find larvae of insects" and "The goal of the activities in various animals of the sympathico-adrenal apparatus as well as of certain cells in the pancreas, is to keep the concentration of blood sugar within relatively narrow limits". However, without loss of meaning or intent, we might just as well replace the term 'goal' by the term 'function' in these statements. Nagel also notes that "*escape from a predator* is said to be the goal of a hare's flight from a hound, but survival itself does not appear to have any function" (all examples in Nagel 1977, p. 263). However, I doubt that there is one biologist who will say that escape from a predator is not *functional*. Functions and goals coincide in these cases. Neither do I believe there is one biologist who will say that survival itself does not have any function: it is, along with reproduction, the ultimate function in biology.

In spite of these doubts about Nagel's (and others') distinction between goal and function ascriptions, and hence about the distinction between teleological explanations *sensu strictu* and functional explanations, I shall, for the moment, go along with him in considering functional explanations as the (to some perhaps paradoxically enough) most problematic type of 'teleological' explanation. Therefore, I will restrict myself in the rest of this chapter to functional explanations, leaving intentional explanations out of consideration, and dealing with 'teleological' explanations only in so far as I consider them to be functional explanations as well. I will show, however, that functional explanations, too, can be reconstrued as causal, deductive-nomological explanations.

7.2.2 Examples of functional explanation

Functional explanations are always answers to questions of the type 'Why do organisms of type x have or exhibit property, trait, process or behaviour y?'. The answers (explanations) are always of the type 'Because y serves for (contributes to, is functional for) z', implicitly or explicitly supplemented by the statement that z is necessary for the adequate functioning, the survival and/or reproduction of x.

Why do vertebrates carry hemoglobin in their red blood cells? Because hemoglobin serves as a respiratory pigment in oxygen transport and because these animals need oxygen transport to their tissues in order to produce energy. Why are the nine amino acids per globin-chain conserved in the hemoglobin molecules of all vertebrate animals? Because they principally serve for (determine) the shape of hemoglobin molecules and because it is this shape that determines the specific oxygen-binding properties of these molecules.

An interesting example related to this is the question why flatworms are (so) flat. The answer is that if these creatures were not flat, oxygen would not diffuse fast enough into their bodies to allow them to survive. Hence, their flatness serves for adequate oxygen transport into their bodies and this is necessary for their survival. Put differently, "the organism's need for oxygen together with the absence of any means of oxygen transport other than diffusion

explains why a (hypothetical) flatworm of more than a millimetre thick would not survive" (Wouters 1995, p. 439). The reverse reasoning holds with regard to the question why larger (thicker) animals have a circulatory system and respiratory pigments (such as hemoglobin). The answer is that they are so big that simple diffusion through their skin would not suffice to supply their tissues with enough oxygen and that, hence, they need a circulatory system and respiratory pigments to do so.

Other related examples are: Why do mammals, along with birds and reptiles, have lungs? To take up oxygen from the air, which they need in order to produce energy. For the same purpose, fish have gills. Why do all these animals have a heart? To pump the blood through their bodies so that (among other things) oxygen reaches their tissues. Why do plants have chlorophyll? Because they need chlorophyll to photosynthesize and they need to photosynthesize in order to (produce sugars and they need sugars in order to) stay alive.

Another well-known example is the explanation of the fanning behaviour of male sticklebacks. After these males have fertilized their partners' eggs, they regularly make fanning movements in front of the nest containing the eggs. The functional explanation of this behaviour is that, unlike other fish, sticklebacks build a tubular nest which would normally not be supplied with enough oxygen, that the males' fanning movements serve to supply the eggs with enough oxygen, so that they don't die, and that the males thereby safeguard their offspring (Tinbergen 1976).

A final example is the explanation of the fact that plovers always seem to lay four eggs, no more and no less. The explanation, which has required a lot of research, is that the number of four eggs guarantees an optimal number of offspring because of a balance between on the one hand the amount of time and energy it takes to raise chicks and on the other hand the number of chicks that eventually reach reproductive age: if these birds lay less eggs, they raise less chicks than they could, given the time and energy the raising of chicks takes with these birds, and when they lay more eggs, relatively less chicks survive per invested amount of energy than when they lay four eggs.

Biology is shot through with such functional explanations and, as the examples indicate, they may concern either components parts and properties, traits, etcetera of organisms, or behavioural patterns they exhibit, as well as processes occurring in them or in their environment. For simplicity's sake, however, I will further speak only of explanations of properties of organisms.

7.2.3 Functions, causes and effects

The main reason for the debate on functional explanations is that they are still laden with the Aristotelian, teleological view that natural objects are determined not only by so-called *efficient causes*, that is, causes preceding their effects, but also by so-called *final causes*, that is, causes following in time after their effects. This is a violation of the modern principle of causal determinism.

Although at first sight functional explanations may give the impression of appealing to final causes, closer inspection reveals that this is not the case. For the statement that hemoglobin serves for oxygen transport conforms to the statement that hemoglobin is a (an efficient) causal factor of oxygen transport and not with the statement that oxygen transport is a causal factor of the presence of hemoglobin. And the statement that male sticklebacks make fanning movements in order to supply 'their' eggs with oxygenated water conforms to the statement

that the fanning movements are a causal factor of the oxygen supply to the eggs and not with the statement that the oxygen supply to the nest is a causal factor of the fanning movements. Thus, functional explanations specify efficient causal relations. In that respect, there is nothing wrong with them.

Still, as mentioned in section 7.2.1, the problem is that in the explanans of functional explanations no antecedent conditions or causes of the property to be explained are being specified, but *effects* or results: adequate oxygen transport is an effect of, among other things, the presence of hemoglobin, not a cause. Oxygen supply to the eggs is an effect of the stickleback's fanning behaviour, not a cause. For precisely this reason reductionists find functional explanations unacceptable as scientific explanations. Whether or not based on efficient causal relations, a reference to the effect of a property does not explain why it is present. From the fact that hemoglobin is a causal factor of adequate oxygen transport in vertebrates it does not follow logically or deductively that these animals have hemoglobin. To a reductionist, functional explanations are unacceptable, because they don't meet the condition that something is explained if and only if its cause(s) is (are) being specified. Effects explain nothing (see in particular Salmon 1984, for an account of causality and of causal explanations).

Because they are nevertheless of the opinion that there is a valid, deductive argument involved in functional explanations, several neo-positivist philosophers have tried to reconstruct functional explanations in terms of the standard model of causal, deductive explanations. The best-known examples of these are Nagel (1961/82) and Hempel (1965) (but see also Ruse 1973). In what follows I will first discuss the analyses by these authors and some of the objections raised against them. After that, I will discuss the alternative, non-standard analysis by Kuipers (1986, 1997), which does more justice to the specific content of functional explanations. However, I will also criticize this non-standard analysis and in the end I will provide my own analysis. I will show that the question whether reductionists are right in asserting that functional explanations are to be replaced by causal explanations, is irrelevant, for the simple reason that, in a particular sense to be specified, functional explanations *are* causal explanations.

7.2.4   The standard analyses of Nagel and Hempel

Both Nagel (1961/82) and Hempel (1965) have tried to reconstruct functional explanations as causal, deductive-nomological explanations (though with different intents).[42] Characteristic of such explanations is that the explanandum appears as the conclusion of a deductive argument. In the case of functional properties this is the statement that organisms of type x have property y, formally given by H(x,y). In giving the reconstruction schemes of Nagel and Hempel I will make use of Kuipers's (1986, 1997) description and notation of them. In both schemes MP stands for meaning postulate.

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[42]Nagel aimed to show that functional explanations can be reconstructed as valid deductive arguments, whereas Hempel aimed to show the opposite.

Nagel's scheme looks as follows:

H(x,z)	organisms of type x have (perform, produce) property (process, phenomenon, behaviour) z
N(x,y,z)	property y of organisms x is causally necessary for property z
MP	if (Nx,y,z) then: if H(x,z) then H(x,y)

H(x,y)   organisms of type x (must) have property y

It should be noted that Nagel's meaning postulate (MP) is a nomological premise. Its non-formal counterpart states that if property y of organisms of type x is causally necessary for property z, then, if these organisms have property z they must also have property y.

Hempel's scheme looks quite different from Nagel's:

A(x)	organisms of type x function adequately
A(x)→H(x,z)	property z of organisms x is a necessary condition for A(x)
S(x,y,z)	property y of organisms x is causally sufficient for property z
MP	if S(x,y,z) then: if H(x,y) then H(x,z)

H(x,y)   organisms of type x (must) have property y

The chief difference between these schemes is that Nagel takes functional properties to be *necessary* conditions for their effects (property y is causally necessary for property z), whereas Hempel takes them to be *sufficient* conditions (property y is causally sufficient for property z). As a result, whereas Nagel's scheme (argument) is logically valid (indicated by the uninterrupted line), Hempel's isn't (indicated by the interrupted line): from the fact that property y is a sufficient condition for property z it doesn't follow logically that organisms x have property y.

The reason for this difference is that Nagel did not, whereas Hempel did, take into account what is generally considered to be the major problem with regard to functional explanations: the *problem of functional equivalents*. This problem is formed by the fact that there are often alternative properties, which are functionally equivalent to the property to be explained, that is, can fulfil the same function. Vertebrate animals have hemoglobin as respiratory pigment, but there are invertebrate species who use hemocyanin for the same purpose. There are animals who breath through lungs, but there are others who use gills for the same purpose, while plants use stomata for their respiration. Many plant species have chlorophyll for their photosynthesis, but there also plants (certain algae) who use other pigments (such as cytochrome) to photosynthesize. Prey may escape from predators by flight but also by camouflage.

This means that the second premise in Nagel's scheme is often untrue, that is, that functions generally may not be regarded as necessary conditions. This relates to another objection that has been raised against Nagel's scheme, namely that it implicates a symmetry of explanation and prediction which in the context of functional explanations generally does not apply: it is often possible to explain the presence of some property (functionally), but not to predict it. For their might just as well be a functionally equivalent property and it seems impossible anyway to predict the evolution of species and their properties.

Contrary to Nagel, Hempel did leave room for functional equivalents. In doing so, he escapes from the objections raised against Nagel's reconstruction but has a high price to pay. For, as mentioned, his argument is not logically valid: instead of property y organisms x might just as well have some functionally equivalent property y*. This means that, when Hempel's account would nevertheless provide an adequate description of the structure of functional explanations, these explanations would not contain a valid argument. As this runs counter to the intuition of most biologists, and also to that of many philosophers, we may decently conclude that there is something wrong with Hempel's account. I will return later to the problem of functional equivalents and to the objections raised against Nagel's and Hempel's accounts, but first discuss Kuipers's alternative, non-standard account.

7.2.5 Kuipers's non-standard analysis

Kuipers (1986, 1997) adds to the afore-mentioned objections against Nagel's and Hempel's reconstructions that they assign no particular role to specific functional statements, that they don't include an explicit evolutionary component, and that, therefore, they do not correspond to the actual research practice of biologists. Kuipers claims that his analysis does and thereby follows more closely the train of thought of biologists. This analysis runs as follows.
It starts with the statement

1. H(x,y)   organisms of type x have property y.

The question following this statement is

2. H(x,y)?   why do organisms of type x have property y?

To biologists this means: what is the function of y? and Kuipers reconstrues this as the generation of the unspecific functional hypothesis

3. FH(x,y)   property y of organisms of type x is functional.

According to Kuipers, the meaning of this hypothesis can be explicated by the following meaning postulate

MP1: $FH(x,y) \approx (\exists z)\ FH(x,y,z)$.

that is, there is a property z such that property y of organisms x is functional for property z. The question is of course what this specific property z is, that is, what the specific function of property y is. From the perspective of biology this is of course the tough question, but philosophically there is not much to say about it, because it belongs to the context of discovery, to the heuristic phase of research. Suppose, however, that biologists come up with a specific idea about the function of y. Kuipers reconstrues this as the generation of the specific functional hypothesis

4. FH(x,y,z)   the (or a) function of property y of organisms x is to contribute to property z.

According to Kuipers, this statement can be decomposed in terms of a second meaning postulate

MP2: FH(x,y,z) ≈ H(x,y) & H(x,z) & P(x,y,z) & P(x,z,∞) .

In this meaning postulate H(x,y) and H(x,z) are descriptive hypotheses (stating that organisms of type x have properties y and z, respectively) and P(x,y,z) and P(x,z,∞) are supposed *causal relationships* (in fact, causal-nomological premises). P(x,y,z) means: property y of organisms of type x is a positive causal factor for property z. P(x,z,∞) means: property z of organisms of type x is a positive causal factor for the survival and reproduction (∞) of organisms x. Based upon the literature, assuming that z does not equal ∞, Kuipers calls P(x,y,z) the *proximate* component and P(x,z,∞) the *ultimate* component of the meaning postulate. He states that the ultimate component is equivalent to what (evolutionary) biologists call the *survival value* or the *adaptive value* of a property. "More specifically, the claim of the theory of evolution is that, as a rule, y became a trait of x-organisms due to selection along the lines suggested by the combination of the ultimate and proximate component" (Kuipers 1986, p. 111).

Naturally, the specific functional hypothesis must be tested for its tenability and this means that after the preceding heuristic phase a testing phase now starts in which the hypothesis may be either falsified or verified. When it is being falsified, the biologist has to start again and come up with a new hypothesis. When it is being verified, he is ready and may go on to the next research question. In Kuipers's scheme, this is rendered as

5.1. not-FH(x,y,z)   falsification, back to step 3, or
5.2. FH(x,y,z)!   verification of the specific functional hypothesis: property y of organisms x is indeed functional for property z.

Finally, there is, in Kuipers's view, a deductive phase in which the unspecific functional statement is being derived:

6. FH(x,y)!   property y of organisms x is indeed functional.

This final step occurs with the help of the first meaning postulate and the logical rule of existential generalization. With this rule, one can derive from the fact that FH(x,y,z) that y is indeed functional and thereby, given MP1, that FH(x,y).

As noted by Kuipers, this scheme was developed for proximate functional explanations, that is, for cases in which z is not equivalent to ∞, but it can easily be adjusted to fit ultimate functional explanations by omitting the proximate component.

7.2.6   Are functional explanations deductive arguments?

The most conspicuous difference with the accounts by Nagel and Hempel is of course that in Kuipers's account the product of the functional explanation, its conclusion, is not the statement about the property to be explained, H(x,y), but the corresponding functional statement FH(x,y) (or the specific functional statement FH(x,y,z)). I agree with Kuipers that his reconstruction indeed more closely resembles the train of thought and research practice

of biologists, and thereby the logic of functional explanations. Nevertheless I find his reconstruction on a number of points unsatisfying.

This concerns, first of all, the final, deductive step in his scheme, the derivation of the unspecific functional statement. Kuipers notices himself that "the valid implication of the corresponding general [unspecific, RL] functional statement .. [is an interesting by-product]: it explains the philosopher's conviction that there is, in some way or other, a valid argument involved [in functional explanations]" (Kuipers 1986, p. 112). There is no way of denying that this is a valid, deductive argument. However, I don't think it establishes *the* deductive argument involved in functional explanations and I don't think it is an interesting by-product. On the contrary, to me it boils down to nothing but a reformulation of the principle of functionality in biology, which, incidentally, Kuipers refers to himself (p. 112). The purport of this principle is that, some apparent exceptions notwithstanding (see 7.4.4), properties of organisms are generally functional, because non-functional or dysfunctional properties will sooner or later be eliminated from a population by natural selection. However, this is not an interesting by-product of functional explanations, nor what makes them into valid arguments, but rather the starting point for investigations into the possible functions of properties. This is evident also in Kuipers's scheme, where the generation of the unspecific functional hypothesis is one of the first steps involved. However, I have never noticed a biologist deriving from the functional explanation of some property that this property be indeed functional. Formally, this may be a valid logical step, but to a biologists it is entirely superfluous and I am convinced that no biologist will claim that this step is the deductive step (argument) in a functional explanation.

Naturally, this leads to the question what then is the argument involved in functional explanations, if there is any. Assuming that the argument is not contained in the final step, my second objection to Kuipers's reconstruction is that I am unable to find any other deductive argument in it. Of course, there is a hypothetical-deductive element in the test phase, but this is unrelated to the structure of the explanation (see 7.4.5). Apart from this, Kuipers's reconstruction contains nothing like a deductive argument, while I am convinced that such an argument is involved in functional explanations.

Clearly (or so I will show), the argument is concealed in Kuipers's second meaning postulate, in the proximate and ultimate components of a specific functional statement. In my view, this meaning postulate is the strong and valuable element in Kuipers's reconstruction, since, beside displaying a proximate component, functional explanations always appeal to the ultimate function of a property, to its contribution to the survival and reproduction of the respective organisms. In most cases, one can discern both a proximate and an ultimate component in functional explanations, such as in the examples of the function of hemoglobin in oxygen transport, the function of the heart in circulating the blood, or the function of the circulatory system in supplying the tissues with enough oxygen. These are all proximate components of the corresponding functional explanations, but the major power of these explanations is that they show that without the property the organisms could not survive and reproduce themselves. In some cases there is only an ultimate component, such as in the example of the clutch size of plovers: this relates directly to the reproduction of these birds.

The problem with Kuipers's meaning postulate is, however, that it is indeed no more than a formal reconstruction of the meaning of a specific functional statement. It tells us nothing about the structure of functional explanations. In the following sections I will show in what sense this structure is hidden in his meaning postulate.

7.3   The problem of functional equivalents

I think there is a simple reason why, apart from the last step, Kuipers's reconstruction does not contain a deductive argument. For the same reason Hempel's scheme (argument) is invalid while Nagel's scheme, though valid, is considered inadequate. Nagel's scheme is considered inadequate, because his second premise is considered to be, in general, false: properties of living organisms are generally considered not to be causally necessary for the respective function. Hempel's scheme is invalid, because organisms of type x might just as well have a functionally equivalent property y* instead of y.

It seems, then, that the major problem underlying the problem of functional explanations is the problem of functional equivalents. Thus, one will have to solve the latter problem in order to solve the former.

Now the problem of functional equivalents is unsolvable as long as one assumes that there are indeed functional equivalents for most properties. It follows that the only way to solve the problem is by showing that there are no functional equivalents or that they are irrelevant. In what follows I will provide two arguments in favour of this solution. The first argument is that, as a rule and contrary to the objection raised against Nagel's account, properties of living beings must be considered necessary conditions for their survival and/or reproduction and that, therefore, functional equivalents are indeed irrelevant. The second argument supports the first one and boils down to the fact that eventually one will have to provide an answer to the question why organisms of type x have property y and why not some functional equivalent property y*. This answer can only be a causal explanation of the presence of y, but I will show that in this causal explanation the function of y plays an essential role.

7.3.1   The specificity of biological laws

One can explain the presence of hemoglobin in vertebrates functionally in terms of its contribution to adequate oxygen transport in these animals, and one can explain the adequate oxygen transport in these animals in terms of, among other things, the presence of hemoglobin in their red blood cells. In both cases, one appeals to the same causal-nomological relationship between the presence of hemoglobin and adequate oxygen transport. However, whereas the causal explanation is generally considered to be legitimate, that is, in accordance with the standard view of deductive-nomological explanations, the corresponding functional explanation is always saddled with the problem that there are also animals transporting oxygen with the help of hemocyanin.

The reason for this asymmetry is that in the causal explanation it is assumed that the explanation pertains to vertebrates and not to invertebrates. That is to say, the fact that there are also invertebrates and that invertebrates transport oxygen by means of hemocyanin is considered completely irrelevant to the explanation of why vertebrates are able to transport oxygen by means of hemoglobin. This has everything to do with the restricted domain, the non-universal character, of most biological laws. Biological laws are often restricted to certain species, families, classes or at most a phylum (see also van der Steen & Kamminga 1991; Schaffner 1993b; Tuomivarra 1994; Mahner & Bunge 1997).

To biologists this is not so much a problem as something that is given and must be accepted. Biological laws may not be universal, they nonetheless pertain to large or very large numbers of organisms and are therefore interesting regularities. When confronted with the

causal explanation of oxygen transport in vertebrates, there is no biologist who will ask why these animals don't have hemocyanin, nor is there a biologist who, when confronted with the causal explanation of photosynthesis in green plants, will ask why these plants don't have cytochrome. Similarly, when confronted with the functional explanation of hemoglobin in vertebrates or of chlorophyll in green plants, no biologist will ask why these animals don't have hemocyanin or why these plants don't have cytochrome.[43] (As a matter of fact, biologists may ask these questions, but only after the acceptance of these explanations and as a subsequent research question.)

Thus the problem of functional equivalents and the associated problem of the specificity of most biological laws are not so much biological but rather philosophical problems and it is mostly philosophers who make an issue of it. This is related to a preoccupation among philosophers with deductive-nomological explanations based on universal laws. However, the non-universal character of biological laws concerns causal explanations just as much as it concerns the corresponding functional explanations. Nevertheless, these causal explanations are generally accepted by philosophers as legitimate deductive-nomological explanations. Many philosophers, such as Nagel, also accept intentional explanations as legitimate explanations, even though these explanations, too, appeal to non-universal regularities. Intentional explanations may even pertain to just a single individual. According to Nagel, however, they are legitimate causal explanations (Nagel 1977, p. 264; see 7.2.1). The same applies to explanations of goal-directed behaviour or of goal-directed processes (Nagel 1977, pp. 277, 299; see 7.2.1). I conclude from this that (a) we may take a more liberal stance towards the requirement of universality of causal laws, and (b) the non-universal character of most biological laws is irrelevant to the structure of functional explanations.

7.3.2 Functional equivalents are irrelevant

Given that we are dealing with vertebrates, there really is no functional equivalent for hemoglobin. If we were to replace hemoglobin by hemocyanin in these animals, they really wouldn't survive. Given that we are dealing with mammals, birds and reptiles, there really is no functional equivalent for lungs. If we were to replace lungs by gills or stomata in these animals, they wouldn't survive. Given that we are dealing with green plants, there is no functional equivalent for chlorophyll. If we were to replace chlorophyll by cytochrome in these plants, they wouldn't survive. Given that we are dealing with sticklebacks, there is no functional equivalent for fanning. If we would force these fish to do what other fish (who don't build tubular nests) do, namely to swim around and enjoy life, their eggs wouldn't survive.[44]

In short, given the respective organisms *as they are in other respects*, there really are no alternatives to their functional properties. Given that we are dealing with mammals, birds and

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[43]Suppose that all organisms would have the same properties, that is, would have 'found' the same solutions to the problems of life. Then there would be little left for biologists to explain, or study at all, for that matter.

[44]In providing (justifying) functional explanations, biologists often make use of this kind of counterfactual reasoning. See also Wouters (1995).

reptiles, we can derive from the fact that these animals breath and the fact that *they* cannot breath without lungs, that they must have lungs. The presence of lungs is accepted as something that is given in these animals - it is, after all, the property to be explained. That other types of organisms have gills or stomata is an interesting fact, that leads to the subsequent research question of why mammals, birds and reptiles have lungs instead of gills (see 7.4), but it is irrelevant to the functional explanation of lungs.

This means that functional properties may be considered as necessary conditions for the adequate functioning of the respective organisms after all. The existence of functional equivalents merely indicates that, on a global level, the presence of a certain property in some creatures may not be the only way to serve some function. It merely indicates that, globally, there may be different ways to solve some problem. However, given a certain solution on a local level, that is, given a certain property in some type of organisms, then, given these organisms as they are in other respects, this property can be considered a necessary condition for the survival and/or reproduction of *these* organisms.

Incidentally, Nagel (1977) seems to have reached the same conclusion: "For example, a convincing case can be made for the claim that in normal human beings - that is, in human bodies having the organs for which they are at present genetically programmed - the heart *is* necessary for circulating blood; for in normal human beings there are in fact no alternative mechanisms for effecting the blood's circulation" (Nagel 1977, p. 292; see also Wouters 1995, p. 444). As to Hempel's objections to this view, Nagel notes that "Despite his doubts that such premises can be validly asserted, he does assume that there are *necessary conditions* (such as the elimination of wastes) for the proper working of organisms. He must therefore have had in mind organisms which are actually found in nature in determinate environments and which must satisfy certain conditions if they are to flourish. For if we are free to exercise our imagination and deal with mere possibilities, with no limitations placed on the kinds of organisms that may be considered, organisms can be imagined that produce no waste materials and have, in consequence, no need for eliminating them. However, if necessary conditions can be discovered for the "proper working" of organisms in their natural state, what reasons are there for doubting, on general principle, that certain organs and other parts of organisms may be necessary for the performance of the functions that are associated with those organs and parts? In point of fact, examination of standard treatises on the physiology of the human body, shows that the great majority of its organs and parts *are* necessary for the performance of their several functions" (Nagel 1977, p. 293). To this may be added that Hempel does take the property z, for which in his view the property y is a sufficient condition, to be a *necessary* condition for the adequate functioning of organisms x (see the scheme in 7.2.4), even though z may just as well be a property for which there are, globally, functional equivalents.

7.3.3   Functional properties as INUS-conditions

A way to account on the one hand for the existence, on the global level, of functional equivalents and on the other hand for the claim that functional properties are necessary for the adequate functioning of organisms, is to make use of Mackie's (1965) notion of INUS-conditions. An INUS-condition is an Insufficient but Necessary part of an Unnecessary but Sufficient condition. This notion seems perfectly suited for functional explanations and for the problem of functional equivalents: a functional property can be seen as an insufficient but

necessary part of an unnecessary but sufficient condition. To stay with the example of lungs: lungs are insufficient for the breathing of mammals, birds and reptiles (this requires also a mouth or nose and a windpipe), but they are a necessary part of an unnecessary (there are functional equivalents) but sufficient condition.

Thus, when we take a more liberal stance towards causality and when we use this (Mackie's) notion of necessity, functional properties can indeed be considered necessary conditions for the adequate functioning of organisms. And this means in turn that, when we fill in this notion of necessary conditions as INUS-conditions in Nagel's scheme (see 7.2.4), functional explanations can be reconstrued as deductive explanations à la Nagel after all. Naturally, the truth or adequacy of a functional explanation depends (as with any explanation) on the truth of its premises, that is, in this case, on the truth of the specific functional statement that a certain property is necessary, but this means only that, as indicated in Kuipers's scheme, this statement must be tested for its tenability. Given its verification, however, nothing stands in the way of accepting the deductive nature of the explanation. I will return to the testing (and supporting) of functional statements later (7.4.4), but first I will now enter into the second way of showing why functional equivalents are irrelevant to the status (structure) of functional explanations.

7.4 The unity of causal and functional explanations
7.4.1 The emergence of functional properties

Since outside the group of vertebrates there are functional equivalents for hemoglobin, the functional explanation of hemoglobin in vertebrates must eventually be supplemented with an explanation of why these animals don't have hemocyanin or some other respiratory pigment. More generally, functional explanations will usually lead to the subsequent question why organisms of type x have property y and why not some functionally equivalent property y*. The only way to answer this question is by providing a *causal* explanation of the presence of y in x. The only way, from the biological perspective, to really solve the problem of functional equivalents is to causally explain a functional property.

In causal explanations we can also, as in functional explanations, make a distinction between proximate and ultimate explanations, or between proximate and ultimate components of these explanations. A *proximate* causal explanation of the presence of hemoglobin in vertebrates consists of a specification of the causal factors which have led to the production of hemoglobin during the *ontogeny* of these animals, that is, their development from fertilized eggs into mature organisms. Among these factors are the production of the porphyrin molecules and of the amino acids in the globin molecules, and the information for this is encoded in certain genes which these animals have inherited from their parents. Thus, vertebrate animals carry hemoglobin in their red blood cells, because in their genome they have certain genes which code for the production of this protein during the ontogeny of these animals.

In the end, however, a causal explanation of the presence of hemoglobin in vertebrates, and more in particular of its coming into being in historical time, will have to be an *ultimate* causal explanation. This explanation consists of a specification of the causal factors which have led to the emergence of hemoglobin during the *phylogeny*, that is, the evolutionary development, of vertebrate species. The only biological theory with which this development can presently be explained is the neo-Darwinistic or synthetic theory of evolution. As is well

known, this theory specifies a mechanism for the evolution of species and properties in terms of variation and natural selection. A property comes into existence as a (random, non-purposeful!) variation on what already existed due to mutations and/or recombinations in the genetic make-up of an organism. A property is maintained by natural selection, a process that may be pictured as a kind of sieve of biotic and abiotic environmental factors which eliminates unfavourable variations and allows favourable variation to pass on to next generations. Favourable variations are variations that have adaptive value, that is, given a certain selection environment, increase the fitness of an organism relative to the fitness of organisms in which the variation has not occurred. This enables the organism in which the variation occurred to produce more offspring than its unvaried fellows, as a result of which the variation may spread in the population over the next generations (and eventually supplant the unvaried form completely, but that need not be the case). Thus, when applied to hemoglobin, the theory states that hemoglobin came into existence as a result of genetic mutations and/or recombinations in some ancestral species and was maintained and spread throughout the population by natural selection, because it had (and has) adaptive value for the organisms in which it occurred: it increased the rate at which they could take up and release oxygen and thereby enabled them to produce more energy. More specifically, the conservation of the nine amino acids in the globin-chains of all vertebrate species can be explained as a result of such a variation and selection process in an ancestral species, which, because of its adaptive value, has been retained during the later speciation, in the phylogenetic spread that led to the present species.

7.4.2 Functional properties as adaptations

I have now reached a most interesting and important point which, in my view, is decisive for the debate on functional explanations. For notice that the above ultimate causal explanation of the presence of hemoglobin, as well as that of the conservation of the nine amino acids, appeals to the adaptive value and, hence, to the *function* of hemoglobin (and of the amino acids, respectively)! A causal explanation of the presence of hemoglobin in present vertebrates in terms of the variation and selection model would be absolutely unsatisfying if it would not state explicitly *why* the selection operated in favour of hemoglobin, and the answer to that question is precisely the functional explanation of hemoglobin! In other words, it is impossible to give a satisfactory ultimate causal explanation of the presence of hemoglobin when its proximate function is unknown and when this proximate function is not stated explicitly in the explanation.

Suppose in general that organisms of type x have property y which has the function of contributing to another property z and thereby to the survival and reproduction ∞ of x. A full, be it admittedly rough, causal explanation of the presence of y would then run as follows: organisms x have property y, because (1) y is being produced under the influence of certain genes g of x, which (2) have emerged due to mutations and/or recombinations within genes g* of forefathers x* of x and which have been maintained and spread in the population by natural selection, because (3) y contributed to property z of x and thereby (4) increased the fitness f of x relative to the fitness f* of x*, such that (5) y (through the genes g coding for its production) was (and is) passed on to next generations of x. Schematically, this explanation looks as in the following figure:
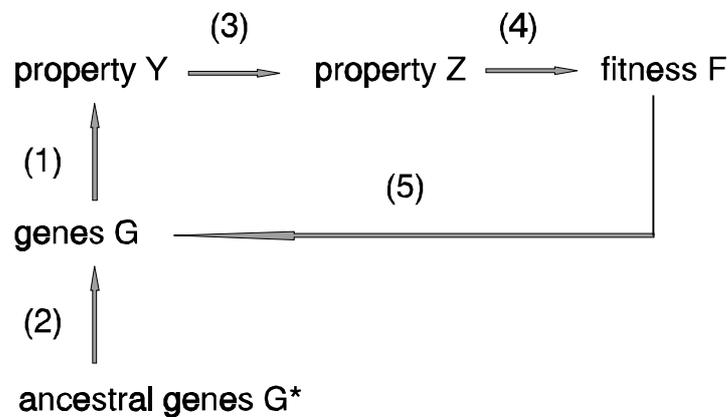
Figure 5: Schematic representation of a complete causal explanation of a functional property y, having proximate causal (1), ultimate causal (2), proximate functional (3) and ultimate functional (4) components; (5) stands for reproduction.

7.4.3   Natural selection and the principle of functionality

Figure 5 shows that both causal-nomological components of a functional explanation (indicated by 3 and 4) are *essential* parts of a full causal explanation of the presence of y. This makes functional explanations principally indispensable in biology. It is often impossible, moreover, to find empirical evidence for the hypothesis that some property has come into existence through mutations and/or recombinations and has been retained by natural selection, for the simple reason that the past of these processes is often inaccessible to empirical research. In such cases, the only way to find evidence for the hypothesis is by showing that the property is (ultimately) functional, that is, has adaptive value and endows its bearers with a selective advantage over non-bearers. This makes functional explanations also practically indispensable. It indicates that functional explanations may be seen as a kind of 'short-hand' for causal, evolutionary explanations (Looijen 1987; Maynard-Smith 1990), and it is in this sense that my earlier remark, that functional explanations *are* causal explanations, should be taken.

  Figure 5 shows also that the contribution of a property y to the survival and reproduction of organisms x, which is stated in a functional explanation of y (directly, or indirectly through its contribution to another property z) is an *ultimate cause* of its presence in x. That is to say, apart from the fact that it must first emerge as a (random) variation, the effect of y, its adaptive value or function, can be seen as an ultimate cause of its presence (preservation) in x. And that, in turn, is to say that the effect of y, its contribution to z and ∞, can be seen after all as an *antecedent condition* for its presence (preservation) in x, indicating once more that we are dealing with a species of causal explanation. The only (but not a slight) problem raised by this account is the question what came first: y or z? What came first: lungs, or animals

that needed lungs (or to whom lungs came in handy in their past selection environment, during their transition from life in water to life on land)? Was there first chlorophyll, or did photosynthesis come first? Did the circulatory system come first, or were there first large animals which needed such a system? Instead of speculating endlessly about these questions, I will confine myself to the statement that they are, in my view, chicken and egg questions, which can be answered only by empirical (historical, paleontological or possibly population-genetical and ecological) research.[45]

   This unity of functional and causal-evolutionary explanations is underlaid by a deeper relationship which is expressed by the afore-mentioned principle of functionality: as a rule, properties of living beings are functional, because non-functional or dysfunctional properties will sooner or later be eliminated from a population by natural selection. Only properties that are functional, that contribute to the survival and reproduction of their bearers, outlive this selection. Because of this relationship between functional and evolutionary explanations it should come as no surprise that it is especially evolutionary biologists like Simpson, Mayr, Ayala, Dobzhansky, Futuyama and Maynard-Smith who defend the role of functional explanations in biology (but see for the conception of functions as adaptations also philosophers like Ruse 1973; Wright 1976; Brandon 1981; Millikan 1984, 1989; Sober 1984; Neander 1991; and Kuipers 1986, 1997).

7.4.4   Exceptions to the functionality principle?

One generally assumes that the past selection environment, in which a property arose as an adaptation, is (roughly) the same as the present selection environment, or at least not so much different that the function which a property had in the past selection environment was different from the one it has in the present selection environment. However, this need not be the case. There are several possibilities.

   In the first place, it may be that a property that was functional in the past selection environment has lost its function. Well-known examples of this are our coccyx and perhaps our tonsils and appendix. As long as such properties are not dysfunctional, however, they may be maintained in a population. Naturally, there is no present functional explanation for such properties, but there may have been a functional, as well as an evolutionary, explanation with regard to the past selection environment.

   A second possibility is that a property, which had a certain function in a past selection environment, has received a new function in a new selection environment, or, in other words, that the function of a property may have changed in the course of evolution. A nice example of this is the tail. Assuming that life originated in the oceans, the tail was first developed as a propulsive organ, a function which it still has in fish, sharks and whales. Later, in animals who developed on land, the function of the tail changed into, for instance, a supporting or balancing organ (in, amongst others, kangaroos), a steering organ (in birds), a grasping organ (a sort of fifth limb in monkeys), a fly-flap (in many hoofed animals) or a show-piece (in

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[45]See Wouters (1995, pp. 451-2) for a not particularly convincing argument, in terms of chicken and egg questions, against the conception of functional explanations as short-hand for evolutionary explanations, or against the view that the adaptive value (function) of a property is a cause of its present occurrence.

many birds like peacocks) or impressing organ (in for example horses). In frogs and toads the tail has almost completely disappeared, though it still exists (as a propulsive organ) in tadpoles (which live in water). In all cases where the tail still exists, it is possible to give a functional as well as an evolutionary explanation fitting the present selection environment.

A third possibility is that a property may have emerged as a side-effect of another (functional) property, but has, or appears to have, no function itself. The standard example of such a property is the sound of the heart-beat. Though the heart-beat serves to circulate the blood through the body, the sound it produces seems to be a side-effect that has no function itself (except perhaps a reassuring or comforting one for embryos). Another example, provided by Grant (1963, in Nagel 1977, p. 298), is the colour of yellow onions. Although yellow onions are resistant against a particular fungous disease, while white onions are susceptible to it, the colour of the yellow onions appears to have no function (adaptive value) itself. To this should be added, however, that colours generally do have important functions in biology and that it may be that in the future even for the colour of yellow onions a functional explanation will be found. It should also be noticed that, if or as long as no function can be ascribed to some property, there is no functional explanation (yet) for it and, therefore, neither a 'problem of functional explanation'.

A fourth possibility is that a property may have side-effects which *are* functional (so that we might better be talking about several functions of the same property, such as the many functions of the liver), and which may have emerged in different evolutionary periods (and hence in possibly different selection environments). In such cases there will be different functional explanations corresponding to different evolutionary explanations.

A final, and most interesting, possibility is that there may be exceptions to the functionality principle in the way of (either or not apparently) dysfunctional properties. Naturally, there can be no functional explanation for such properties. (Many genetically induced diseases may fall under this heading). However, there are interesting cases of (apparently) dysfunctional properties which can be given an evolutionary, and therefore also a functional, explanation. A familiar example is the occurrence of sickle-cell anaemia in humans. Humans having normal red blood cells are homozygous (say AA) for the gene that codes for these cells. Humans having abnormal, sickle-shaped red blood cells are homozygous (aa) for the aberrant gene. They usually die before reaching reproductive age. However, all other things being equal, heterozygotes (Aa) may normally stay alive. It appears that, contrary to expectation, the aberrant allele (a) remains present with relatively high frequencies in certain parts of the world. The cause of this is that heterozygotes appear to be much more resistant against a certain form of malaria than either homozygote. Therefore, in parts of the world where this form of malaria reigns, heterozygotes have a selective advantage over homozygotes and transfer the aberrant allele (a) on to next generations, whence it is retained in the population despite the fact that elsewhere it is dysfunctional and leads (in 'aa' homozygotes) to premature death. This is an example of *balanced selection*, and more in particular of *heterosis* (or advantage of the hybrid), one of the mechanisms through which populations may be endowed with a diverse gene-pool or various genotypes allowing them to adapt to various selection environments.

7.4.5 Co-operating research programmes

To conclude this chapter I will show that in the context of functional explanations there is

also a mutual dependence of holistic and reductionistic research programmes. This occurs in two areas: (1) deductive support of functional statements, and (2) causal explanations of functional properties.

As noticed before (see also Kuipers's scheme in 7.2.5), the statement that a certain property y of organisms x is functional for another property z and thereby for the survival and reproduction ∞ of x, will first be generated as a hypothesis which must next be tested for its tenability. Such testing means that one goes in search of an underlying theory with which the function of y can be explained, or, in other words, with which the functional statement can be deductively supported. From this theory, joined by the required auxiliary hypotheses, one can derive deductively that organisms x need property y in order to have property z and that, hence, y is functional for z (see note 37). In the case of hemoglobin this underlying theory is the theory of allostery, supplemented by the theory of chemical bonding. In order to prove the function ('role') of hemoglobin biochemists and molecular biologists had to show that the uptake and release of oxygen by the blood rests with the binding and release of O_2 molecules by hemoglobin molecules and that the accelerated uptake and release of oxygen by the blood is the result of the allosteric properties of these molecules. In the case of flatworms, McNeill Alexander (1979) needed Flick's diffusion law to deductively support his claim that flatworms of more than a millimetre thick could not survive (Wouters 1995).

In other words, functional statements must be deductively supported before they can be accepted as genuine explanations. And that means that in cases of functional explanation we can see the same sort of mutual dependence between holistic and reductionistic research programmes as in cases of reductive explanation. For if, following holists like Mayr and Simpson, we associate functional explanations with holistic research programmes, and if we associate their deductive support with reductionistic programmes, we can talk here also of a holistic guide programme that generates a problem which it cannot solve itself: the support of a functional hypothesis. For the solution of this problem it depends on a reductionistic programme which sets itself to supporting the hypothesis. If it succeeds in doing so, the reductionistic programme acts as a supply programme for the holistic guide programme. However, it is itself dependent on the guide programme, because it can only provide the deductive support after the need for this has arisen at the level of the guide programme.

In the second place there is a mutual dependence of holistic and reductionistic research programmes in the sense that, as noted above, functional explanations generally lead to the subsequent question of why organisms x don't have a functionally equivalent property y* instead of y and that the answer to this question can only be a causal explanation of the presence of y in x. When we associate functional explanations again with holistic programmes and now associate the proximate and/or ultimate causal explanations with reductionistic programmes, we see again the mutual dependence of both types of programmes. Holistic programmes depend on reductionistic programmes for causal answers to the question of why organisms x have property y instead of y*, and reductionistic programmes depend on holistic programmes for generating the question.

7.5   Conclusions

I have shown that functional explanations specify 'normal' efficient causal relations and that, therefore, they are not in contradiction with the principle of causal determinism. I have also shown that, using Mackie's INUS-conditions, functional explanations can be reconstrued as

deductive-nomological explanations à la Nagel (1961/82), where functional properties appear as necessary conditions for the survival and reproduction of the respective organisms. Besides that, I have argued that functional properties can be seen as adaptations and that, therefore, functional explanations can be regarded as 'short-hand' for more comprehensive causal-evolutionary explanations. This means that the function or adaptive value of a property can be seen as an ultimate cause, and hence as an antecedent condition, for its present occurrence in organisms, indicating that in this respect too, functional explanations can be seen as a species of causal explanation. Finally, I have argued that in the context of functional explanations too, there is a mutual dependence of holistic and reductionistic research programmes, both because functional hypotheses must be deductively supported and because functional explanations (in the narrow sense) must eventually be supplemented with (proximate or ultimate) causal explanations of the respective property.

Thus, the conclusion we can draw is that holists or autonomists are right in asserting that functional explanations are indispensable in biology. On the other hand, reductionists or provincialists are right in asserting that functional explanations can be replaced by causal explanations, where one should bear in mind, however, that 'being replaced by' actually means 'being placed under', because ultimate causal explanations cannot do without proximate and ultimate functional components. Given the fact that functional explanations specify causal-nomological relations, which form, or may form, essential parts of more comprehensive causal-evolutionary explanations, we can also draw the conclusion that they provide no obstacles to reductions but rather contribute to them.