Etiological Theories of Functions and Functional Explanations in Biology

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Abstract

My thesis will be a study on how etiological theories of functions relate to functional explanations in biology. Focusing on the problem of distinguishing between evolutionary explanations and functional explanations, I will show why the modern history theory of functions, along with the whole etiological account, cannot support this distinction by itself. This is a serious problem because etiological theories define functions in terms of the traits' evolutionary history, and thus, they take functional explanations to be a kind of evolutionary explanations. Biologists, however, employ functional explanations independently from evolutionary ones. My objection to the way in which the modern history theory draws the distinction will target two assumptions on which this account relies: that selected effect functions can account for both kinds of explanations and that functional explanations are a kind of historical selection explanation. These two assumptions are not supported by the practice of biologists, who use different concepts of functions and other methods beside the historical method in their explanations. As a consequence, functional explanation, as defined by etiological theories is unable to offer satisfactory accounts for the fitness contribution of traits. In the end, I will show that the distinction can be made with the help of different concepts of functions: causal role, biological advantage, or propensities. I conclude that the function debate should take a turn towards biological explanations and the explanatory relations between the different concepts of functions.

Contents

Introduction

There are more kinds of explanations in biology, relating to the different questions that may be relevant when studying a certain organism, trait, or behavior. I will be concerned with the distinction between functional explanations and evolutionary explanations. Upon making an inquiry over a certain trait present in an organism, biologists may refer to its current contribution to fitness or to its evolutionary history. A functional explanation will say how that particular trait helps in sustaining a process that proves to be important for that organism's survival and reproduction. An evolutionary explanation will track the trait's presence in the organisms' ancestors and make a claim about the selection pressures that led to the trait's propagation. I will argue that etiological theories of functions unduly blur this distinction.

Starting from the general framework set by etiological theories and going through the specifications made by modern history theories of functions, I will show that this distinction cannot be made on the basis of a fully etiological concept of function. I will argue that the failure in making this distinction rests on a conceptual mistake: the supposition that functions analyzed only by virtue of their selection history are adequate for the function ascriptions present in both functional explanations and evolutionary explanations that biologists employ.

Inquiries into the different explanations concerning function ascriptions show that there is a clear distinction between traits performing a certain function within an individual organism and traits having been selected for a function in a species' past. The former case amounts to functional explanations (how that trait relates to other processes and proves to be fitness increasing), the latter to evolutionary explanations (where the present trait originates and in what

ways it affected past population dynamics). Since etiological theories define functions through an evolutionary history, on their account functional explanations should fall within the category of evolutionary explanations, not stand by themselves as a distinct category. Upon asking, for example, what the function of the heart is, etiological theories of functions take the presence of the heart in current organisms to be the *explanandum*, while the *explanans* refers to the past selection of hearts for blood pumping. An explanation that follows this structure, while rightfully ascribing the heart the function of pumping blood, takes the function ascription to rely mainly on the evolutionary history of the trait (how did species with a heart evolve, what were the selection pressures etc). However, what biologists use as a functional explanation in this case would refer to the blood pumping function of the heart relating to the more complex process of blood circulation and its contribution to the survival of the organism. On this type of explanation, the *explanans* refers to current processes and conditions present in the organism in question, and not to past selection. By taking past selection to be explanatory for present function ascriptions, etiological theories take functional explanations to answer the same question that evolutionary explanations address: what is the trait's selection history and how it determines the current existence of the trait.

One unlikely consequence that etiological theories would have to concede if they maintain this conflation would be that when providing explanations in physiology or anatomy one should always refer to the evolutionary history of the traits studied. The practice of biologists shows that this is not the case: functional biology and evolutionary biology are considered separate fields (see Mayr), and considerations on anatomical or physiological aspects are independent from the evolutionary history of the traits in question. From the more general point of view of investigating living organisms and the traits or processes characterizing them,

inquiries into the functions of particular traits and their evolutionary history are connected. Function ascriptions can be made pointing to the system in which the trait contributes to certain, more complex processes; there is also a more general explanation of the trait's existence that relates to its contribution to the survival and reproduction of a certain species. However, upon accounting for the fitness value of the different traits, one may step out of the historical account and find other ways of investigating how those traits are useful and how they increase fitness. The connection is not as etiological theories of functions point it out to be: not all claims on functions amount to claims on evolutionary history. The two explanations are distinct and investigations on various organisms can specify the functions of different processes without investigations into their history. Moreover, sometimes evolutionary considerations start from the present functions one ascribes to a trait, or process. This shows that there is a need to make a distinction between the two domains of inquiry.

There are two assumptions on which I am going to rely in building my criticism of the etiological account. The first is what is called "pluralism" with respect to the analyses of functions in the philosophy of biology: there is no one single concept of function to incorporate all the function ascriptions found in biology. Apart from selected effect functions, the other concepts relevant to my investigation will be causal role functions (as in Cummins) and functions as biological advantage (as in Wouters). The second assumption will be that there are three kinds of explanations used in biology, relating to the previous three concepts of functions (but not limited to them): the historical selection explanation, the mechanist explanation, and the design explanation. (distinction found in Wouters). This assumption will be relevant in pointing out how the particular analyses of functions answer the different questions biologists ask. My point will be that in order to account for the distinction and the relations between the different

explanations, the etiological account must make use of another analysis of functions. While I will not investigate the further problems that causal role functions or functions as biological advantage may have, these accounts help shed some light on some possible solutions to the objections raised against etiological theories.

My criticism against the etiological account, and particularly the modern history theory, will be that functional explanations, as used by biologists, cannot ultimately rely on selected effect functions and, consequently, on a selection history explanation. The distinction drawn with reference to the time of selection (as in Godfrey-Smith) makes functional explanation a kind of historical explanation. I mean to show that this does not capture what functional explanations amount to. Taking functional explanation to account for cases of recent selection only would not be enough for what biologists call functional explanation. Without referring to a causal process working within a system, or to some sort of counterfactual involving comparisons between organisms, etiological theories cannot draw a line between the distinct categories of selection history explanations and functional explanations.

One important consequence of this critique would be that etiological theories of functions, while having several advantages, have a serious problem in relating to biological explanations. This shows that the debates on functions should focus more on the concepts used in biology and on the problem of functional explanation than on other aspects that led the debate, such as finding one main analysis of functions, or the issue of normativity. Another implication would be that, as biologists work with various notions of functions and various explanations, assuming that they can be captured within a single analysis of function or explanatory project would be too restrictive. Finally, clarifying the difficulty that etiological theories have with functional explanations and revealing that the historical account of functions fails to answer it

can show what one can expect from a biological explanation and what are the important factors taken into consideration by those explanations: it is not a problem posed in terms of the time of selection only, as etiological theories assume, but it also relates to the fitness and the adaptiveness of traits.

Chapter 1

Analyses of Functions

In this first chapter I will explain the main concepts I am going to work with and focus on the etiological theory of functions, which will constitute the object of my criticism in the following chapters. I will also discuss the connection between function ascriptions and explanations in biology. While functional explanations became a problem within the more general concern with the structure of scientific explanation, and various answers have been given, the current debate starts from two accounts: selected effect functions as defined by etiological theories (as in Wright, Millikan, Neander) and causal role functions as described in systematic accounts (Cummins). Apart from these two concepts, I will also discuss the biological advantage approach to functions (as in Wouters) and the resulting explanatory project, design explanation. Another concept of function, the propensity view (as in Bigelow and Pargetter), will be briefly discussed in the final chapter.

1. Selected effect and causal role functions

According to Millikan (1984), Amundson and Lauder (1993) and Godfrey-Smith (1994), among others, the distinct causal role and selected effect analyses are not necessary rivals and could account for different explanatory projects, both used by biologists. While their views diverge upon considering one analysis as being the main one or opting for pluralism, it is agreed that selected effect functions are employed mostly in evolutionary biology and causal role

functions work in anatomy or physiology. The two explanatory projects could be summarized as follows:

1. Explaining why a trait exists in the form it does.
2. Explaining how a component of a system contributes to the system performing a more complex capacity.

The former explanatory project relies on an etiological account for functions, while the latter uses a systematic theory. An explanation in the sense provided by (1) will be historical. The explanation scheme, as shown by Godfrey-Smith (1994) takes the *explanandum* to be the existence of current members of the family, while the *explanans* is a fact about prior members. Using the well-known heart example, one could say that present hearts (as tokens) exist now because of their membership to a type which incorporated tokens that exercised the same capacity in the past. On the other hand, an explanation such as (2) would mention that the heart contributes to the circulatory system by pumping blood. I will present the two accounts in the following sections.

a) Functions and selected effects

In Wright's original formulation, the selected effect analysis of functions holds that:

> The function of X is Z means:
> (a) X is there because it does Z,
> (b) Z is a consequence (result) of X's being there. (Wright 1973: 161).

One point that should be mentioned here is that while etiological theories of functions rely on this kind of analysis, in Wright's formulation it is not obvious that functions are described historically. Etiological theories explain a trait's current presence in terms of its past

selection. Taking the standard example, the heart's pumping capacities in humans will be explained via the past selection of hearts for their blood pumping capacities. Another important aspect is that Wright's analysis was supposed to apply to both biological functions and artifacts. In the refinements brought by Millikan and Neander, the etiological theory works mainly for biological systems, although an account for artifacts is generally considered possible. Millikan (1984) describes traits as being members of a family produced by certain lines of copying. Thus, an eye, for example, is member of a family of traits selected for sight and it is passed to further organisms by means of reproduction. This is not the case for artifacts. According to Millikan, the proper function of m is to F if m is the member of a reproductively established family R and if

> (1) Certain ancestors of m performed F.
> (2) In part because there existed a direct causal connection between having the character C and performance of the function F in the case of these ancestors of m, C correlated positively with F over a certain set of items S which included these ancestors and other things not having C.
> (3) One among the legitimate explanations that can be given of the fact that m exists makes reference to the fact that C correlated positively with F over S, either directly causing reproduction of m or explaining why R was proliferated and hence why m exists. (Millikan 1984: 28)

Godfrey-Smith's definition of functions, endorsing an explanation of the former kind, goes as follows:

> The function of m is to F iff:
> i. m is a member of family T,
> ii. members of family T are components of biologically real systems of type S,
> iii. among the properties copied between members of T is property or property cluster C, which can do F,
> iv. one reason members of T such as m exist now is the fact that past members of T were successful under selection in the recent past, through positively contributing to the fitness of S, and
> v. members of T were selected because they did F, through having C. (Godfrey-Smith 1994: 359)

As will be pointed out in the next chapter, Godfrey-Smith's account of functions differs from standard etiological theories with respect to the time of selection; instead of distant past, it relies on more recent history of the traits.

An advantage that comes with etiological theories is that they permit the use of normative notions in biology. Using a concept of function that refers to the selected effect one is able to say that a trait has a certain function, for which it was selected in the past, but it might be currently unable to perform it. On this account, it is possible to say that most tokens of a type perform their function, but, in certain circumstances, some of them may not, and this does not render them functionless. As Godfrey-Smith puts it, an etiological theory

> can say without strain that some particular thing which is in principle unable to do F now, nonetheless has the function to do F. It has this function in virtue of its membership in a family which has that function. Whether this member can do F is irrelevant to its family membership, as long as it was produced by lines of copying that are generally normal enough. (Godfrey-Smith 1994: 347)

If a trait is currently selected for a past capacity, that capacity can still count as its proper function even if, in a given organism, the trait is unable to perform it for the time being. For example, a malformation to an individual's heart that renders it unable to pump blood does not cancel that particular heart's function to pump blood. On a systematic account, as we shall see, if the heart does not contribute to the circulatory system, then it has no function. Although the normativity of function ascriptions is a controversial issue (see Davies 2000), an account for malfunctions can count as an advantage for etiological theories. This could be relevant especially when talking about biological functions, since in biological systems malfunctions are often in need of explanation.

b) Functions and causal roles

Cummins' account was initially a rival of etiological theories. Cummins points out the assumptions that underlie the investigations of the concept of function:

1. Functions ascriptions in science should explain the presence of the trait that is functionally characterized.
2. A trait performs a function if it has certain effects on a containing system, the effects contributing to some activity or condition of that system.

These assumptions are found in Hempel (1959) and Nagel (1961), but also in Wright's previously mentioned analysis. While keeping the latter assumption, Cummins considers that the former should be dropped and that an analysis of functions should not be concerned with explaining the existence of a functional trait.

Cummins' theory need not make any claims about previous traits. He considers that the function of a trait consists in exercising a capacity within a system and thus contributing to the system performing a more complex process. The function ascription is made by virtue of the causal role the trait performs in a more complex capacity exercised by the organism:

> x functions as a φ in s (or: the function of x in s is to φ) relative to an analytical account A of s's capacity to ψ just in case x is capable of φ-ing in s and A appropriately and adequately accounts for s's capacity to ψ by, in part, appealing to the capacity of x to φ in s. (Cummins 1975: 762).

This definition also shows how the first presupposition underlying selected effect analyses is rejected. As Cummins puts it, "what we can and do explain by appeal to what something does is the behavior of a containing system" (Cummins 1975: 748). Also, the notion of function is no longer normative: if the heart no longer has the capacity of pumping blood, then one cannot

ascribe it that function since it no longer contributes to the body's more complex capacity of sustaining blood circulation.

2. Function, biological advantage, and design explanation

Defining function through the biological advantage it provides to the organism having a certain trait is interesting because it involves some considerations on functional explanation that are not present in the previously mentioned approaches. Wouters (2003) takes function attributions to answer four questions, corresponding to four concepts of function:

1. What does it do? (function as activity)
2. How is it used? (function as causal role)
3. How is it useful? (function as biological advantage)
4. For what effect it was selected in the past? (function as selected effect)

For example, the heart has the property of contracting rhythmically, an activity which it performs by itself (function in the first sense). Based on this property, the heart pumps blood, which is its biological role within the more complex circulatory system (function in the second sense). Thus, the heart contributes to the circulatory system, which is more advantageous than a diffusion system because oxygen is transported faster (function in the third sense). The efficiency of having a circulatory system has favored the vertebrates which to this day have a heart whose function is to pump blood (function in the fourth sense).

In this section, I will only discuss (3) and its specific explanatory project, which differs from the previous considerations of Godfrey-Smith. Wouters grounds his concept of function, in connection to biological advantage on a particular kind of investigation upon traits made by

biologists: comparing organisms having the trait in question with organisms that may not have that trait or that may have a different one. One of his examples is that of the circulation of the blood. Upon looking for the heart's function as biological advantage, one asks why is it useful to have a system that circulates blood. Referring to Krogh's (1941) conclusion that within a circulatory system oxygen is transported much faster than in a diffusion system, one could claim that the faster oxygen transportation is the biological advantage of having a circulatory system. This function ascription is made through a comparison between different systems. Formally put,

> one biological advantage to organisms in condition *c* of having trait *t* rather than trait *t'* is that those organisms can do *v* better if they have *t* than if they had *t'*. (Wouters 2003: 645)

Also, Wouters mentions fitness as the ultimate criterion that determines which traits are the most advantageous. This will become important in the following chapters, since upon using functional explanations, one has to resort to the fitness value of those traits.

Moving on to the problem of functional explanation, Wouters considers that there are more senses in which one could account for functional explanations. According to etiological theories, functional explanations are a kind of historical selection explanations (the presence of traits is explained via their past contribution to fitness). According to systematic approaches, functional explanations are a kind of mechanistic explanations (as Wouters calls them, biologists would call them causal explanations). Wouters' own account, called design explanation is that functional explanations have a complex structure, based on counterfactual comparison. They involve causal role function attributions in the first place and, on a second stage, functions defined through biological advantage to show why is it advantageous for the trait to perform the ascribed function in the way it does rather than in some other way. Only the employment of biological advantage can permit counterfactual comparisons.

While I will not investigate whether the structure of functional explanations, as biologists use them, should fit one kind of these explanations over another, I take the historical, mechanistic and design aspects to be relevant and worthy of being taken into consideration when distinguishing functional explanations from other biological explanations. Even more relevant for the point I am going to make is Wouters' claim, against Cummins and Godfrey-Smith, that none of the explanatory projects is committed to a single concept of function. For example, historical selection explanations require both selected effect functions and biological advantage functions, for reasons that will become clear in chapter 3. While the conceptual framework set by Wouters goes against the way in which etiological theories deal with functional explanations, I consider that the whole project of distinguishing functional from evolutionary explanations needs more investigation, especially from the point of view of a comparison with how biologists use explanations. I will make my critique of etiological theories in chapter 3, and I will then use some of the distinctions set by Wouters.

Chapter 2
From Ancient Selection to the Modern History Theory

In this chapter I will point out some of the problems that etiological theories of functions have to face and how they try to answer them within the framework of the modern history theory of functions (as in Godfrey-Smith 1994). My main focus will be on the distinction between evolutionary and functional explanations, particularly on the problem that theories relying on ancient selection history of traits fail to draw the line between the two explanations as biologists use them. I will first mention two other objections which will be relevant to my criticism of Godfrey-Smith's solution to the problem of distinguishing functional from evolutionary explanations.

Most of the problems that etiological accounts of functions encounter relate to rendering the function dependent upon the original selection of a trait. As pointed out by Schwartz (1998), there are three main reasons for adding a modern history requirement to the analysis of functions.

First, as Godfrey-Smith (1994) notes, an ancient history approach to functions will ascribe a trait the function that connects to its original selection. However, the selection may have favored a completely different effect than the one that is now considered to be its proper function. For this reason, etiological theories have difficulties in dealing with exaptations.

Secondly, as Griffiths (1993) points out, an account for vestigial traits (i.e. traits that had previously had a function but have currently lost it) is needed. Relying exclusively on the ancient history of a trait, e.g. the appendix in humans, will take us back to its original function. However, what we want to say about a vestigial trait is that while it *had* a function, it no longer has one.

Thirdly, as Kitcher (1993) and Godfrey-Smith (1994) show, etiological accounts do not make a proper distinction between two kinds of explanation currently used by biologists: evolutionary explanation and functional explanation. According to Tinbergen (1963), the explanations that biologists work with take into consideration four kinds of questions concerning causal relation, survival value (or function), evolutionary history or ontogeny. Since in etiological theories functions are defined through the past selection of traits, the explanations for survival value (or function) are not a distinct category, but a kind of evolutionary explanations. As Godfrey-Smith puts it,

> Tinbergen's distinctions are often endorsed in the opening pages of books about animal behavior […]. This is clearly an embarrassment for any historical theory of function which seeks to capture biological usage: on the historical view there should be three questions, not four, as the functional question *is* a question about evolutionary history, as long as the rest of (F2) [i.e. the standard etiological account for functions] […] is satisfied. (Godfrey-Smith 1993: 10)

This is happening because, as mentioned earlier, the explanatory project endorsed by etiological theories takes function statements to answer the question "why does a trait exist in the form it does?". While one could see evolutionary explanations answering this question, it is harder to fit functional explanations within the same framework. Etiological theories do that by supposing that functional explanations are a kind of evolutionary explanations. Disclosing this presupposition, however, shows that this way of accounting for functional explanation does not correspond to the manner in which biologists operate with functional and evolutionary explanations, so it is not really informative in understanding biology. Investigations on physiology, for example, are made independently from evolutionary biology. An apparent solution, such as relating to the other explanatory project, and switching from "why?" to "how?"

would bring causal role functions into question and further strengthen the claim that etiological theories of functions cannot account for functional explanations by themselves.

1. Function, adaptation and exaptation

In his final considerations on the modern history approach to functions, Godfrey-Smith mentions the distinction between adaptations and exaptations made by Gould and Vrba (1982). While adaptations have been selected for certain functions, exaptations may have served no function in the beginning, or may have had a different function, being later co-opted for another function. While I will not discuss the views on functions that might result from Gould and Vrba's considerations (on Godfrey-Smith's account, they support some sort of propensity view; i.e. explaining the presence of a trait through its future effects on fitness), it is important to note that the whole adaptationism issue is connected to how one may approach functions. For etiological theories, the traits explained through past selection are mostly adaptations. That is why cases of exaptations provide them with difficulties: relying on ancient history would provide an explanation of the initial selection of the trait, which in the case of exaptations differs from current selection. In the case of constrains that have later been co-opted for fitness-increasing effects, things seem to get even worse, since according to the ancient history they serve no function.

According to a point made by Griffiths (2006), etiological theories have trouble in dealing with exaptations because they are centered on adaptations. When talking about adaptive traits, one has to employ causal role functions, and "by definition, every adaptation was once an adaptive trait, but not all adaptations are still adaptive and not every adaptive trait is yet an

adaptation. If we use the language of functions, a trait is *adaptive* in virtue of some of its CR functions." (Griffiths 2006: 2).

Thus, etiological theories can only account for functions as long as they are ascribed to traits that actually constitute adaptations. But an adaptation can have a use different from the one it was selected for, and thus be adaptive in a way different from what its ancient evolutionary history specifies. In order to account for its new function one has to resort to a systematic account, explaining how that particular function sustains a process that is advantageous for the organism. The same kind of explanation would be required from an adaptation that lost its adaptive value due to changes in the environment (e.g. the wings of the insects which from a windy environment end up causing them more harm than helping). Of course, in this case functions are no longer in question, since a maladaptation is at issue, but an explanation for the presence of the wings could still relate to etiology and the ancient selection history, and it would not be a functional explanation. Therefore, etiological theories relying on the ancient selection history are limited to function ascriptions involving traits that are adaptations.

On a modern history account of functions, the distinction between ancient and recent past selection manages to offer a satisfactory account on exaptations. Their functions are those that presently contribute to fitness, not the ones that were originally selected. Using another example from Gould and Vrba, bones are essential for the survival land-dwelling vertebrates, but they originate in sea animals. While the recent use for bones is support, they were originally selected as deposits for phosphates. On a modern history theory, this would be a good explanation of the function of the bones.

If having an account for exaptations is a challenge for etiological theories relying on the ancient past, a recent past approach would answer that worry. However, as it shall later become

obvious, the problem of adaptations and exaptations and an account of how traits are fitness increasing comes back due to the general historical account on explanations provided by etiological theories. There is a more general problem affecting modern history theories: the history of a trait is determined by its contribution to inclusive fitness. Thus, an inquiry over evolutionary history needs to explain how a trait increased inclusive fitness. Since inclusive fitness is generally defined in terms of population dynamics, establishing how a trait was fitness-increasing involves observing how the trait was present in past generations. While ancient history theories may look at the population dynamics over a period of time long enough to assess how a trait contributed to fitness, modern history theories, even though they are talking about the adaptiveness of traits in terms of inclusive fitness, cannot rely on the same method. Since a trait is evaluated in terms of its recent contribution to fitness, modern history theories have to explain how the trait under discussion in currently adaptive. Thus, they need an approach to fitness that could evaluate the fitness-increasing traits via a different way than going back to the original selection and propagation of the trait in past populations. What is even more problematic is that they will have to do that on an exclusively selected effect concept of function. As it shall be pointed out in chapter 4, a possibility would be to consider a propensity view on fitness (fitness considered as the disposition to survive and leave offspring as in Beatty and Mills 1979), but that could count as a move towards a forward looking view on functions, since it no longer relies solely on past selection.

2. *Vestigial traits*

As pointed out by Griffiths (1993), a theory of functions needs to distinguish between traits that serve a current function and vestigial traits. The case of traits losing their function but being maintained for a new function is part of the discussion concerning exaptations. However, there is still the case where a trait loses its original function but it is still found within a species due to lack of genetic variation. As Griffiths puts it, "a successful account must allow non-atrophied vestiges. But it will not do to make every trait that cannot perform its functions vestigial." (Griffiths 1993: 417).

Vestigial traits are a problem for etiological theories because explained through their original selection they should serve a function. Due to the normative character of the selected effect analysis of functions, one could always say that they do have a function, but they are unable to perform it. This, however, is not a satisfactory answer, since it is not sensitive to the distinction between traits malfunctioning and traits that lost their function. An account for functions should allow traits to malfunction, to have functions they cannot perform at a given time, without being vestigial traits. Even when a trait is malfunctioning it must still have a proper function.

From a broader point of view, this is a problem for etiological theories because, on their account, all function ascriptions should go back to their past adaptive history. The inference from the past adaptive history to the current adaptive value is problematic because it does not simply say that function ascriptions are justified by the evolutionary history of the traits in question. The structure endorsed by etiological theories opens up the space for a problematic claim: every trait that has an evolutionary history must also have a function. The problem can be traced back to the question that selected effect theories answer, "why does a trait exist in the form it does?" and the

definition of function relying on the model "T is there because it does F" and T does F on the basis of T having done F in the past and having been selected for doing F. Since, implicitly, ancient past is taken into consideration one could say that the eyes of a mole are there because they enable sight (they do have an evolutionary history). However, the explanation one would wish in this case is that the eyes of the mole are there now for no function; they were selected for sight in the past, but have currently lost their function. Explaining functions in a causal framework, and explaining the presence of a trait through its past function yields the inference from past selection to current function. As shown by vestigial traits, and, previously, by exaptations, the inference is not valid. This seems to be less so when considering species and environment conditions as changing over time: the evolutionary history of a trait cannot justify by itself the current function.

Griffiths' answer to this problem is a reformulation of the proper functions theory by relating it to Cummins' account, and adding the proximal selective explanation, according to which selection forces act during the last evolutionary significant period. The distinction between functional and vestigial traits is possible within the following account of functions:

> where i is a trait of systems of type S, a proper function of i in S 's is F iff a proximal selective explanation of the current non-zero proportion of S's with i must cite F as a component in the fitness conferred by i. (Griffiths 1993: 418)

As Griffiths' solution shows, the issue of vestigial traits points towards a possibility of combining the different accounts of functions. Upon mentioning functions as being part of a system, Griffiths is using the concept of function as causal role, as well: a trait has a function if it belongs to a system in which it contributes to fitness by performing a certain process. This, although it is related to the recent history of traits, is not part of the modern history account that

Godfrey-Smith endorses. Godfrey-Smith's solution is meant to account for this problem strictly from within the boundaries of an etiological theory. By making the maintenance of a trait relevant for its current function, the problem of vestigial traits is solved. According to its ancient history, the appendix had a function in the ancestors of humans, but according to the more recent history, it does not serve any function. If functions are defined through recent history, one can say that the appendix does not serve any function and thus it is not a malfunctioning trait either. However, by answering the difficulty in this way, modern history accounts are opened to another drawback: the problem of distinguishing between traits selected for a certain function from those maintained due to lack of variation. This problem, as pointed out by Schwartz, is more serious for recent history accounts, unlike in ancient history approaches. I shall come back to this in chapter 4.

3. Kinds of explanations

The final objection starts from Tinbergen's considerations on ethology and his distinction between four questions that biologists ask, related to four different areas of investigation: cause, survival value, evolutionary history, and ontogeny. Tinbergen points out that the survival value of a trait should not be attributed exclusively to natural selection, being open to experimental endeavor:

> While I agree that the selection pressures which must be assumed to have moulded a species' past evolution can never be subjected to experimental proof, and must be traced indirectly, I think we have to keep emphasizing that the survival value of the attributes of present-day species is just as much open to experimental inquiry as in the causation of behavior or any other life process. (Tinbergen 1963: 418).

Relying only on a trait's past contribution to fitness, etiological theories leave out the experimental inquiries mentioned by Tinbergen which may yield functional explanations. In Tinbergen's classification, there is, on the one hand the evolutionary history of a trait and its original selection, and, on the other, the current contribution of that trait to the organism's fitness. They may be the same, or may differ when the environment conditions change. Adepts of etiological theories think they can explain the latter in terms of the former, but as biological examples show, that is not always the case.

Another way of explaining this difficulty is by referring to a distinction made by Bock and Wahlert (1965) between function and biological role: in a similar manner to Tinbergen, Bock and Wahlert consider that functions may be determined through experimental inquiry, independently of the effects favored by selection. While I will return to Bock and Wahlert in the next chapter, at this point it should be mentioned that, at least as function ascriptions go, looking at the past selection of the trait is not the only method. Functional explanations, thus, may be grounded in considerations independent of evolutionary history. This is important for the present discussion because, as pointed out by Wouters (2005: 130), a very unlikely consequence of the failure of distinguishing between the two explanations, is that if functional explanations were to be a kind of historical selection explanation, then the study of function should be a branch of evolutionary biology. However, as shown earlier, biologists make a distinction between the study of function and the study of evolution.

The modern history theory of functions, as formulated by Godfrey-Smith manages to make this distinction by separating the original selection of a trait from its current maintenance:

> Functions can be seen as effects of a trait which have led to its maintenance during recent episodes of natural selection. The distinction between 'functional' and 'evolutionary' explanations can be cast as a distinction between the explanation for the original

> establishment of the trait, and the explanation, which may be different, for its recent maintenance (…) Thus we can make sense of biological usage while retaining the idea that in giving a function we are, ipso facto, giving an explanation for why the functionally characterized thing exists now. (Godfrey-Smith 1993: 202).

His full account of functions, as previously mentioned, corresponds to the etiological project, with the addition of a modern history requirement: both ancient uses and recent uses correspond to a selected effect notion of functions, the two explanations differ only with respect to the time of selection.

As Perlman (2010) points out, in the modern history theory functions no longer rely on natural selection, but on current maintenance of a trait. Of course, selection still occurs, but what is relevant for a function ascription is the recent existence of the trait. This manages to solve the problem of distinguishing the two kinds of explanation, by ascribing an evolutionary explanation to the ancient selection of the trait and a functional one for its current maintenance. Also, the cases where natural selection did not operate in the first place are no longer a threat for this account, because functions match the trait's recent contribution to fitness. As mentioned earlier, Godfrey-Smith's modern history theory does not step out of the etiological account. Function moves from natural selection to current maintenance, but the theory is still backward looking, as etiological theories generally are.

Another point to be made here is that the modern history account solves the aforementioned problems in a distinct way from the propensity view (see Bigelow and Pargetter 1987), which Godfrey-Smith opposes. Although I will not discuss this view in detail, I take it to be important for the unification accounts (i.e. defining functions by reference to both their past selection and their propensity to increase fitness in the future; see Kitcher 1993), which manage to solve the further difficulties of modern history theories at the expense of a purely etiological

way of accounting for functions. Briefly, propensity, or forward-looking views consider that functions are propensities: the presence of a trait is explained through its future contribution to the fitness of organisms. Godfrey-Smith's objection to this account is that it cannot offer a satisfactory explanation, since the structure has the current existence of a trait as *explanandum* and its past selection as *explanans*. One cannot explain the current existence of a trait in terms of its future effects. Godfrey-Smith takes the right place to make this distinction to be between ancient past and recent past. Distinguishing between past and future would go through these problems, but would encounter further issues with the explanation structure. However, a more general objection would concern the way in which these theories account for exaptations, or vestigial traits, or types of explanations by relating to time. In a precise way, they are all historical. The question that arises is whether a historical perspective over functions is sufficient. In the next chapter I will try to show why it is not.

To sum it up, the modern history theory of functions manages to draw the distinctions between adaptations and exaptations, functional and vestigial traits and evolutionary and functional explanations by operating the distinction between the original selection of a trait and its current maintenance. It does so on a purely etiological account where recent maintenance is relevant for ascribing a function to a present trait, and where functional explanations follow the form "why does a trait exist in the form it does".

Chapter 3

Evolutionary and Functional Explanations

In this chapter I will show why Godfrey-Smith's attempt, along with the whole etiological project, fails to offer a satisfactory account on functional explanations. First, I will show how the distinction between functional and evolutionary explanations is rooted in the different causes involved in biology and, consequently, why an account taking the time of selection as crucial would be insensitive to the two kinds of causation. I will then consider cases of functional explanations ascribing functions independently of the time of selection. Mainly, this point is made by biologists when claiming that certain functions and uses of traits may be established through experiments. Secondly, I will discuss the explanatory relation between selected effect and other concepts of function, relating it to the questions *whether* traits are adaptive and *how* traits are adaptive, and show how it is relevant for the problems that etiological theories face. I connect the explanatory relations in which selected effect functions stand with respect to other functions to the problems pointed out earlier about exaptations and vestigial traits. The concluding point of this chapter would be that the two assumptions that etiological theories use (that selected effect functions can account for both explanations, and that functional explanations are a kind of historical explanations) cannot match the points made by biologists and do not support the explanatory relations between selected effect functions and biological advantage functions. The modern history theory, although it attempts a distinction, does so by virtue of past selection and is open to the same kinds of objections as etiological theories relying on distant past.

1. *Causes and functions*

Ernst Mayr (1965) points out that functional biology and evolutionary biology work with different kinds of causation. In terms of explanations, he considers that functional biology answers how-questions, while evolutionary biology investigates why-questions. What I take to be important in Mayr's considerations is that the main tool used in functional biology is the experiment. Mayr goes as far as to say that by sufficiently isolating a phenomenon from the other conditions in an organism, the functional biologist may work with the precision of the physicist or chemist. (Mayr: 1965: 1502) This could be taken as a call for mechanistic explanations which could work very well in functional biology and, again, the point is more favorable to causal role functions. Moreover, even in principle, the idea that in doing functional biology, a function may be singled out by means of experiment alone casts a serious doubt on the view that function attributions should necessary relate to etiology (be it ancient or recent history). This problem could be solved, nevertheless, if experiments are a way to peer into the past. But this, again, would yield evolutionary explanations: current function ascriptions would help shed some light of what happened in a trait's history.

Further, Mayr (1965) distinguishes between proximate and ultimate causes, constituting the objects of the two different types of explanations:

> proximate causes govern the responses of the individual (and his organs) to immediate factors of the environment while ultimate causes are responsible for the evolution of the particular DNA code of information with which every individual of every species is endowed. (Mayr 1965: 1503)

Since there are two different kinds of causation here, the distinction between functional and evolutionary is obvious. Again, in order to see the immediate responses of certain traits, or

organisms, one does not necessarily need to resort to their evolutionary history. When explaining a function, one may refer to current environment conditions and responses, rather than to the recent history of the trait. More importantly, as long as it concerns ultimate causes, and not proximate ones, recent history should relate to the genetic material one finds in the species, and not to how a certain trait is currently used. It is the different kinds of causation, and not the time of selection that are relevant for the distinction here. Etiological theories of functions cannot support this way of drawing the distinction because they do not acknowledge two kinds of causation, and they ground functional explanations on a causal process that leads to selective retention. While I will not address the issue whether the distinction should be grounded in two kinds of causation, I wish to point out that etiological theories, when making the distinction, refer to what Mayr calls ultimate causation. Regardless of the fact that there may be different kinds of causation or just different explanations in biology, etiological theories need to allow functional explanations to be established independently of evolutionary history claims.

Another important point to be drawn from the claims made by biologists is that there may be a further distinction concerning functions. Bock and Wahlert (1965) distinguish between what they call function and biological role. Functions may be studied in laboratory conditions, independently from the environment, relating only to the organism's anatomy. This technique may also reveal functions of features that might have never been used by an organism, Bock and Wahlert's example is that of a muscle that may shorten up to 40 percent, but has never been shortened more than 10 percent. The muscle's property of shortening up to 40 percent has a function, but since that feature has never occurred, one cannot make a function ascription based on past use, but only on studying the structure of the muscle. These studies on functions are to be completed by inquiries into the biological roles of traits which involve the environment and the

uses of a trait in the course of an organism's life. Their distinction is further reflected in the distinction between functional anatomy (operating with functions) and biological anatomy (operating with biological roles). Here, Bock and Wahlert make a point similar to what we find in Mayr and Tinbergen: some functions may be studied independently from their evolutionary history. The difference is that they restrict this to a purely mechanistic account of the traits' potentiality to perform certain processes that may later become fitness increasing. This also leaves space for preadaptations, as they put it (or, employing Gould and Vrba's term, exaptations). What Bock and Wahlert call biological role may be assimilated to causal role functions (see Wouters 2003 for this interpretation). Relating to the previous section about explanations, one may note that Bock and Wahlert are talking about functional explanations, their testability in experiments (in laboratory conditions, or in the natural environment of a species) without bringing about evolutionary history. A recent history of a trait would not specify its possible uses, and it would be difficult even to reveal the current uses without the proper experimental techniques, solely on the basis of selection history.

While not decisive for showing that the etiological theories cannot properly account for functional explanations, the previous considerations show that the work of biologists at least does not support the distinction as drawn by the modern history theory. When considering functional explanations, experiments and immediate conditions seem to be crucial, and more important than recent selection history. Furthermore, they manage to provide examples of functional explanations that work in that way. I take the examples from biology to show that, even if the distinction were operable conceptually speaking, it would be at least methodologically problematic. One would want function attributions to relate to what is currently happening in biology; and if most functional explanations refer to proximate causes or

are grounded in experiments, defining them as involving recent selection of traits would not be very fruitful for understanding how biologists work.

2. Selected effect and biological advantage. Which explains which?

Another point that should be highlighted from the previous discussion is that from the distinctions made by biologists, functional explanations appear to have similar structures to either mechanistic explanations or design explanations. Upon investigating why this seems to be the case, the differentiation between selected effect functions and functions as biological advantage becomes important. The question that arises concerns the explanatory relation between these two concepts of functions.

As Wouters (2003) specifies the difference between the two concepts of functions, selected effect functions are trait-centered, etiological, factual, and non-comparative, while functions as biological advantage are organism-centered, evaluative, hypothetical, and comparative. Taking another one of Wouters' examples, upon asking why snakes have forked tongues, the selected effect approach would refer to the past presence of the trait, and to the variants that occurred in various populations. From the point of view of biological advantage, the explanation would refer to the forked tongue's enabling the simultaneous sampling of two chemicals in a trail following mechanism. While selected effect functions follow the history under which the trait evolved up to present organisms, biological advantage focuses on how the trait is useful in a certain organism by comparison to hypothetical variants (e.g. why would a forked tongue be more advantageous than a non-forked tongue?) As Wouters explains the difference: "advantage articulations report about what would be advantageous to the organism in

certain circumstances relative to certain alternatives, while attributions of selected effect report about the causes of what actually happened in the history of a trait." (Wouters 2003: 652)

These characteristics further lead to an asymmetric relation between the two concepts of functions: biological advantage is explanatory for selected effect, but not the other way around: "The fact that those effects are advantageous in those circumstances with respect to the then existing alternatives, together with the observation that the relevant alternatives and circumstances were there, explains why the trait was selected." (Wouters 2003: 652)

Thus, the selection of certain traits, and consequently, their current presence is to be explained in terms of why those traits are useful. This relation between selected effect and biological advantage functions can be moved to the level of explanations, making it possible to ground selection history explanations in design explanations. Upon investigating the function of a trait, one may say, following its selection history that it may be now present in an organism for various fitness-related reasons, but one cannot say that it is advantageous now for the organism in question only because it was selected in the past. If Wouters' contrast between selected effect and biological advantage functions is accurate, it becomes clear why evolutionary explanations cannot incorporate functional explanations. Often, claims about fitness are explanatory for reconstructing a trait's evolutionary history, and can give rise to hypotheses. However, as shown for the case of exaptations and vestigial traits, evolutionary history is not always explanatory for current uses of traits. As a case of exaptation, before being used for support in land-dwelling vertebrates, bones were selected for depositing phosphates, thus the selection for depositing phosphates, while explaining the presence of bones in land-dwelling vertebrates, does not explain why they are currently useful. A case of vestigial trait would be the wings of ostriches,

which were originally selected for flight, but currently serve no function; again, an explanation of their selection history will not be relevant for a function ascription.

At this point the weakness pointed out when discussing vestigial traits proves to be relevant to the distinction between the two explanations as well. Etiological theories employ a reverse inference, from past selection to present use, but it is the use that explains selection. Thus, while one can justify function ascriptions by the evolutionary history of the traits, one cannot fully explain a present function through evolutionary history. By taking functional explanations to be a kind of evolutionary explanations, etiological theories succumb to the error of explaining use exclusively in terms of selection. I should mention here that this objection stands against etiological theories as long as they seek to distinguish between adaptations and exaptations or vestigial traits, or between evolutionary and functional explanations by themselves. Upon employing a different concept of function, to explain present use, relying on past selection history would provide a good justification for function ascriptions. However, when selected effect functions are the only concepts supposed to handle this distinction, selection history becomes the only means of ascribing functions to traits. As shown earlier this leads to some problematic consequences for function attributions and functional explanations, from both a conceptual and methodological point of view. First, it is the way in which a function is adaptive that explains its selection. Secondly, functional explanations in biology establish current use and fitness contribution before resorting to selection history.

Since the distinction made by the modern history theories mainly draws a line between two selection history explanations, separated only in terms of time of selection, functional explanations should be of a historical kind. As pointed out earlier, the biologists' approaches to explanations do not seem to support this view. Furthermore, considering the explanatory value of

selected effect functions, it seems that etiological theories are reversing the relation to be considered: traits are selected because they are useful, and not the other way around. While having a selection history, one may ask about the way in which those traits were useful. This is Wouters' design explanation and it is of a different kind from an explanation involving recent selection history: it is counterfactual and involves comparisons with hypothetical traits or organisms.

These considerations point to another important problem of the way in which etiological theories deal with the distinction between the two explanations: they do not consider the possible explanatory relations between selected effects and other analyses of functions. This would not even be possible within an account that is not meant to step out of the bounds of the etiological project. In the next section I will analyze how the etiological account relates to other ways of investigating functions and the fitness value of certain traits.

3. Functional explanations and fitness

The final point I am going to make against the distinction, as drawn by modern history theories, is that it cannot offer an account for satisfactory functional explanations for certain traits under investigation. The limitations are partly due to the heavy reliance on the time of selection, partly to the exclusive employment of selected effect functions.

First, there are some clarification issues regarding functions as being centered on traits or organisms. Recent history theories ascribe functions to traits according to their modern history. Taking an example of exaptation, of feathers in Archaeopteryx and in birds, one may say that the recent history of feathers shows their selection for flight. Their original selection, however, is

connected to thermoregulation. Taking an evolutionary explanation to relate to thermoregulation and a functional explanation to take flight into consideration may raise some problems. Switching to species, one may ask whether in the case of Archaeopteryx there is still a distinction between the evolutionary and functional explanations, since both refer to thermoregulation. This problem would be solved if one considers the more recent history of a now extinct species (Archaeopteryx). However, there should be additional requirements relating to organism, rather than trait history, and also to what Griffiths (1993) calls evolutionary significant period.

The point where the distinction proves to be inefficient for what is considered to be functional explanation in biology is where one takes an actual case of explanation. As shown earlier, functional explanations may relate to causal role or biological advantage functions, they may be conceived either as mechanistic or as design explanations. Within the etiological project, however, they are a kind of selection history explanations. In the remaining part of this chapter I will show why functional explanations cannot be a kind of historical explanations, and how this leads to the failure of the distinction, as made by Godfrey-Smith.

I am taking an example of exaptation where a trait continues to serve the function for which it was selected in the distant past and that has also been co-opted for a different function in the more recent past. The black egret's wings are used both for flight and for catching fish (it spreads its wings upon the surface of the water, casting a shadow which attracts fish that prefer a shady environment over open water). Upon asking about the function of the black egret's wings, one could refer to their evolutionary history, mentioning flight, or to the more recent uses, mentioning flight, as well as catching fish. Looking at a sample of population, their number of offspring and the perpetuation of wings to the next generations would reconstruct their

evolutionary history. These are both historical explanations, and according to the modern history theory of functions we should count the former (flight) as an evolutionary explanation and the latter (flight and catching fish) as a functional explanation. There is a problem here however: looking at the evidence given by the historical method one may say whether the trait was adaptive or not, but not why it was adaptive, how it contributed to fitness. Besides studies of past population dynamics one may employ the experimental method (e.g. see how birds using both of their wings' functions fare over birds using only one of them). Upon investigating evolutionary history one may employ certain hypotheses relating to the fitness value of a trait, but most of these hypotheses need to relate to a current function, established independently from evolutionary history. Observing that a trait has been present in a population for many generations may count as evidence that it serves a certain function, but that does not necessarily specify its function. A similar point is made by Ruse as a methodological point: in order to find out how what happened in the past, biologists must employ hypotheses about current function. (Ruse 2002: 47)

Functional explanations, as used by biologists, are helpful in constructing evolutionary explanations because they relate to fitness claims. However, while evolutionary explanations have the structure of a historical explanation, functional explanations, although they fit the larger picture of the evolution process, involve more than a trait's history. An important method used by biologists is the experiment. As mentioned earlier, Tinbergen makes the claim that the fitness value of a trait may be studied in a different way from referring to past effects on population dynamics.

At this point one may ask why cannot etiological theories relate to different ways of investigating fitness, and they remain committed to a kind of historical explanation? I take the

problem to be that a distinction between evolutionary explanations and functional explanations cannot be made exclusively in terms of selected effect functions. Going back to the black egret example, one could easily talk about the adaptiveness of the wings by asking how they are contributing to the more complex functions that the organism sustains. This, however, would involve causal role functions. The point that selected effect functions mainly concern adaptations, while causal role functions account for adaptive traits is made by Griffiths (2006). In the next chapter I will analyze a few other attempts of solving the problem that will further support my claim that a functional explanation that could account for fitness and adaptiveness needs to rely on more than selected effect functions.

To sum it up, the attempt to draw a distinction between functional explanation and evolutionary explanation from within the boundaries of etiological theories fails for more reasons. One would be that there seems to be a difference in the structure of the two explanations to which etiological theories are not sensitive: evolutionary explanations are selection history explanations, while functional explanations may involve mechanistic, or design explanations. This claim is justified by their use in separate fields of biology.

Secondly, etiological theories cannot grasp the different structures by themselves because they employ only selected effect functions. Other concepts of functions, such as biological advantage, may prove explanatory for selected effect functions, and thus be able to draw the distinction relying on a method different from the historical one: counterfactual comparison between organisms. A more serious problem for etiological theories as this point is the fact that function is explained only through evolutionary history, which leads to a reversed relation between use and past selection. It is precisely this inference that generates the further problems, of accounting for exaptations and vestigial traits.

Finally, functional explanations, as characterized within the etiological theories are unable to give a satisfactory account for inclusive fitness; they cannot incorporate other methods apart from the historical one. This, again, is due to the assumption that functional explanations are historical and that they only employ selected effect functions. In the next chapter I will show that the failure to deal with the distinction does not compromise the whole etiological account as such, but it opens the way for pluralism.

Chapter 4

Moving towards Pluralism

As shown earlier, the modern history theory of functions has some major difficulties in trying to account for functional explanations as being a different category from evolutionary explanations. In this chapter I will analyze other attempts of drawing the distinction. The point of the analysis will be that while the distinction may be drawn in several ways, it requires that selected effect functions be backed up by a different concept of function. In the following sections, I will show how etiological theories relate to forward looking theories of functions and unification accounts and then deal with an objection against both of them, connected to the aforementioned concept of biological advantage function. First, though, I will consider a possible modification of the modern history theory and see whether it can account for the distinction from a purely etiological approach.

1. Modern history and continuing usefulness

As mentioned in chapter 2, distinguishing between evolutionary and functional explanations is not the only problem that modern history theories have to face. On an account by Schwartz (1998), a serious objection that these theories need to answer is that it is always possible that a trait may have been maintained due to lack of variation or due to some other effect than its assigned function. On ancient history accounts this possibility is more remote,

since the trait in question is traced for a far longer period of time. In order to solve this difficulty, Schwartz introduces the concept of continuing usefulness to the analysis of function:

> a trait has the proper function F if and only if, first, the trait was favored by selection for doing F at some point (perhaps far in the past), and, second, the trait has recently contributed to survival and reproduction by doing F. (Schwartz 1998: S211).

Going back to the problem of explanations, one may ask whether the concept of continuing usefulness could help in dealing with the problems which affect the modern history theory. However, Schwartz's considerations explicitly take functional explanations to be a subset of evolutionary explanations: they stand for traits that still perform the effects for which they were selected. (Schwartz 1998: S220) I consider this point to be important because it is an explicit statement of the presupposition that underlies etiological theories: functional explanations are a kind of evolutionary explanations and both of them ultimately resort to selected effect functions. There are two problems with this way of amending the modern history theory. One relates to the previous considerations on explanations as used by biologists. The other is a worry with regard to the boundaries of etiological theories.

As shown earlier, functional and evolutionary explanations are being employed by biologists to answer different questions. While Schwartz's account makes the assumption of etiological theories clear, it does in no way justify it. Moreover, upon considering a functional explanation to involve continuing usefulness, one may leave out ways in which traits are or become adaptive. If functional explanations are always derived from evolutionary explanations, then each function ascription must refer to the evolutionary history. As shown earlier, this is not the case. I consider Schwartz's take on functional explanation to be limited only to those traits which are adaptations and have maintained their function over a long period of time. Since these

aren't the only traits to which biologists assign functions, Schwartz's account for function ascriptions is even narrower that Godfrey-Smith's.

Secondly, it is difficult to assess where Schwartz' approach stands with respect to the classification of the different accounts of functions. As long as his concept of continuing usefulness is not clarified, one cannot specify whether this would enable him to solve the difficulties etiological theories have without stepping out of their account. One could extend the continuous contribution to fitness to the present functioning of a system (pointing towards causal role functions) or to the future (pointing towards forward looking theories).

Leaving these issues aside, Schwartz's approach is vulnerable to the same kind of criticism as Godfrey-Smith's: the distinction between evolutionary and functional explanations is cast as a distinction between selection operating in the distant or the more recent past, and functional explanations are seen as having the same structure with historical explanations, thus it cannot capture what biologists employ as functional explanations.

2. Forward looking theories and unification

Up to this point I have shown how, even in a different version, the modern history theory of functions cannot make a distinction between evolutionary and functional explanations that would do justice to functional explanations. I will now turn to a different way of making this distinction, by reference to a different concept of function. I will focus on the propensity view.

Instead of relying on the evolutionary history of a trait, forward looking theories take the function of a trait to be the feature which, by its presence in an organism will contribute to that

organism's fitness: "a character or structure has a certain function when it has a propensity for selection in virtue of that character or structure's having the relevant effects." (Bigelow & Pargetter 1987: 194) This account is inspired by the view which specifies that, in order to answer the circularity objection, fitness should be defined as a propensity for surviving and leaving offspring (as in Beatty and Miller 1979). I will not be concerned with this account as it stands alone, but with the accounts that bring together backward looking and forward looking concepts of functions. I take these approaches to be interesting because they can make the distinction between evolutionary and functional explanations through reference to time, as in modern history theories, except that a functional explanation is pointing towards the future, not the present. Although the reference to time may be conceived as a common weakness, as I will show later, the reference to future steps out of the historical view on explanations, and this proves to be relevant for overcoming the criticism that troubles etiological theories. Also, the fundamental difference is that pluralist accounts step out of the bounds of etiological theories.

A version of this solution is found in Walsh (1996), and his considerations on explanations are particularly interesting:

> there are two sort of explanations for which functions are invoked in biology: aetiological and propensity. Aetiological explanations explain the current prevalence of as trait in terms of that trait's contribution to survival and reproduction in the past. Propensity explanations explain current fitnesses of individuals in terms of the contribution a trait makes to the current propensity of individuals to survival or reproduce. (Walsh 1996: 572)

If the two explanations that Walsh is mentioning overlap with the distinction between evolutionary and functional, he seems to be narrowing the etiological account to evolutionary explanations. For functional explanations a forward looking theory is necessary. Under this view, selected effect functions work only applied to evolutionary explanations, while functional

explanations require functions as propensities. Another important point made by Walsh is that in investigating functions one needs to employ an ahistorical element precisely because the history of the trait may indicate a function different from current uses. His full account takes functions not to be intrinsic properties of traits, but relational properties holding between the trait and the environment. His full account on relational functions goes as following

> The/a function of a token of type X with respect to selective regime R is to m iff X's doing m positively (and significantly) contributes to the average fitness of individuals possessing X with respect to R. (Walsh 1996: 567)

There are two important points made by Walsh, which I take to be relevant for any etiological account for functions. First, selected effect functions work for evolutionary explanations, but functional explanations need propensities or a different way of accounting for present fitness. Second, a function attribution should be based on something more than the history of the trait. These points show that etiological theories cannot account by themselves for all function attributions there are. Going to the distinction under discussion, it seems that precisely the ahistorical elements taken into consideration can make the difference. Again, functional explanations are pointed out to be something else than historical explanations.

Another version of pluralism, involving unification this time, is found in Kitcher (1993). According to Kitcher, the modern history theory is committed to the following claim:

1. The function of *X* is *Y* only if selection of *Y* has been responsible for maintaining *X* in the recent past.

By contrast, forward looking theories go as follows:

2. The function of *X* is *Y* only if selection for *Y* is currently responsible for maintaining *X*.

Kitcher does not agree with Godfrey-Smith's dismissal of (2) and considers that in order to account for both explanations and predictions in biology, the two accounts need to be unified. Thus, his own account:

3. The function of *X* is *Y* only if selection of *Y* is responsible for maintaining *X* both in the recent past and in the present.

This account goes past Godfrey-Smith's considerations on explanations, since it includes prediction as well. Also, it overcomes the difficulty of distinguishing between the two explanations in a way similar as that pointed out by Walsh: functional explanations require a forward looking perspective. One may notice again, functions as propensities are involved here as well.

A point that should be made with reference to the use of a forward looking concept of functions is that they fit Tinbergen's distinction better than etiological theories. Tinbergen considers that explanations for survival value are forward looking, estimating how a certain behavior might increase an organism's chances of surviving and leaving offspring. This is not the case for evolutionary history, when one has to reconstruct what has happened in the past. I take this aspect to be a good motivation for using functions as propensities to solve the problem of different explanations involving functions.

3. Time of selection revisited

Along with purely etiological theories of functions, these accounts are criticized by Wouters, who takes the distinction between evolutionary and functional explanation to be made by biological advantage, not by the time of selection. Although the previously mentioned

theories are not fully historical, they still employ a distinction by referring to time (past and future). By employing functions as biological advantage and his concept of design explanation, Wouters is able to operate the distinction in a different manner. Also, the kind of reasoning he is pointing at when talking about functions as biological advantage is not accessible from the perspective driven by etiological theories. As he puts it,

> in a design explanation the actual organism is compared with hypothetical organisms in which the trait to be explained is replaced by another. Such a comparison relates to selection only if the variants used for comparison are the variants that actually occur in the population. (Wouters 2003: 663)

Obviously, his account does not fit etiological theories because for historical accounts only the traits that occur in the population are the ones that matter. Wouters makes a more general point here, going against all analyses of functions that make reference to time.

While I presented my criticism against modern history theories and their attempt to draw the distinction related to past selection, I will make a few remarks of Wouters' more general criticism of making the distinctions by referring to the time of selection.

First, drawing the distinction between the two explanations need not necessarily resort to an exhaustive either/or choice between the time of selection and the concept of biological advantage. It is a notable difference between two ways of understanding the living world that evolutionary explanations need to refer to the past and functional explanations may refer to the present or future. My criticism of etiological theories is that they try to fit functional explanations under those explanations which mainly refer to past. I take this to be due to their emphasis on selected effect functions, and to the reverse inference they are employing when explaining functions. As long as one takes a function to contribute to an organism's fitness, and fitness may be measured as a propensity, bringing together a forward looking concept of function with the

etiological theories should offer a satisfactory account. Wouters' concept of function as biological advantage points out some features of functions which escaped previous controversies over functions, and captures the complexity of biological explanations. That does not mean, however, that this concept of function is the only valid way of drawing the distinction.

Second, I take Wouters to be right in claiming that biological explanations employ more than one concept of function. The very idea that the distinction I have been discussing could be made by employing different concepts of functions shows that pluralism is more fruitful than arguing for a single analysis as being *the* analysis of functions. Furthermore, the fact that all the suggested possibilities rely on more than one concept of function points at pluralism as being better suited for dealing with biological explanations. The examples of causal role, biological advantage and propensity analyses of functions should be illustrative.

Finally, as pointed out in the previous chapter, the whole problem might be due to trying to apply the same concept of function to two distinct areas of biology, studying different aspects of the living world. The debate over fitting more functions under one account or over unification also shows that there are more senses in which biologists use the concept of function, all of which are useful in the different kinds of explanations they are employing.

Conclusions

At this point, several considerations can be made about the different analyses of functions I have been discussing and the problem of drawing the distinction between evolutionary and functional explanations. Some of them concern the connection between investigations on functions and the problem of explanation on biology. Others are related to the connection between function ascriptions and the problem of defining fitness. Finally, I will make a more general point on how my study on etiological theories might be important for the whole function debate in the philosophy of biology.

The very problem I sought to investigate, whether etiological theories of functions can handle this distinction by themselves shows there is a connection between the different accounts on functions and biological explanations. In the light of the considerations made in the last two chapters, the two separate explanatory projects I was presenting in the beginning no longer appear as satisfactory. It is highly doubtful that each type of explanation used by biologists should be limited to a single concept of function. It is even more difficult for an account to extend its concept of function to separate explanations. I meant to show that selected effect functions only work within historical explanations, and since functional explanations are not historical, selected effect functions cannot account by themselves for this kind of explanations. From a more general perspective, the explanatory projects which various approaches endorse need a more detailed analysis.

My criticism of the solution employed by etiological theories for distinguishing evolutionary from functional explanation is based, in part, on the previous considerations on

biological explanations. Another important part of my criticism is related to the distinctions made by biologists and how different explanations in biology may refer to different causes or to different approaches to investigating the living world. As long as selected effect functions cannot permit these distinctions within their account and base their views on functions exclusively on evolutionary history, it is unlikely that their views on functional explanations could coincide with the biologists' considerations.

A final point on explanation concerns the explanatory relations that may arise between different concepts of functions. In a pluralist framework, one would be interested to see which functions explains which, and this would give further indications about which concepts of function are being used in a particular explanation. For my current argumentation, biological advantage functions being explanatory for selected effects functions proved to be an important point, showing that etiological theories are working on a reverse view on the explanatory relation: they are justifying function ascriptions by evolutionary history, but evolutionary history itself is determined by the advantages that the traits confer to organisms.

Another link that proved to be important for my argumentation was between function ascriptions and fitness. In fact, one could say that the whole problem of etiological theories depends on how biologists solve the problem of fitness. I have shown that biologists employ the experimental method, or compare organisms in order to determine the fitness contribution of various traits. Etiological theories work under the assumption that the historical method is the only valid method for fitness claims. Under this presupposition, it is clear that they leave out important aspects which characterize the biologists' work and function ascriptions.

Finally, while criticizing the heavy reliance on historical explanations and using Wouters' concepts of function as biological advantage and design explanation, I have expressed my

skepticism over criticizing all of the theories of functions which bring about the time of selection. Claims referring to present or future fitness contributions are not historical, and they can have predictive value. While it might not be the best criterion to distinguish between evolutionary and functional explanations, talking about past selection in the former and present or future contributions to fitness in the latter are nevertheless important features of the two explanations.

Bringing these considerations together, a quite different picture of the problem of functions and biological explanations may be grasped. First, pluralism seems to be a better approach to function ascriptions but it is still open to question which analyses of functions work better in the case of different explanations, or fields of biology. The more interesting issue that arises is how analyses of functions should account for the different fields of biology. Are there different methods, and thus, different concepts of functions? How should the analyses of functions relate to these methods? I think these are queries to which theories concerning functions and functional explanations in biology should try to answer. With respect to these issues, my investigation on etiological theories has shown that selected effect functions do not take into consideration other ways of determining fitness and that claims on present fitness should have an important part in function ascriptions.

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