

## Chapter 7: The etiological theory

### 7.1 Introduction

In chapter 4 I argued that Hempel's and Nagel's classical accounts of design explanations in terms of the inferential theory of explanation, fail. Generations of philosophers have talked about these attempts as if they were "the received view" (the last representative of this tradition is probably Sandra Mitchell (1989: 214)). The expression 'received view' is probably used merely as a proper name, rather than as a definite description. In this chapter I discuss what might be called the received view of our time: the "etiological account". On the etiological account function attributions in biology inform us about the evolutionary history of the item to which the function is attributed. More specifically, function attributions identify the effects for which a certain trait was selected in the past. For example, on the etiological account hearts are said to have the function of propagating the blood, if and only if propagating the blood is what hearts did that caused them to be favoured by natural selection.

The etiological account as it is defined here was originally proposed by Karen Neander (1980, 1983, 1991a, 1991b), and, independently, by Ruth Millikan (1984, 1989b, 1989a, 1993a). Other proponents of etiological theories are Mitchell (1989), Brandon (1990), Griffiths (1993), Sober (1993), and Godfrey-Smith (1994). Forerunners of the etiological theory were proposed by Ayala (1970) and Wright (1973, 1976). According to the latter theories, functions are determined partly, but not wholly by a selection history. Millikan (1993a: 33) claims that she arrived at her theory without knowing Wright's work and she tends to play down the similarities between an etiological account and Wright's theory of function. The other authors generally acknowledge Wright's influence on their work.

The etiological theory of function is first and foremost concerned with the definition of the term 'function'. The role of function attributions in explanations receives much less attention. However, the etiological account has a very attractive feature for philosophers who favour a causal theory of explanation: the etiological account promises to reconcile the idea that function attributions concern consequences with the idea that function attributions are explanatory on a causal theory of explanation. The designer of the causal theory, Wesley Salmon, was among the first to appreciate this connection between the causal theory of explanation and the etiological account of function (Salmon 1989: 111-116). The point has been made most forcefully by Neander (1991b) and by Mitchell (1993). At first sight function attributions seem to be both explanatory and concerned with consequences. However, on the causal theory of explanation, explanations are explanatory to the extent that they detail the mechanisms by which

the phenomenon to be explained was produced. But how could an appeal to consequences causally explain the presence of an item, since those consequences occur only after the production of that item? The answer of the etiological theory is as ingenious as it is simple: the functions of a certain item in a certain individual are a subset not of the present consequences of that item but rather of the past consequences of that item in ancestral organisms. Past consequences, of course, can be causally effective and the etiological account identifies the functions of an item with those past consequences that *were*, as a matter of fact, causally effective in the evolution of the item to which the function is attributed.<sup>1</sup>

Both Neander and Millikan claim that function attributions have an indispensable role in categorizing items and behaviours and that among the current theories of function the etiological theory is the only one that accounts for this role of function attributions. According to them biological categories such as ‘heart’, ‘kidney’ and ‘mating display’ collect items together on the basis of their function. It is obvious that a certain biological category may include normal members that do not actually perform their function (e.g. many attempts to escape fail and most sperm cells will never fertilize an egg cell) as well as defective members that are not even able to perform their function (a malformed heart is still a heart). The etiological theory accounts for this feature by defining the function of an item or behaviour not on the ground of the actual properties and propensities of that item or behaviour but in terms of its history. On the etiological theory a certain sperm cell is a sperm cell because fertilizing eggs is what the precursors of that cell did that accounts for the existence of the sperm cell in question. Similarly, propagating the blood is the hallmark of hearts and a malformed heart is yet a heart because propagating the blood is what precursors of that malformed heart did that accounts for the existence of that malformed heart.

In this chapter I am concerned with the question to what extent the etiological theory accounts for the use of the different kinds of function attributions in functional biology. I focus on Millikan’s account because this is currently the most elaborated etiological account of function. As she has emphasized recently (Millikan 1993a: 31), her definition of what she calls “proper functions” is not meant to capture the biologist’s usage. Millikan is primarily interested in solving certain problems in the philosophy of language (Millikan 1984) and in the philosophy of mind (Millikan 1993b). Her definition of ‘proper function’ is meant as a stipulated, technical term, the use of which does not depend on the extent to which it captures the use of

---

<sup>1</sup>Neander (1991b: 462) rightly points out that this is true only of biological functions. Functions of human artefacts are effects of which the designer or user believes or hopes that they will occur and for which the item is selected. Such effects need not have occurred in the past. Since I aim to account of biological functions only I shall ignore this point.

function attributions in biology. Nevertheless there are three good reasons for considering the question whether or not her theory applies to biological function.

The reason for considering Millikan's theory is obvious: Millikan has offered a powerful general account of function. This alone is sufficient reason to consider its application to biological function.

The second reason is that many philosophers of biology have arrived at accounts similar to that of Millikan (Mitchell 1989, Brandon 1990, Neander 1991b, Neander 1991a, Griffiths 1993, Sober 1993). All these authors claim that when biologists attribute a function to an organ, process, behavioural pattern, characteristic or whatever they make a claim about the evolutionary history of those items or traits.

The third reason is that Millikan herself repeatedly suggests that her theory applies to almost all function attributions in biology. Some of her favourite examples of function attributions are 'the heart has the function to pump the blood around', 'sperm cells have the function to fertilize an egg cell' and 'the colour of the chameleon's skin has the function to camouflage its bearer'. How could such examples make sense if Millikan does not think that her theory applies to these examples? Indeed in her "In Defense of Proper Functions" (1989b: 293) Millikan explicitly claims that her theory explains all ordinary uses of the terms 'function' and 'purpose', including their use in biology:

The definition of "proper function" is intended as a theoretical definition of function or purpose. It is an attempt to describe a unitary phenomenon that lies behind all sorts of cases in which we ascribe purposes of functions to things, which phenomenon normally *accounts for* the existence of the various analogies upon which applications of the notion "purpose" of "function" customarily rest. My claim is that actual body organs and systems, actual actions and purposive behaviors, artifacts, words and grammatical forms, and many customs, etc., all have proper functions and that these proper functions correspond to their functions or purposes ordinarily so called. Further, it is *because* each of these has a proper function or set of proper functions that it has whatever marks we tend to go by in *claiming* that it has functions, a purpose, or purposes (Millikan 1989b: 293).

In the same year she publishes a paper in *Biology and Philosophy* (Millikan 1989a) in which she distinguishes two different kinds of function: "Cummins-style functions" and "selected functions". The latter ones are also called "proper functions". These kinds of functions correspond to the kinds of functions I call 'function as causal role' (function<sub>2</sub>) respectively 'function as selected effect' (function<sub>4</sub>). Associated with these two kinds of function Millikan distinguishes two kinds of functional explanation: "functional explanations in Cummins sense" and "functional explanations that make reference to natural selection". These two kinds of functional explanation correspond to the kind of explanations I call 'capacity explanations' respectively 'selection explanations'. Millikan maintains that the use of Cummins-style functions is

restricted to functional explanations in Cummins sense, whereas selected functions may “enter into” functional explanations that make reference to natural selection. Although Millikan seems to acknowledge that both kinds of function have their use in biology she still maintains that selected functions are “the only kind of function that is well defined” (Millikan 1989a: 174). Indeed, four years later she argues that Cummins’s definition of function does not suffice to define biological function (Millikan 1993a: 33, 35-39).

I will argue that the etiological theory is not relevant to understand reasoning about functions in functional biology.

## 7.2 Proper functions and selection

### 7.2.1 The etiological account of function

In the first two chapters of her *Language, Thought and Other Biological Categories* (1984) Millikan develops a recursive definition of what she calls “proper function”. This definition is a general definition applicable to such diverse things as organs, behaviours, artefacts, customs, parts of organizations, words and grammatical forms. Although Millikan’s examples include functions of organs of organisms such as hearts and kidneys, her intended domain of application is the philosophy of mind and language. As I am interested only in the application of the theory to biology, I restrict this summary to those definitions that allow one to attribute functions to parts and behaviours of living organisms.

On Millikan’s theory functions are attributed to things that have been reproduced repeatedly, that have been selected to be reproduced, and that were selected because of what they did. The proper function of such a device is to do what its ancestors did that explains why those ancestors were selected for reproduction. That is, to do the things that explain why the device exists, why it exists in the place where it exists, or why it is as it is:

Putting things very roughly, for an item *A* to have a function *F* as a “[direct]<sup>2</sup> proper function”, it is necessary (and close to sufficient) that [...] *A* originated as a “reproduction” (for example, as a copy, or a copy of a copy) of some prior item or items that, *due* in part to possession of the properties reproduced, have actually performed *F* in the past, and *A* exists because (causally historically because) of these performances (Millikan 1989b: 288/9).

---

<sup>2</sup>Actually, Millikan gives two disjunctive conditions. The first condition is satisfied by “direct proper functions”, the second by “derived proper functions” (functions derived from the proper functions of the devices that produce them). I have quoted only the first condition. Derived proper functions are not of interest here.

The definition of the proper function of the parts and behaviours of organisms is complicated by the fact that the parts and organs of a certain organism are not copied from the parts and organs of the parents of that organism. It is the genes that help to produce those items which are copied, not the items themselves (see fig. 7.1). This means that, to attribute proper functions to the organs of organisms the notion of reproduction must include more than copying. Millikan needs a notion of reproduction that allows, for example, my lung to be a descendent of the lungs of my parents.

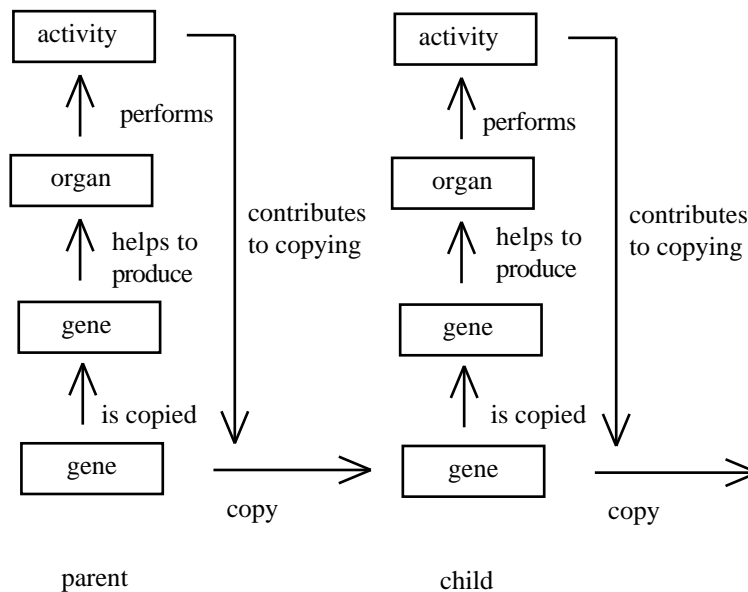


Fig 7.1: reproduction in organisms

Millikan solves this problem by means of a recursive definition. Proper functions are defined with respect to entities that have been reproduced. The class of entities that have been reproduced includes (i) entities that have been copied, and (2) entities that have been produced with help of entities that have been reproduced and that have the proper function to help to produce those entities. Genes belong to the first category of entities that have been reproduced, organs to the second.

Now for the details. The recursion starts with entities, such as genes, which are copied. The hallmark of copying is that the copies are similar to the original. The copies of an entity which is copied establish a “first-order reproductively established family”:

Any set of entities having the same or similar reproductively established characters derived by repetitive reproductions from the same character of the same model or models form a *first-order reproductively established family* (Millikan 1984: 23).

According to this definition the subsequent copies of a gene constitute a reproductively established family, provided that those copies are sufficiently similar to each other.

Next, Millikan uses the definition of proper function to attribute functions to entities that originate from copying. In order to have proper functions the entities must not only originate from copying (or from other kinds of reproduction), there also must have been a kind of selection process. That is, there must have been competitors with a different character which were not reproduced or were less extensively reproduced because due to their different character they performed a certain activity less well. According to Millikan's definition of proper function an entity that originated as a reproduction of a reproduction (...) of another entity has an activity  $F$  as a proper function if (i) some of its ancestors competed to be reproduced with entities of a different character, (ii) the proportion of entities that did  $F$  was higher among the entities with the ancestor's character than among the entities with the different character, and (iii) those ancestral entities were selected for reproduction over their competitors because they did  $F$ . The character due to which ancestral entities performed  $F$  and, hence, due to which they were selected, is called the 'reproductively established' or 'Normal' character of that type of entity.

Where  $m$  is a member of a reproductively established family  $R$  and  $R$  has the reproductively established or Normal character  $C$ ,  $m$  has the function  $F$  as a direct proper function iff:

- (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 indirectly causing reproduction of  $m$  or explaining why  $R$  was proliferated and hence why  $m$  exists (Millikan 1984: 28)

Millikan does not give an example of an attribution of a function to a member of a first-order reproductively established family but one might think of  $m$  as a gene of a certain organism (let's call that organism  $i$ ) and of  $C$  as the order of the nucleotides of that gene.  $F$  might be the production of a certain peptide, say haemoglobin.  $R$  consists of all the genes in  $i$  and in related organism which are both homologous with and sufficiently similar to  $m$ . According to the above definition gene  $m$  of  $i$  has the function to produce haemoglobin if and only if (1) some ancestors of  $m$  produced haemoglobin, (2) beside the ancestors of  $m$  with nucleotide sequence  $C$  there existed variant genes with a different sequence; because the ancestors had nucleotide sequence  $C$  they produced haemoglobin whereas the variants did not produce haemoglobin (or less haemoglobin, or a less efficient kind of haemoglobin), (3) the existence of  $m$  might be explained by appeal to the fact that (due to the fact that the order of their nucleotides was  $C$ ) the ancestors of  $m$  produced haemoglobin whereas the others did not (or produced less haemoglobin, or less efficient haemoglobin). Suppose there is reason to assume that from time to time there occur mutants of the gene for haemoglobin that produce a less effective kind of

haemoglobin (think of genetically induced anaemia) and that the fitness of those variants is lower than that of the normal kind of haemoglobin. Then we might also assume that some ancestors of  $m$  were in competition with such mutants and we might explain the existence of  $m$  by appeal to the differences between the normal variant and the mutant.<sup>3</sup> Hence, we might attribute the proper function to produce haemoglobin to  $m$ .

This shows that the above definitions of first-order reproductively established family and of proper function allow us to attribute proper functions to genes. In order to be able to attribute functions to other items such as organs, Millikan introduces the notion of a “higher-order reproductively established family”. This definition uses the notions of proper function and of Normal explanation. A Normal explanation tells us how ancestral items performed the activity for which they were selected, for example a Normal explanation might explain how past copies of a gene were used to produce haemoglobin. The conditions that enabled ancestral items to perform the activity that resulted in selection of that item are called the ‘Normal conditions’.

Any set of similar items produced by members of the same reproductively established family when it is a direct proper function of the family to produce such items and these are all produced in accordance with Normal explanations, form a *higher-order reproductively established family* (Millikan 1984: 24)

On this definition the parts and organs of an organism form a reproductively established family. As I showed above, on the basis of the definitions of first-order reproductively established family and of proper function one may attribute the proper function to produce a certain molecule (such as haemoglobin) to a certain gene. Because that gene is a member of a reproductively established family and because the members of that family have the proper function to produce haemoglobin, haemoglobin is a member of a higher-order reproductively established

---

<sup>3</sup>Note that this is my reconstruction of what Millikan would say of this example, not my own opinion. Part (3) of Millikan’s definition of proper function requires that the existence of  $m$  can be explained by appeal to selection. For that reason, I assume that Millikan would claim that the selection explanation in my example explains why  $m$  exists. I would not agree with her. The selection explanation in my example explains how the character of the members of  $R$  was maintained in the evolutionary history. This explains why the members of  $R$  have the character they have and, hence, why  $m$  has the character it has, but not why  $m$  exists. Indeed, I fail to understand what it would mean to explain why  $m$  exists by appeal to selection. Because I feel awkward in saying that the selection explanation in my example explains the existence of  $m$  and because I would agree that  $m$  has the proper function to produce haemoglobin I think that part (3) of Millikan’s definition of proper function is defective. This defect can be repaired easily by replacing the requirement that one may explain why  $m$  exists by appeal to selection with the requirement that one may explain why members of  $R$  have the character they have by appeal to selection.

family. Similarly, hearts form a higher-order reproductively established family because there are several genes that have the proper function to (help to) produce hearts.

As the definition of proper function applies to all kinds of reproductively established families, it is now possible to assign functions to organs and behaviours. Because my heart is a member of a reproductively established family, it has the proper function to pump blood if pumping blood is what its ancestors did that account for its presence in my body. In that case  $m$  refers to my heart,  $C$  to those properties of hearts that enable it to pump blood,  $F$  is propagating the blood and to  $m$  belong all hearts which are both homologous and sufficiently similar to each other.

As I said, Millikan's theory is meant as a general theory which allows one to attribute proper functions to a lot of entities, provided that these entities are reproduced and that their structure or existence can be explained by appeal to selection. When applied to the living world the relevant selection process is natural selection. The term 'natural selection' refers to the situation that (i) there is variation among the individuals of a population in some trait, (ii) the life chances of these variants vary as a result of that variation (the different variants differ in fitness due to the different possession of that trait), and (iii) the possession of that trait is inheritable. In short, natural selection consists in heritable fitness differences. Natural selection results in (i) differences in the frequency distribution of the characteristic among age classes, and (ii) a change in relative frequency of that characteristic among generations (if the population is not at equilibrium). Note that these effects might also result from other sources. Differences in trait frequency distribution among age classes might be the result of ontogenetic development (the fact that the frequency of baldness increases with the age is for example not an effect of selection), changes in trait frequency among generations might be the result of direct environmental effect or of genetic drift.

Whereas Millikan pretends indifference to the applicability of the etiological theory to biology, Neander's theory is explicitly meant as an analysis of the biologist's usage. Neander defines proper functions directly in terms of natural selection. Neander defended this theory in a paper she presented at the AAP conference in 1980 (Neander 1980). That paper circulated widely among philosophers of science with an interested in biology but remained unpublished. Neander elaborated on the etiological theory in her PhD thesis (Neander 1983). Her first published defence of the etiological theory appeared in 1991 in *Philosophy of Science* under the title "Function as Selected Effects":

This paper defends the etiological theory of proper functions, according to which, roughly speaking, biological proper functions are effects for which trait were selected by natural selection. (Neander 1991a: 196).



More specifically:

It is the/a proper function of an item ( $X$ ) of an organism ( $O$ ) to do that which items of  $X$ 's type did to contribute to the inclusive fitness of  $O$ 's ancestors, and which caused the genotype, of which  $X$  is the phenotypic expression, to be selected by natural selection. According to this theory, for instance, hearts have their proper function of pumping blood, because pumping blood is what hearts did that caused them to be favored by natural selection (Neander 1991a: 174).

For example

it is the function of your opposable thumb to assist in grasping objects, because it is this which opposable thumbs contributed to the inclusive fitness of your ancestors, and which caused the underlying genotype, of which opposable thumbs are the phenotypic expression, to increase proportionally in the gene pool. In brief, grasping objects was what the trait was selected for, and that is why it is the function of your thumb to help you to grasp objects (Neander 1991a: 174).

### 7.2.2 Selection explanations

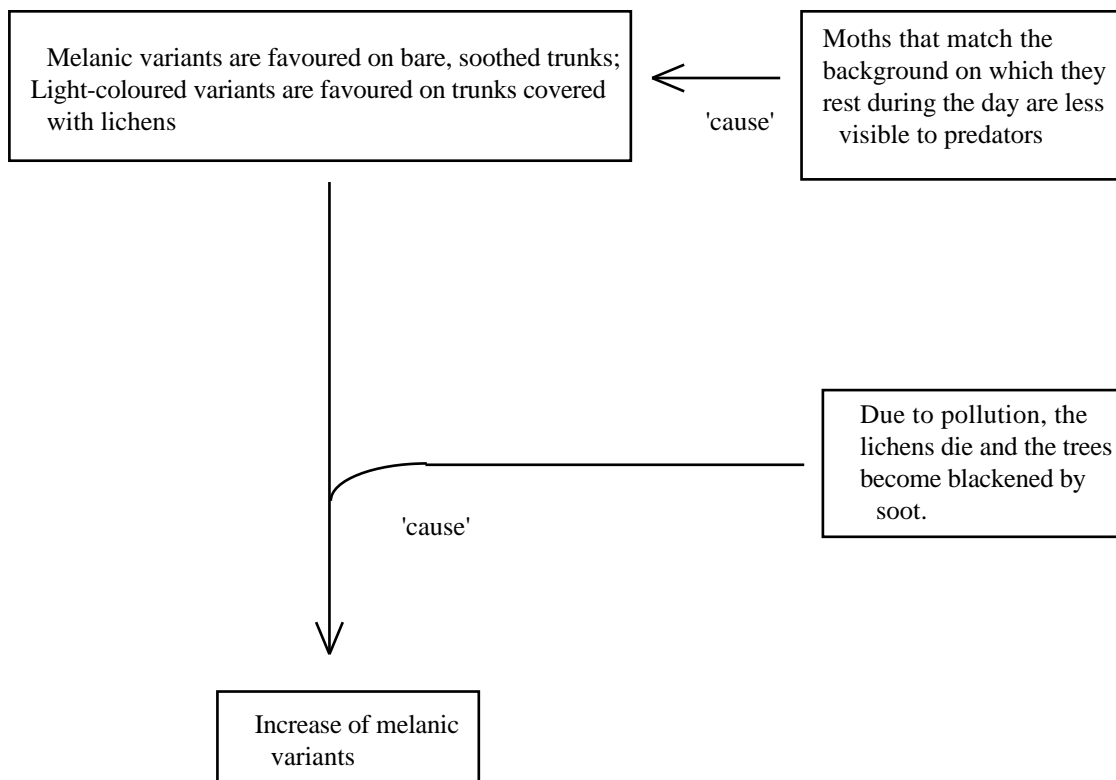
It will be clear from the above account that on the etiological theory there is a tight connection between attributions of proper functions and explanations that appeal to natural selection. In this section I take a closer look at such explanations. I distinguish two kinds of selection explanation: evolutionary selection explanations and equilibrium selection explanations. Evolutionary selection explanations explain the presence or character of a certain item or behaviour by telling how and why that item or behaviour was modified by natural selection in the course of evolution (see section 2.3.2). Equilibrium selection explanations explain why a certain variant is maintained by natural selection in the population at a certain frequency.

In evolutionary selection explanations the present character of an item is viewed as the result of a series of changes of an ancestral item. Each of these changes is explained as the result of natural selection, which is a process that operates at the population level (this is what distinguishes evolutionary explanations from physiological, developmental and design explanations, all these explanations are concerned with processes, mechanisms and/or relations at the individual level)

A well-known example of an explanation of an evolutionary change by appeal to natural selection is Kettlewell's (1959) explanation of the increase of melanic (black) variants of various species of moths in the industrial areas of nineteenth century England. In the area around Manchester the first black variants of the peppered moth (*Biston betularia*) were caught in 1848; by 1895 this variant took up 95% of the total population in that area. Kettlewell explains this increase as follows. The various species of moths rest during the day on the exposed parts of trees. The resting moths form a favourite dish for many insect eating birds. Before the rise of

industrialization the trees were covered with light-coloured lichens. Against this background the light forms of the moth were difficult to see. Lichens are very sensitive to air pollution and with the advent of industrialization the lichens disappeared and the bare trees became blackened by soot. Against this background the melanic form is less conspicuous than the light form. As a result the melanic variants were less easily caught by their predators than their lighter relatives and their share in the population increased rapidly.

Kettlewell has performed a series of experiments to support this explanation. In 1953 he released marked individuals of both variants in the polluted woods near Birmingham. About 90% of the natural population in this woods is melanic. More than twice as many dark as light variants were recaptured after one day in the wild. A repetition of this experiment in 1955 yielded approximately the same results. In the same year the experiments were also repeated in the unpolluted woods of Dorset, where the trees are covered with lichens and about 95% of the natural population is light-coloured. The results are the reverse of those of the Birmingham experiment: more than twice as many light-coloured as black-coloured forms were recaptured. In addition, in co-operation with Tinbergen, he observed the resting moths from a hide. In the Birmingham area they observed 58 moth being captured by birds, 43 of the captured moths were light-coloured and 15 melanic. In Dorset of 190 moth observed to be captured more than 86% were melanic and less than 14% light-coloured.



*Fig 7.2: selection explanation of the evolution of industrial melanism*

Hence, the phenomenon to be explained is the increase of melanic variants in the population in a certain period (see fig. 7.2). This phenomenon is explained by two factors, namely (1) differences in relative fitness between the melanic variants and the light-coloured variants in different environments (melanic variants are favoured on bare, soot-covered trunks and light-coloured variants are favoured on trunks covered with lichens), and (2) a change in the environment (due to pollution the colour of the trunk became bare and blackened by soot). The fitness differences in their turn are explained by the fact that moths with a pattern of colours that match the background on which they rest during the day are less visible to their predators. (This account of industrial melanism is derived from Kettlewell 1959, Kettlewell 1973, Keeton & Gould 1993: 480-481)

Kettlewell primarily explains a past increase of melanic variants in the population, but this secondarily explains why the wings of current moths have the colour pattern they have. That is it explains why certain items (the wings) have the character (colour pattern) they have.

Evolutionary selection explanations, as I have defined them, are concerned with changes at the population level. Do we need such an explanation to attribute a function according to the etiological theory? At least in Millikan's view the answer to this question is no. Millikan reminds us that selection might not only explain evolutionary change. It might also explain why a certain item or behaviour has not changed (has not evolved) in the recent past:

If natural selection accounts for a trait, that is something that happened in the past, but that past might have been, as it were, "only yesterday". Indeed, *usually* the relevant past is "only yesterday": the *main business* of natural selection is steady maintenance of useful traits by continual selection against new intruders in the gene pool (Millikan 1989a: 173).

The idea is that in the course of time in a population there regularly turn up mutant variants in which the character of an item has changed in such way that that item performs a certain activity less well, for example, there regularly turn up mutants in which due to a change in the heart's structure the heart pumps the blood less well. These variants are subsequently weeded out by natural selection because they perform that activity less well, for example, because they pump blood less well. In those cases the character of an item or behaviour is maintained by selection and on Millikan's theory it is justified to call the activity concerned a proper function of that item:

A trait's function is what it actually did — did most recently — that accounts for its current presence in the population, as over against *historical* alternative traits no longer present (Millikan 1989a: 174).<sup>4</sup>

---

<sup>4</sup>Note that in this paper Millikan attributes functions to traits. In her other work functions are attributed to items which is closer to the way biologists talk of functions.

It is useful to distinguish two kinds of selection explanations: evolutionary selection explanations and equilibrium selection explanations. Evolutionary selection explanations explain changes at the level of the population and equilibrium selection explanations explain the maintenance of a certain trait at a certain frequency in the population. Similarly it is useful to distinguish two variants of etiological theories: an origins variant and a maintenance variant. The origins variant defines the functions of a trait as the effects that caused the past increase of that trait in the population. The maintenance variant (endorsed by Millikan) emphasizes the effects that have maintained a certain trait at its present level in the population in addition to the effects that caused its original increase. On the origins variant to attribute a function to a trait one needs evidence that the trait increased in the population due to natural selection for performing that function, on the maintenance variant one needs evidence that in the recent past the trait has been maintained by natural selection for performing that function.

### 7.3 The proper place of proper functions

In this section I discuss the extent to which the etiological theory helps us to understand the use of function attributions in explanations in functional biology.

As I said Millikan on the one hand maintains that her definition is not meant to capture the biologist's usage and on the other hand she gives the impression that she thinks that her definition applies to almost all function attributions in biology (among others because her examples of function attributions include standard function attributions in biology such as "a function of the heart is to pump the blood around"). Anyway Millikan does not give a detailed example of the way in which biologists come to attribute a function to an item or behaviour, neither does she study how those attributions are actually used in biology.

Neander's theory is explicitly meant to capture the biologist's usage. However, her main published defence of the etiological theory (Neander 1991a) deals with philosophical objections against the etiological theory. She does not give detailed examples and does not show in detail that her theory applies to biological practice. The lack of detailed examples makes it difficult to understand to what kinds of function attributions she thinks her theory applies and in what kind of explanations she thinks these function attributions are used. Anyway, as the above quotations show she thinks that her theory applies to at least two function attributions that on my definition are attributions of function as causal role (namely the attribution of the function to pump blood to the heart and the attribution of the function to assist in grasping objects to my opposable thumb).

I argue that the etiological theory is of no relevance to understand talk of functions in functional biology. I have three arguments:

- 1) The kind of evidence biologists bring up when they attribute functions to the parts, organs and behaviours of organisms is not the kind of evidence one would expect on the etiological account. This shows that the etiological theory does not apply to this kind of function.
- 2) The kind of functional explanations sketched by the proponents of the etiological account have only a remote resemblance to the explanations offered by functional biologists.
- 3) The interpretation of biological categories as categories that unite items and behaviours by their function is wrong.

The etiological theory is at best an account of the fourth notion of function (function as selected effect) and this notion of function does not play an important role in functional biology.

### 7.3.1 The evidence against proper functions

Although the meaning of a statement is not equivalent to its evidence, it seems that there must be a relation to what is asserted by means of a certain scientific statement and the evidence brought up to support that thesis: the relevant scientific community must think that the evidence gives them an indication of the truth of what is supported. But this means that the evidence brought up in support of a certain kind of thesis, gives us some indication about what is asserted. In other words, one need not be a verificationist to maintain that the evidence which is brought up in support of a certain kind of thesis provides an important way to evaluate whether a philosophical theory applies to theses of that kind. Neander, for example, maintains that the kind of conceptual analysis in which she is engaged

involves trying to describe the criteria of application that the members of the linguistic community generally have (implicitly or explicitly) in mind when they use the term (Neander 1991a: 170).

If the etiological theory would apply to such function attributions as “the heart has the function to pump the blood around” and “the function of my opposable thumb is to assist in grasping objects” what kind of evidence would one expect for these function attributions? As selection consists in heritable fitness differences and results in , we might expect:

- (i) evidence that variation occurred in regard to the relevant trait,
- (ii) evidence of natural selection, that is evidence that
  - (a) in the environment in which those organisms lived organisms having the trait performed the function-to-be-attributed different from their competitors, and
  - (b) in that environment the way in which the function was performed by the organisms having resulted in better life chances than the way in which that function was performed in organisms lacking the trait,

- (iii) evidence that this variation is heritable,
- (iv) evidence that the predicted results occur.

Natural selection is not easy to detect. The authoritative guide to detecting selection in natural populations is John Endler's *Natural Selection in the Wild* (1986). Endler discusses ten different kinds of methods to detect natural selection. Problems may result among others from statistical bias and from incomplete knowledge of genetics, population structure and ontogenetic development. Endler presents a lists of all known direct demonstrations of natural selection (p. 129-53). These demonstrations are distributed among 314 traits, and among 141 species. This is quite impressive as a demonstration of the occurrence of natural selection in the wild, but it fails as a justification of the common function attributions in biology. Moreover, most of these studies are concerned merely with demonstrating *that* natural selection occurred, but not with the *why* of selection. None of this studies is concerned with the function attributions philosophers usually mention as examples, such as the functions of heart and kidneys, the function of sperm and so on. This means that if the etiological theory applied to these function attributions biologists would have no support for their standard function attributions.

If one requires that a function attribution tells us something of the origin of the trait (rather than on the maintenance) the problems increase. Amundson & Lauder (1994) have spelled out these difficulties. I quote from this paper:

There are enormous practical difficulties in determining just what the selected effect of a structure was in the first place. Many structures are ancient, having arisen hundreds of millions of years ago. During this time, environments and selection pressures have changed enormously. How are we to reconstruct the ancient selected effect?

If there is enough palaeontological information, it is sometimes possible with help of physical theories to estimate the likely action of selection in the past and to construct a possible scenario of the evolution of a certain trait, but many structures, in particular in fossils, are not amenable to such an analysis.

More specifically, on Millikan's account (which emphasizes selection for maintenance of a trait in the recent past) one would expect that someone who wants to attribute the function to pump the blood around to the heart comes up with (i) a list of deviations that regularly occur in the heart, (ii) an account which shows that (a) these deviations result in differences in the way in which the blood is pumped, and (b) the life chances of variants which deviate hearts are lower than that of normal organisms due to the difference in the way in which the blood is pumped, (iii) evidence that the deviations are heritable, (iv) an analysis which shows that the percentage of people having the deviant heart decreases with the age (or other evidence of the predicted outcome). I could not find anyone providing this kind of evidence for a function attri-

bution. To avoid misunderstandings, my point is not that this kind of evidence does not exist.<sup>5</sup> Rather my point is that nobody cares to present this evidence in favour of the bulk of function attributions, even if it exists. This is a strong indication that the etiological theory does not apply to those function attributions. When biologists identify functions they seldom delve into the selection history of an item, behaviour or trait. Instead they try to figure out (i) what role a certain part, organ or behaviour has in the maintenance of an organism (in which case the study results in an attribution of a causal role), or (ii) what the survival value is of a certain trait as compared to another trait (in which case the study results in a claim about survival value). I show this by means of some examples.

My first example concerns the attribution to the heart of the function to pump blood. The evidence for this attribution was provided by Harvey in the beginning of the seventeenth century (example 2.1 of section 2.2.2). Harvey's main point in regard to the heart was that the heart movement does not originate from the chest and the lungs but from the heart itself and that the active phase is the expansion phase rather than the contraction phase. Harvey discovered that the heart of some amphibians and reptiles remain active after killing the organisms and used observations of how the heart works in those organisms to argue for his thesis that the function of the heart is to pump blood. He also observed that the heart is hollow muscle. Of course, there is no hint of selection in Harvey's argument.

Neander (1991a) dismisses appeal to Harvey on the ground that her etiological theory is meant as an analysis of present day biology and that the notion of function has changed with the arrival of Darwin's theory. I think she is wrong. The present day attributions of the function to pump the blood to the heart derive from Harvey. Current textbooks on morphology hardly give evidence for function attributions. Evidence is presented only in the rare cases in which the attribution is controversial. In the case of the heart, textbooks confine themselves to saying that the function of the heart is to pump blood without presenting the evidence for that attribution (the function attribution is used to explain such things as how the heart and the circulatory system work, why the heart has the structure it has, how it developed in the course of the evolution (see section 2.3.3)). This means that the attribution is entrenched in morphology to such an extent that textbooks state the function without giving evidence. The attribution became

---

<sup>5</sup>One should not underestimate the difficulty of providing such evidence. For example, in the case of the heart it is not enough to point to the fact that in many hospitals all over the world there are people with heart diseases and that these diseases involve the capability to pump blood. One must show that these diseases have a genetic component, that they influence fitness (it might for example be the case that most heart diseases occur at an age at which they do not influence the expected number of offspring) and it would be nice to have also some evidence that the predicted result of neutral selection occurs. The latter kind of evidence is, perhaps, the most difficult to obtain (as far as I know there are no means to detect deviant hearts at an early age).

entrenched in biology due to Harvey's work. If Neander is right that the meaning of the term function changed with Darwin one would expect that after the arrival of Darwin's theory biologists would point out that the concept of function has changed and that for that reason Harvey's evidence was bad evidence. No such thing happened. Indeed, if any evidence is presented today for attributing the function to pump blood to the heart it is Harvey's evidence. For example, I first learned the evidence for this function attribution, from a movie about Harvey shown as part of a practical course in zoology.

However, I need not appeal to Harvey to argue that the evidence presented in favour of the common function attributions in morphology is not of the kind one would expect if the etiological theory would apply to those attributions. In 1961 Jacques Miller showed that the thymus had a function in the development of the immune system (example 2.2 of section 2.2.2). His evidence consists of the results of extirpation experiments in new-born mice. There is no investigation into the history of the thymus, no list of common mutants, no argument that the mutants are worse off than the normal forms, no investigation into heredity and no investigation of natural populations which could affirm a selection hypothesis. In sum: the evidence Miller provided in support of the hypothesis that the thymus has a function in the development of the immune system is evidence that the thymus is (in current organisms) involved in the development of the immune system not evidence that the thymus was selected for that role.

Especially instructive is my third example: Kurt Schwenk's (1994) argument for the attribution of trail-following function to the tongue of snakes (and some other reptiles) (example 2.3 of section 2.2.2). As I said in section 2.2.2 his evidence consists of: (1) observations of the behaviour of snakes during trail following, (2) experiments showing that removal of the forked portion of the tongue eliminates the ability to follow scent trails, but not the delivery of stimuli to the vomeronasal organ, (3) comparative data showing a rough correlation between depth of tongue bifurcation and ability to follow chemical trails, (4) observations of the nervous system showing circuits suitable for comparing signal strength from each side of the tongue. There is no appeal to history nor to selection in this part of the argument. The example is especially instructive because Schwenk discusses the selection history of the trait in addition to its function (albeit superficially). At this point he does present historical evidence: he fits the trait 'having a forked tongue' on a phylogenetic tree and shows that the forking is a derived character which emerged at least twice in the evolutionary history. He then speculates that the forking might have arisen because it conferred a performance advantage in chemical delivery to the vomeronasal organ and that subsequently the forking increased due to selection to perform this role better.<sup>6</sup> Whereas Schwenk maintains that his conclusion about the function of the tongue

---

<sup>6</sup>This is merely a speculation because Schwenk does not tell us what the performance advantage was and he does not attempt to correlate the emergence of a forked tongue with the need for such a performance advantage.



in trail following is “inevitable” (p. 1574), he is pretty uncertain about why the tongue became forked (at p. 1567 he maintains that “the reason for its initial evolution remains obscure”. “Probably [...] it did initially confer a performance advantage in chemical delivery to the vomeronasal organ.” Subsequent selection for increased efficiency in scent trail-following “may have caused” the tongue to become increasingly forked). The facts that (i) the evidence which Schwenk presents in support of his function attribution differs from the evidence he presents for supporting his hypotheses about selected effect, and (ii) Schwenk is confident about the function attribution and hesitant about the selected effects, support my view that the etiological theory does not apply to the common function attributions in morphology.

My first three examples concerned examples in which the evidence provided in support of a function attribution shows that the attribution was concerned with the causal role of the item in study not with the effects for which that item was selected. Let us now look at an other kind of examples

My fourth example concerns the foraging behaviour of black headed gulls (example 3.1 of section 2.2.3). As I said, Gotmark, Winkler and Anderson (1986) argue that this behaviour has the function to enable each gull to catch more fish than it would have done if it fished alone. They support this attribution by means of a laboratory experiment which shows that gulls in groups catch more fish (per gull) than do gulls that fish solitary and that the number of fish caught per gull increases if the group size increase. I admit that this kind of evidence comes closer to the kind of evidence one would expect if the etiological theory applied (closer than the evidence in my first three examples). The experiments support the view that the fitness of a gull that tends to flock is greater than the fitness of a gull that tends to fish alone. However, these experiments do not provide sufficient evidence for the view that there recently was selection. They do not show that there regularly turn up individuals that tend to fish alone, which survive less well due to this tendency and they do not show that this tendency is heritable.

Similar considerations apply to my fifth example: the egg shell removal behaviour of black headed gulls. The experiments of Tinbergen and his colleagues (1962) show that the actual birds that remove the egg shell would be favoured by selection over hypothetical variants that would not perform this behaviour. According to Millikan's etiological theory, however, functions are attributed not on the basis of “what would happen if”, but on the basis of what actually happened in the past. This requires evidence that the hypothetical selection established by the authors has actually played a role in the evolution or maintenance of the egg shell removal in the past. It should for instance be shown that every now and then a mutant gull turns up that has decreased fitness because it does not remove the empty egg shell, or waits too long before doing

so, or dumps the empty shell at a too short distance. The researchers do not provide evidence of this kind. Yet, they take it that their studies establish the function of the trait concerned.<sup>7</sup>

I have presented five examples in which the evidence provided by the authors differs from the evidence one would expect on Millikan's theory. This may either mean that the authors are over-confident or that they use the word 'function' in a sense different from that of Millikan. In my examples we can safely exclude the first possibility. The examples are either derived from renowned refereed journals such as *Science* and *Nature* (Schwenk, Gotmark, Winkler & Anderson) or else they have become classics in their field (Harvey, Miller, Tinbergen). The conclusion that they use the term 'function' in a sense that is different from Millikan's seems justified. In the first three examples the term 'function' refers to the causal role of a certain part or organ, in the last two examples the term 'function' refers to the survival value of a behavioural pattern. I do not deny that the word 'function' is sometimes used by evolutionary biologists in Millikan's sense of proper function. My point is, rather, that functional biologists often use the term 'function' in a different way and that no account of function in biology is complete if it ignores that other use.

### 7.3.2 Functional explanations

In the preceding section I argued that the kind of evidence put forward in support of the standard function attributions in functional biology is not of the kind one would expect on the etiological theory. This shows that the etiological theory does not apply to these kind of function attributions. In this section I am concerned with the question whether or not the etiological theory offers insight in explanations in functional biology.

In chapter 2 I argued that functional biologists aim to explain the way in which an organism is built and the way it behaves. They do so in four complementary ways: (1) physiological explanations, (2) design explanations, (3) developmental explanations, (4) evolutionary explanations. I also argued that functions as causal roles have a key role in three kinds of

---

<sup>7</sup>The point that evidence of survival value is not evidence of selection has been made emphatically by Tinbergen (1963) and by Hinde (1975). Tinbergen emphasizes the difference in method between establishing survival value and establishing selection. Survival value is, according to him, determined by means of experiments which allow us to attribute survival value beyond any reasonable doubt. Evidence of selection, on the other hand, is provided by means of comparison and hypotheses about selection are rather speculative. Hinde emphasizes that comparison with a hypothetical organism does not establish selection. Hinde distinguishes between strong and weak meanings of function. Function in a strong sense corresponds to my function as selected effect, function in a weak sense to my function as survival value. Functions in the weak sense are established by comparing the real organism with a hypothetical one, functions in the strong sense are established by comparing real competitors. The latter kind of evidence is, according to Hinde, much more difficult to supply.

explanations: capacity explanations (which are a special kind of physiological explanations), design explanations and evolutionary explanations. In this section I am concerned with the question what insights the etiological account provides in these kinds of explanation and whether my account should be revised in the light of the etiological theory.

As I said in the introduction to this chapter, the etiological theory is primarily a theory of function, not of functional explanation. Millikan and Neander, the main proponents of the etiological theory, pay little or no attention to explanation. Millikan makes some scant remarks on “functional explanations” in her “An Ambiguity in the Notion ‘Function’” (1989a) and Neander devotes a paper to the alleged feature that attributions of proper functions generate what she calls “teleological explanations” (Neander 1991b). Neither Millikan nor Neander discuss a detailed example of an explanation in biology.

Although it is clear that on the etiological account function attributions are singled out by their role in selection explanations, it remains unclear what according to the proponents of the etiological theory the relation is between on the one hand selection explanations and the resulting attributions of “proper” functions and on the other hand the explanations which biologists call ‘functional explanations’ (and which I call ‘design explanations’). Would the proponents of the etiological account agree with me that design explanations are a different kind of explanations beside physiological explanations (among which capacity explanations), developmental explanations and evolutionary explanations (among which evolutionary selection explanations)? If so, would they agree with me that these explanations appeal to causal roles and survival values or would they maintain that these explanations appeal to proper functions in their sense? Would they maintain that design explanations appeal to past selection in some way or other? What is the structure of such explanations on their account?

### *Millikan*

In her ‘An Ambiguity in the Notion “Function”’ (1989a) Millikan scorns Horan (1989) and Bigelow & Pargetter (1987) for confusing “two types or senses of ‘function’ and ‘functional explanations’” (p. 172). The two kinds of function are on the one hand “Cummins-style functions (Cummins 1975)” and on the other hand “selected functions” (or “proper functions” — Millikan 1984, 1986, 1989b). “Cummins-style functions” correspond to the kind of function I call “function as causal role” (function<sub>2</sub>); “selected functions” correspond to the kind of function I call “function as selected effect” (function<sub>4</sub>). According to Millikan both kinds of function can be used to explain the presence of the item to which the function is attributed, but the resulting kinds of explanations should not be confused. Millikan distinguishes two types of functional explanations: “functional explanations in Cummins sense” (p. 175) and “functional explanations that make reference to natural selection” (p. 174). “Functional explanations in Cummins sense” correspond to the kind of explanation I call “capacity explanation”, “functional

explanations that make reference to natural selection” correspond to the kind of explanation that I call “selection explanation”. Millikan maintains that functional explanations that make reference to natural selection appeal to functions as selected effect (and not to causal roles), whereas causal roles are used in functional explanations in Cummins’s sense (that is in capacity explanations).

Functional explanations that appeal to natural selection explain the presence of a certain trait simply by saying that that trait has a certain selected function, say *F*. Millikan emphasizes that on her theory to say that a certain trait has a function *F* is just another way of saying that in the past that trait was selected over its competitors because it did *F*.

To say that a trait *T* has the proper function *F* is to say that *T* had a history during which it was selected for doing *F*. So if you want to know why current species members have *T* the answer is, very simply, *because T has the function F*, that is, because *T* was selected for because it *did F*. *F* was not of course the function of the very first tokens selected, even though they did *F* and that is why they were selected. They were not selected “because they had functions” but because they did *F* (Millikan 1989a: 174).

As I discussed in chapter 5, Cummins (1975) maintains that attributions of causal roles have no place in selection explanations. Millikan agrees with him:

It is important to see that Cummins’ sense of function does not fit with the theory of natural selection to help explain the current presence of a trait in a species (Millikan 1989a: 175).

Only attributions of functions of selected effects may be used in selection explanations:

[selected function] is the only kind of function that is well defined and that can enter into functional explanations that make reference to natural selection (Millikan 1989a: 174).

Although Millikan agrees with Cummins that causal roles may not be used in selection explanations, she argues, *pace* Cummins, that there are cases in which the presence of an item might be explained by means of a functional explanation in Cummins sense (and hence by appeal to the causal role (Cummins function) of the item to which the function is attributed). Such cases concern causal roles which help to explain the reproduction of cyclical system (such as “the life cycle of a species” (p. 176)). In such case the presence of a certain item in the current phase of the cycle might be explained by the fact that that item performed its causal role in the preceding phase. For example, the presence of my heart might be explained by the fact that the hearts of my parents performed their causal role (in “the life cycle of the species”) to propagate the blood.

So the Cummins functions of various features of a biological species, when these functions are defined relative to the life cycle of the species, do help to explain the most recent genesis of these various features as present in current individuals (Millikan 1989a: 176).

Millikan's concludes by saying that as (i) most selected functions coincide with a Cummins function that helps to explain "how a species [sic!] has recently been surviving, developing and reproducing" (p. 175)<sup>8</sup> and (ii) both kinds of functional explanations may explain the presence of the item to which the function is attributed the two sense of function and functional explanation are easily confused.

As I have shown in chapter 6, Horan and Bigelow & Pargetter are interested in a third type of function, namely function as survival value (function<sub>3</sub>) which they confuse with function as causal role and erroneously take for the one and only kind of function. Millikan too falls prey to confusion, not only because she fails to see that Horan and Bigelow & Pargetter are interested in a third kind of function, but also because she has a mistaken idea of the explanatory use of functions as causal roles.

Biologists do not use causal role functions to explain the presence of the item to which the function is attributed in the way described by Millikan. It is not clear what Millikan means by "the life cycle of the species" but, of course, someone may explain the presence of my heart by appeal to the fact that the hearts of my parents performed their causal role in the development and reproduction of *my parents* but this has nothing to do with the way in which biologists use the notion of causal role in explanations. In this kind of explanation, the fact that the explanation appeals to the causal role of the item the presence of which is to be explained is accidental. One may just as well explain the presence of my heart by appeal to the fact that my parents *lungs* performed their causal role. This in contrast to the way in which biologists appeal to causal roles in explanations. As I have shown by means of many examples in several chapters, biologists use attributions of causal roles to explain (i) how a certain organism, item or behaviour is able to perform a certain task, (ii) why it is useful to certain organisms that they have a certain item or behaviour, (iii) why it is useful to certain organisms that a certain item or behaviour has the character it has, and (iv) how that item or behaviour got its character in the course of the evolutionary history. In a certain sense of 'why' the explanations ad (ii)-(iv) may be taken as explanations of why a certain trait is present in a certain type of organisms. Explanations ad (ii) (which answer a type 4a question) explain why<sub>2</sub> certain organisms have a certain item or behaviour. They do so by telling us why the causal roles performed by that item or behaviour are useful to those organisms. Explanations ad (iii) (which answer a type 4b question) explain why<sub>2</sub> a certain item or behaviour has the character it has (if one thinks of the character

---

<sup>8</sup>To my mind the very notion of a Cummins function "in the life cycle of species" is confused. It is individuals not species that survive, develop and reproduce. Perhaps Millikan means to say "how the member of a species have recently been surviving, developing and reproducing". Cummins defines functions as capacities of subparts that help to explain the capacities of the part to which the subpart belong. However, the things certain individuals did that contributed to their survival, development and reproduction are activities not capacities.

of an item as a trait one may phrase this as why<sub>2</sub> that trait is present). They do so by telling us why the causal role of that item or behaviour is better performed if the item or behaviour in question has the character it has than if it had some other character. Explanations ad. (iv) (which answer a type 6 question) tell us why<sub>3</sub> a certain item or behaviour has the character it has. They do so by telling us that the item or behaviour in question acquired its character due to the fact that in an ancestral population variants in which the item or behaviour in question had the character it now has were fitter than variants in which that item or behaviour had another character because in the circumstances in which those organisms lived the causal role was better performed by an item or behaviour with the present character than by an item or behaviour with that other character. Note that in all these kinds of explanations the appeal to causal roles of the item in question is essential. One does not explain why the heart is useful by appeal to the causal role of something other than the heart (such as a lung), nor does one explain why it is useful that the heart has the structure it has and why it acquired that structure in the course of the evolution by appeal to the causal roles of other organs.

Millikan's idea that causal roles may not be used in selection explanations is equally mistaken. Consider, for example, Abramson's (1993) study of the structure and evolution of dentition of true lemmings. Lemmings are small rodents that inhabit the tundra's of Scandinavia, Siberia and North-America. There are two subgroups: true lemmings (*Lemmini*) and collared lemmings (*Dicrostonyxini*), both belong to the subfamily of vole (*Arvicolinae*). The structure, trends in variation and rate of evolution of dentition in true lemmings is remarkably different from that of collared lemmings and, indeed, of all other voles. Abramson argues that these differences "can be understood from the quite different functioning of the masticatory apparatus" (p. 687). True lemmings differ in their food preferences from all other vole. They mainly eat graminoids and mosses, which are poor in mineral nutrients and contain a large volume of hardly digestible hemicellulose fibres. This diet imposes demands on the masticatory apparatus which are different from those of other voles with another diet:

Thus the masticatory apparatus of the Lemmini *must* deal with the consumption of far greater quantities of food per unit of time than is the case with voles, containing in addition much higher amounts of hardly digestible cellulose (Abramson 1993: 696, emphasis mine).

These different demands explain both the differences in structure and the differences in evolution. In true lemmings the greater part of the cutting edges of the upper and lower molars form reciprocally curved blades. As a consequence some blades meet along the direction of movement. In collared lemmings, the cutting edges of the upper and lower molar meet obliquely. The arrangement in true lemmings increases the contact area (in comparison to that of other voles). Such curved blades entrap food better, which allows the processing of a larger amount of food

per unit of time. In the conclusions section this point is expressed by means of a functional counterfactual:

It has been shown that with the arrangement of cutting edges characteristic of highly evolved voles, food with a high concentration of cellulose will slip off the masticatory surface instead of being cut (Abramson 1993: 697)

The arrangement of cutting edges in its turn explains the arrangement of the muscles: the arrangement of cutting edges in true lemmings requires an increase in the force normally applied to the occlusal surface and the muscles differ in accordance with this requirement.

The evolution of tooth patterns in vole is a well studied area. The main trends observed in many different lineages are: acquisition of additional triangles (dentoenamel elements) on the rear end of the lower molars and the front end of the upper ones, together with an increase in the degree of alteration of salient angles. These trends are extremely clear in the evolution of collared lemmings. True lemmings, however, show a different trend, namely an increase in the relative width of the molars and a tendency to fuse the triangles. Roughly spoken the trend is towards flattened molars. Both in true and in collared lemmings these trends result from selection for achieving maximum efficiency of the molars. However, due to the dietary differences the means to increase that efficiency differ in these two lineages.

The trend leading to one solution or another depends greatly on the genetic base, and, to a very significant degree, on demands imposed on the masticatory apparatus by the mechanics connected with feeding specialization (Abramson 1993: 695/6).

The flattening of the molars is a means to achieve greater efficiency in herbivores with a low caloric diet.

In Lemmini, with their characteristic chewing movements and the nature of occlusion, increased mastication efficiency is achieved not with the elongation of the cutting edges by the acquisition of new elements, but by the increase in the relative width of the teeth and the fusion of the alternating triangles (Abramson 1993: 693).

**In sum:**

The distinctive means of increasing the efficiency of the masticatory apparatus seen in Lemmini not only reflects definite genetic history but can also be explained by their very unusual food specialization and the demands it imposes on the mechanics of their masticatory apparatus (Abramson 1993: 687)

(The remarks about genetics appear out of the blue and remain unclear).

Note, that Abramson's explanation of the structure and evolution of the molars of true lemmings proceeds in the same way as Schwenk's (1994) explanation of the forked character of the snake's tongue. Both explanations start with the attribution of a causal role to the items in

study. This attribution is subsequently used in both a design explanation and an evolutionary explanation of the structure of the item in study. The design explanation shows that the relevant causal role is better performed if the item has the structure it actually has than if it has another conceivable structure. The evolutionary explanation points out that a certain trend in evolution can be explained as the result of selection of variants that performed the relevant causal role more efficiently in the conditions that apply to the organisms involved. In Schwenk's case the attribution of a causal role in chemosensory tropotaxis to the snake's tongue takes up the large part of the paper; in Abramson's case the attribution to the molars of a causal role in mastication is well established and the explanatory part gets the most attention. Schwenk's design explanation explains why it is useful that the snake's tongue is forked (why<sub>2</sub> the tongue is forked) by pointing out that blunt tongues are of no use in chemosensory tropotaxis. Abramson's design explanation points out that given the dietary preferences of true lemmings the causal role of the molars (mastication) is better performed if the molars have the structure they have in true lemmings than if they had the structure they have in collared lemmings. Schwenk's evolutionary explanation suggests that the tongue of snakes became increasingly forked in the course of evolution due to selection of variants in which the tongue performed its causal role in chemosensory tropotaxis more efficiently. Abramson's evolutionary explanation explains the evolutionary tendency toward flattened molars in the lineage of true lemmings as the result of selection of variants in which the molars performed their role more efficiently. This explanation starts with the observations that the molars have a causal role in mastication and that the diet of true lemmings consists of graminoids and mosses. It then points out that if the diet consists of graminoids and mosses the molars perform their causal role more efficiently if they are more flattened. For that reason in the course of evolution variants with more flattened molars were favoured again and again over variants with less flattened molars, which resulted in the tendency to flatten the molars.

The appeal to causal roles in selection explanations such as the ones provided by Schwenk and Abramson shows that Millikan's idea that selected functions are the only kind of functions that can enter into selection explanations is mistaken. Indeed, when biologists talk of function in the context of selection explanations they seldom use that term in a historical sense—if ever. I have already quoted Millikan explaining how attributions of selection functions are used to explain the presence of a certain trait:

if you want to know why current species members have T the answer is, very simply, because T has the function F, that is, because T was selected for because it did F (Millikan 1989a: 174).

The way in which biologists talk is different in a subtle, but fundamental way. Biologists often say that a certain structure (e.g. flattened molars) was favoured by selection because it increased the efficiency with which a certain function (e.g. mastication) was performed. For example,



according to Abramson the flattened molars were selected because they increased the efficiency of the masticatory apparatus. This means that the selected function (in Millikan's sense) of the flattened molars is to increase the efficiency of the masticatory apparatus. But no biologists will say that “increasing the efficiency of the masticatory apparatus” is a function of the flattened molars. They say that flattened molars were favoured by selection because they increased the efficiency with which the mastication function is performed, but they do not say that “increasing the efficiency of the masticatory apparatus” is a function. The function to which they appeal is mastication (which is a causal role), not increasing the efficiency of a certain item; and this function is attributed to the item (the molar) the structure (flattened) of which is to be explained not to that structure itself. This means that their use of the term ‘function’ does not conform to the etiological theory.

Moreover, these examples show that selection explanations add more to our knowledge than Millikan seems to think. Abramson does not explain the flattened molars *simply* by saying that they were selected because they increased the efficiency of the masticatory apparatus. One of the main points of his explanation is that more flattened molars are more efficient than less flattened ones because of the demands imposed upon their function (mastication) by the kind of food consumed by the true lemmings. Millikan’s idea of selection explanations as consisting of simply an attribution of a selected function completely negates this part of selection explanations.

Let me draw some conclusions. Millikan (1989a) distinguishes two kinds of functional explanations that might explain why certain organisms have a certain item: functional explanations in Cummins sense and functional explanations that make reference to natural selection. I have argued (i) that the way in which biologists use attributions of causal roles in design explanations to explain the presence of a certain trait has nothing to do with Millikan’s “functional explanations in Cummins sense”, and (ii) that Millikan’s account of functional explanations that make reference to natural selection leaves out of sight much of what is achieved by such an explanation because it fails to take into account the attributions of causal roles that are an essential part of such explanations. The conclusion is that Millikan’s (1989a) remarks on functional explanations are of no use if one wants to understand explanation in functional biology.

### *Neander*

Millikan is not the only one who seems to think of functional explanations as consisting of a single attribution of a selected function. This idea seems akin to the etiological approach. Larry Wright, for example, maintained that the “insight” that functional explanations consist of a single function attribution as the foundation of his theory of function, which became a predecessor of several of the current etiological theories, among which is that of Neander. According to Wright the key to a satisfactory account of function is the insight that

merely saying of something, X, that it has a certain function, is to offer an important kind of explanation of X (Wright 1973: 154)

an insight that all other theories of function have failed to take into account.

Neander too gives the impression that she thinks of functional explanations as one sentence attributions of selected functions. In her “The Teleological Notion of Function” (1991b) she maintains that function attributions “universally and intrinsically” “generate” or “justify” “teleological explanations”. As an example of such an explanation she mentions an explanation of why penguins are myopic on land which points out that this is a “by-product of an optical system that has the primary function of providing sharp visual focus under water where the penguins find their food” (p. 454). This explanation is, in her view, teleological because it appeals to what the eyes are for:

The function of the penguins’ eyes of providing sharp visual focus under water explains why the penguins have the eyes they have, and why they have land myopia, by explaining what their particular optical system *is for* (Neander 1991b: 454. emphasis hers).

The terms “generate” and “justify” suggest that, according to Neander, function attributions and functional explanations are different things. But the differences as well as the relations between the two remain unclear. How is a teleological explanation generated from a function attribution? What is the structure of the resulting explanation? Neander contrasts her view that “function attributions universally and intrinsically justify teleological explanation” (p. 458) with (i) the views of Beckner (1959) and Cummins (1975) that “any so-called ‘teleological explanation’ derived from biological function is merely misguided pseudo-explanation” (p. 458), and (ii) the views of Canfield (1966), Ruse (1973) and Wimsatt (1972) who, according to Neander, maintain that “function attributions usually (but not always) justify teleological explanations, and only when combined with background theory extraneous to (not implied by or contained in) the function attribution” (p. 458).<sup>9</sup> Neander’s main argument against these views rests on her judgement that the idea that function attributions are explanatory is “quite robust” (p. 457). According to her, in the past function attributions were standardly interpreted as stating the reasons why God gave a certain organism the item to which the function is attributed.<sup>10</sup> Notwithstanding the insight that “in modern biology” “we cannot properly inter-

---

<sup>9</sup>Neander’s characterization of the position of Canfield, Ruse and Wimsatt is slightly inaccurate. They do not say that function attributions “usually (but not always) justify” such explanations. Rather they say that function attributions are sometimes used in functional explanations (but function attributions have other uses too) and that if function attributions are used in functional explanations they are combined with background knowledge.

<sup>10</sup>Neander does not substantiate this claim, with which I disagree. Perhaps, Neander describes the way in which natural theologians in the first half of the nineteenth century viewed function attributions but natural theology is

pret” function attributions in this way, function attributions are used again and again to explain why certain organisms have the item to which the function is attributed.

That the koala’s pouch has the function of protecting its young does seem to explain why koalas have pouches. That the bee’s dance is for directing other bees to pollen does seem to explain why bees dance  
(Neander 1991b: 457)

According to Neander it is “just barely possible” that this apparent explanatory power is illusory and an account which shows that such explanations are scientifically legitimate is preferable to an account that maintains that “we” are persistently irrational. The etiological theory provides such an account and is for that reason to be preferred over the views she opposes.

Neander is right that philosopher’s should not explain away established scientific practice as irrational. However, her representation of that scientific practice is mistaken. Neander does not substantiate her claim on penguin myopia, koala pouches and bee dances with reference to scientific literature. This makes it difficult to evaluate her representation of scientific practice in these cases. However, in section 6.6.2 I showed by means of several other examples that the explanations which biologists call ‘functional explanations’ (and which I have called design explanations) do not explain why certain organisms have a certain item or why an organism performs a certain activity simply by citing the function of that item or activity.<sup>11</sup> Design explanations come in two kinds. One kind, answers type 4b questions: they explain why a certain items or behaviour has a certain character. The other kind answers type 4a questions: they explain why an organism has an item that performs a certain task. Both kind of design explanations start by attributing a causal role (function<sub>2</sub>) to an item. But this attribution is the first step in the explanation, not the whole explanation. To yield a design explanation the function attribution is explicitly combined with other statements. This shows that, contrary to what Neander claims, an account according to which function attributions are explanatory only when combined with other statements represent scientific practice better than an account according to which function attributions are intrinsically explanatory.

Perhaps, the idea that biologists routinely explain the presence of an item or behaviour by uttering a sentence of the form ‘the function of ... is ...’ rest on a failure to distinguish attribu-

---

only a minor influence in the history of biology. In the traditions of Aristotle, Cuvier and Von Baer functions were interpreted as roles in the maintenance of the organism.

<sup>11</sup>In regard to Neander’s examples I’m pretty sure that the explanations offered by biologists are much more complex than Neander maintains. For example, to explain the penguin’s myopia it is not sufficient to point out that the eyes have the function to provide sharp visual focus under water. In addition, one should connect the myopia to that function for instance by explaining why an eye that provides sharp visual focus under water does not provide sharp visual focus on land.

tions of causal roles (function<sub>2</sub>) from attributions of survival value (function<sub>3</sub>). Neander's examples are examples of attributions of causal roles. Attributions of causal roles might be converted to the standard form 'the function<sub>2</sub> of item *i* is to do *f*' or 'item *i* has the function<sub>2</sub> to do *f*' but they are not explanatory without any addition. To yield design explanations function<sub>2</sub> attributions are either combined with statements which say why it is useful to the organism to perform role *f* or with statements which say why it is useful that an item that has role *f* has the character which item *i* has. Attributions of survival value are design explanations but they have a much more complex structure than attributions of causal roles and they can not be converted without loss of information to a sentence of the form 'the function of .... is ...'.

### *Kuipers & Wisniewski*

A detailed account of the structure of functional explanations in the spirit of the etiological theory comes from Kuipers and Wisniewski (1994). In a series of papers Kuipers (1985, 1986b, 1986a, 1996) has distinguished two main kinds of explanation: 'explanation by subsumption under a law' and 'explanation by specification'. The latter fall into three types: functional explanations, intentional explanations and explanations by specification of a cause. Kuipers and Wisniewski (1994) outline the common structure of explanations by specification (discovered by Kuipers) in terms of the logic of questions developed by Wisniewski. For obvious reasons, I will restrict myself to their account of functional explanations.

Kuipers and Wisniewski's main example of a functional explanation in biology is "the biological function of the systematic fanning movement of stickleback is to supply the eggs with oxygen". Their analysis consists of two parts: an analysis of the meaning of function attributions and a reconstruction of the train of thought underlying the search for functional explanations. Kuipers & Wisniewski's analysis of the meaning of function attributions (they call them "specific functional statements") falls within the scope of an etiological theory. According to this analysis function attributions of the form "the biological function of trait of organisms of type is " state that:

- (a<sub>1</sub>) of is a positive causal factor for ,
- (a<sub>2</sub>) is a positive causal factor for the reproduction and survival of ,
- (a<sub>3</sub>) both and were causally, i.e. evolutionary effective, for having (Kuipers & Wisniewski 1994: 382).

The train of thought underlying the search for a functional explanation starts with an explanation-seeking question of the form 'why do organisms of type have trait '?' (e.g. "why do male sticklebacks show systematic fanning movement?"). As a first step in answering this question one accepts as a hypothesis to be tested an "unspecified functional statement" of the form "trait of organisms of type is functional" (e.g., the systematic fanning movement is

functional”). The main point of the functional explanation is to establish a specification of this unspecified statement in the form of a function attribution of the form “the biological function of trait of organisms of type is ” (e.g. “the biological function of the systematic fanning movement of sticklebacks is to supply the eggs with oxygen”). Such a function attribution provides a direct answer to the question “what is the biological function of trait of organisms of type ?”.

According to Kuipers & Wisniewski this function statement might also be seen as an answer to the original explanation-seeking why-question:

Each direct answer to a question of the form [what is the biological function of trait b of organism of type a?]<sup>12</sup> may be regarded either as an answer to the corresponding question of the form [why do organisms of type a have trait b?] or as a sentence which entails such a statement (Kuipers & Wisniewski 1994: 384).

Kuipers & Wisniewski do not provide an argument for this thesis, but it is clear that they think that the specification of a function in itself accounts for the presence of the trait to which the function is attributed.

Kuipers & Wisniewski do not give references to biological literature. However, one might expect that their example of a functional explanation (“the biological function of the systematic fanning movement of stickleback is to supply the eggs with oxygen”) refers to the experiments Kristensen performed in the 1940s. Let us have a look at this example.<sup>13</sup> Male sticklebacks build a tubular nest and guard it with a complex pattern of behaviour. They alternate periods of swimming around the nest with periods as long as 30 seconds in which they stay before the nest in a slanting position, head down, moving their fins in a quick regular rhythm. Kristensen performed a series of experiments which showed that this behaviour has the causal role to supply the nest with oxygen. He showed that the eggs die if the male is removed from the nest and also if the nest is shielded from the fanning male with a watch glass. However, if oxygen rich water is directed to the nest by means of a tube, the eggs survive the removal of the male. Ventilation is needed because of the tubular nest, fish species who lay their eggs on leaves in running water do not need to ventilate the eggs. This example shows that Kuipers & Wisniewski are mistaken at two points. First, Kuipers & Wisniewski’s analysis of the meaning of biological function errs in defining biological function in evolutionary terms. Kristensen is concerned with the role and survival value of the fanning behaviour not with its evolution. Second, Kuipers & Wisniewski account of only a part of the insight provided by Kristensen’s explanation. They ignore the part which explains the need for ventilation by appeal to the tubular form of the nest. The question ‘why do male sticklebacks show systematic fanning move-

---

<sup>12</sup>I have substituted the formulae in Kuipers & Wisniewski’s quote by appropriate sentences

<sup>13</sup>As I couldn’t find the original literature I use Tinbergen’s (1976: 12) account of Kristensen’s experiments.

ment?’ is a typical type (4a) question which is answered by a design explanation. The attribution of the function to supply the nest with oxygen is but the first step in answering the question. In addition Kristensen explains why this function is needed by appeal to the tubular form of the nest.

### *Conclusion*

The accounts of functional explanation offered by Millikan, Neander and Kuipers & Wisniewski are inspired by a picture of functional explanations as consisting of a single function attribution in answer to a question of the form ‘why do .... organisms have [trait] ....?’. However, the explanations put forward by functional biologists seldom consists of a single function attribution and the accounts proposed by these philosophers leave much out of sight of what is achieved by functional explanations of the character of the item or behaviour to which the function is attributed. Function attributions are a first step in design and selection explanations and the etiological theories fail to account for the insights provided by the other steps. As I showed in chapter 6 one of the most interesting questions concerning functional explanations is: how can it be explanatory to compare real organisms with hypothetical organisms that may never have existed and may have played no role in the genesis of the trait to be explained. The etiological account ignores this question.

### **7.3.3 The normative role of function attributions**

Both Millikan and Neander claim as one of the main merits of the etiological theory that it can account for the alleged fact that the parts and behaviours of organisms are classified on the basis of their function. In this section I argue that the assumption that biologists classify the items and behaviours of organisms in terms of their function is wrong.

Millikan starts the first chapter of her *Language, Thought and Other Biological Categories* (1984) by claiming that the different things which are called ‘hearts’ belong to the same category because they have the same function:

That a heart is a heart certainly has something to do with pumping blood (Millikan 1984: 17)

However, as there are both diseased or malformed hearts that are unable to pump blood and things such as water pumps which are not hearts that are able to pump blood or that in fact pump blood (artificial hearts), the heart’s function cannot be something the heart actually does or is capable of doing.

It is not then the actual constitution, powers or dispositions of a thing that make it in a member of a biological category (Millikan 1984: 71)

Rather, what is relevant to being a heart is what it is “designed to” do or “supposed to” do. According to Millikan this notion of “designed to” or “supposed to” can be spelled out in a “naturalist, nonnormative and nonmysterious” way if ‘function’ is defined in historical terms:

My claim will be that it is the “proper function” of a thing that puts it in a biological category, and that this has nothing to do with its powers but with its history (Millikan 1984: 71).

Millikan repeats the idea that biological categories are historical categories in a paper published in 1986:

Biological categories are carved out not by looking at the actual structure, actual dispositions, or actual functions of the organ or system that falls within the category but by looking at (or speculating about) its history (Millikan 1986: 51)

Hearts, for example, may have many different forms (they may be large or small, they may be three-chambered or four-chambered) and they may also be unable to pump blood, yet, they are all hearts. They are hearts, at least according to Millikan, because they were reproduced by mechanisms that proliferated in the course of the evolutionary history due to the fact that they pumped blood. In the same way the other parts of organisms are classified on the basis of what they did that caused them to be selected.

Every body organ or system falls in the biological or physiological categories it does due to its historical connections with prior examples of kinds that have served certain functions or, typically, sets of functions. So whether or not it is itself capable of serving any of these functions, every organ or system is associated with a set of functions that are biologically “proper” to it, functions that helped account for the survival and proliferation of its ancestors. I call these functions “proper functions” of the organ or system (Millikan 1986: 52)

Millikan (1989b) talks of “function categories” instead of “biological categories” but the story remains the same: “function categories are *essentially* categories of things that need not fulfil their functions in order to have them” (p. 296, emphasis hers) and an analysis in terms of proper functions is the only one that is capable to account of this fact.

In the same vein, Neander (1991a: 180) claims that the etiological account of function is the only one that can account for “one of the most important theoretical roles of the notion [of function] in biology”, namely that “most biological categories are only definable in functional terms”. A definition of biological categories in terms of similarities in form does not work because biologists need categories that may include items that differ in form:

Biologists need a category that ranges over different species, and hearts are morphological diverse: fish have a single pump with one auricle, but amphibians and most other [sic!] <sup>14</sup> reptiles have a single pump

---

<sup>14</sup>Amphibians and reptiles are two different classes.

with only one auricle, and while many reptiles have the ventricle partly partitioned, only crocodiles, birds and mammals have the two separate ventricles (Neander 1991a: 180).

Moreover, the relevant notion of function must be a notion not of what an item is capable of doing but of what an item is supposed to do:

for the purpose of classifying hearts what matters is not whether the organ in question manages to pump blood, but whether that is what it is supposed to do. The heart that cannot perform its proper function (because it is atrophied, clogged, congenitally malformed, or sliced in two) is still a heart (Neander 1991a)

The etiological theory accounts for this ability by defining the proper function of an item in terms of its selection history. The definitions of ‘function’ provided by Cummins (1975), Wimsatt (1972) and Boorse (1976), on the other hand, fail to account for this role of the notion of function in classifying the items and behaviours.

The arguments of Millikan and Neander can be represented in the following scheme:

- (1) biological items and behaviours are categorized in terms of their function;
- (2) a biological category may include items that fail to perform their function or are unable to perform their function;
- (3) a biological category may include items that differ in form;
- (4) the features ad (2) and (3) can be accounted for if the categories are seen as historical categories;
- (5) it follows from (1) and (4) that function is to be defined in historical terms.

I argue that claim (1) is mistaken and that for that reason conclusion (5) does not follow, although (2), (3) and (4) are right.

Let me start by providing some counter examples against the claim that biological items are categorized in terms of their function. Perhaps all hearts have the function to pump blood, but there are many other biological categories that include items that differ in their function. A clear example is the category “tail”. The tails of sharks, bony fishes, tadpoles, crocodiles, beavers and whales have a propulsive function, the tails of cows and many other ruminants have the function to keep fly’s away, in many monkeys the tail has a function as a steering organ, some monkeys use the tail as a grasping organ as well, many mammals use their tail as a balancing organ, the hippopotamus uses its tail to spread its excrements and the tails of kangaroos have a supporting function.<sup>15</sup> Other examples are the categories ‘pharynx’, ‘wing’ and ‘limb’. In non-vertebrate chordates (such as tunicates and amphioxus) the pharynx has the function to filter food from water, in aquatic vertebrates the pharynx has a respiratory function. In most birds the

---

<sup>15</sup>Frogs, apes and man lack tails. The tail of birds is reduced. The function of the tail feathers that arise from the tail’s stump might have differs in different species. In many birds the tail feathers have a steering function during flight, the peacock’s tail has the function to attract females and to make them willing to mate.



wing has an important function in flight. Penguins are not able to fly and their wings have a function as a swimming organ. In most land vertebrates limb movements have a function in generating thrust. In salamanders, however, thrust is generated by means of undulations of the body and the limbs are stationary organs by means of which the push of the body movements is exerted on the ground. The forelimbs of lizards do have a function in generating thrust but their main function is in steering. The forelimbs of humans have a function in grasping objects but not in locomotion. The main function of the mole's forelimb is in digging.

My examples show that the categories biologists use to classify the parts of animal bodies do not only include items that differ in character (as Millikan and Neander emphasize) but also items that have different functions (as their first claim denies). I would agree with Millikan and Neander that many gross organs such as hearts, livers, kidneys and eyes have a similar function in many vertebrates, but this does not hold for such items as individual bones and muscles. I challenge the proponents of the etiological theory to come up with functional descriptions of categories like 'clavicle', 'humerus', 'thumb' or 'hand' which (i) applies to all the items that belong to this category in all the different classes of vertebrates, and (ii) is detailed enough to distinguish the items that belong to that category from all other parts of the body.

The fact that many biological categories include items with quite different functions shows that not all biological categories collect items in terms of their function. It does not follow, of course, that none does. Millikan and Neander might maintain that at least some of the categories used by biologists collect items in terms of their function, that those categories might include morphologically diverse items, as well as items that do not perform their function or are not able to perform their function and that those features are best explained by assuming that those categories collect items in terms of their selected effects ("proper functions"). I argue against this view that there is a better explanation of those features, namely that those categories collect items on the basis of their evolutionary origin (homology).

All biology students learn in their first year<sup>16</sup> to distinguish between three ways to classify the items and behaviours of organisms, namely:

- (a) on the basis of similarities in character (form and function<sub>1</sub>),
- (b) on the basis of their causal role (function<sub>2</sub>),
- (c) on the basis of common descent (homology).

All three types of criteria (note that 'selected effect' (function<sub>4</sub>) is not among them) have some use in biology and some categories are based on criteria of different types. For example, something is called a lung if it has a causal role in respiration (which is a criterion of the second type) and an invaginated structure (which is a criterion of the first type). However, the basic relation of *being the same thing* is homology. Two items in different individuals are (by defini-

---

<sup>16</sup>See for example: Keeton & Gould (1993: 521), Romer (1986: 9-11), Russell-Hunter (1968: 2)

tion) homologous (the same) if they are derived from a single item in a common ancestor. My heart is the same organ as your heart not because they are both supposed to pump blood but because they are derived from the same item of a common ancestor. Similarly, the lungs of mammals and the lungs of birds are the same organ not because they are both lungs, but because of their common evolutionary origin.

To avoid misunderstandings I should, perhaps, emphasize that my point is a point about categories not about names. Perhaps my heart is *called* a heart because it is supposed to pump blood, but my heart and your heart are the same organ not because they both are supposed to pump blood but because they have a common evolutionary origin. The names biologists use do not always reflect the categories. In many cases the same name is used for organs that belong to different categories. Insect hearts and vertebrates hearts are both *called* ‘hearts’ (perhaps because they are both supposed to pump blood), but as they are not homologous they belong to different categories. There are also many cases in which things with different names turned out to be homologous. The swim bladder of a teleost fish is a modified lung, despite the fact that lungs and swim bladders have different names, because the swim bladder originated as a lung in primitive osteichthyes (the common ancestors of both teleost fish and land vertebrates). The reason that the names do not reflect the categories is, of course, that many organs already had a name before their phylogenetic relationships were cleared up. If a category includes things with many different names biologists sometimes take resort to words which are seldom used in daily language. An example is the term ‘appendage’ which includes such things as fins, limbs, wings and flippers.<sup>17</sup>

The idea that the parts and organs of an organisms are to be classified primarily in terms of their function was abandoned by biologists in the beginning of the nineteenth century, long before Darwin. The term ‘homology’ was introduced by the English morphologist Richard Owen in 1843, but the idea that the parts and organs of members of different species are not only similar but in a certain sense “the same” goes back to the work of the French morphologist Étienne Geoffroy Saint-Hilaire (1772-1844). At the end of the eighteenth century the similarity between organisms belonging to different taxa was an important object of research in French morphology. The leading morphologist of that time, George Cuvier, maintained that those simi-

---

<sup>17</sup>For my purposes it is sufficient to define the notion of ‘homologous items’. Biologists also talk of ‘homologous characters’. The character of an item in certain individuals is homologous to the character of an item in other individuals if the items in question are homologous and the corresponding item of the most recent common ancestor had that character. The wings of bats and birds are homologous because they both originate from the forelimbs of a primitive terrestrial reptile-like ancestor. However, as the forelimbs of that common ancestor did not have a winged character, the winged character of the forelimbs of bats is not homologous to the winged character of the forelimbs of birds.

larities should be explained as the result of common functional requirements. Geoffroy argued against Cuvier that underneath the functional adaptations was a structural similarity that could not be explained by appeal to common functional requirements. He maintained that all animals are built in the same way and that the structural differences between organisms of different taxa are modifications of the same parts and organs in response to different functional requirements. Cuvier was quick to point out that the meanings of terms like ‘modification’ and ‘the same part or organ’ are unclear. Although Geoffroy’s work remained highly controversial he convinced the morphological community of his time that not all similarities between organisms could be explained on functional grounds. Two decades later, Owen (1843: 374-379) came up with a clear distinction between two ways to classify organs: homology and analogy. Owen defined “homologue” as “the same organ in different animals under every variety of form and function” and “analogue” as “a part or organ in one animal which has the same function as another part or organ in a different animal”. However, we had to wait until Darwin’s (1859) theory of common descent to clear up the vague ideas of ‘modification’ and of ‘the same organ’. According to this theory modification should be taken far more literally than was done before. Darwin himself did not delve into the notion of ‘sameness’, but he maintained that similarities between the same (i.e. homologous) item in members of different taxa can be explained as the result of common descent, and that the similarities between non-homologues items can be explained as the result of natural selection acting in the same direction. After Darwin, morphologists came to *define* ‘sameness’ (homology) in terms of a common origin. The first definitions of homology in terms of a common origin were given in 1870, by the English morphologist Lankester 1870<sup>18</sup> and, independently, by the German morphologist Gegenbaur.<sup>19</sup>

The definition of ‘sameness’ in terms of common descent (homology) is important in functional biology, first and foremost, because it enables biologists to say that a certain item has changed in character and/or has acquired a different causal role in the course of evolution. A famous example are the ossicles of the middle ear which were once part of the jaw of our fish-like ancestors and appear even earlier in the evolutionary history as part of the support of the gills of ancestral vertebrates. If in the course of the evolutionary history the character of a

---

<sup>18</sup>Actually, Lankester proposed to drop the term ‘homology’ altogether, because that term was also used to indicate relations that had nothing to do with common origin such as the relation between the appendages of different segments of an arthropod. He proposed to call “structures which are genetically related, in so far as they have a single representative in a common ancestor” “homogenous” instead (Lankester 1870: 36).

<sup>19</sup>The first edition of Gegenbaur’s *Grundzüge der Vergleichende Anatomie* was published in 1859, the genetic definition of homology appears in the second edition of 1870, after Gegenbaur had adopted Darwin’s theory of common descent. In this latter edition ‘homology’ is defined as “the relation which obtains between two organs which have had a common origin, and which have also a common embryonic history” (Gegenbaur 1870: 64).

certain item changed extensively it might be difficult to track the evolutionary origin of that item. Two useful criteria are the position relative to other organs and the embryonic origin.

Furthermore, as both the character and the causal role of an item might change in the course of the evolutionary history, the concept of homology enables biologists to put items that differ in character and / or causal role in the same category.

The concept of homology enables biologists to say that a sperm cell which does not fertilize an egg cell is a sperm cell and that a malformed hearts is a heart. This is because (in contrast to what Millikan and Neander take for granted) being a sperm cell (that is being the same as the parts which in other organisms are called “sperm cells”) has nothing to do with fertilizing egg cells. Whether something is a sperm cell or not depends on its ancestry and has nothing to do with its function. Similarly a malformed heart is a heart not because of some function it is supposed to perform but because it originates from another heart. The case is not different from the swim bladder. A swim bladder is a modified lung because it is derived from an ancestral lung and a malformed heart is a modified heart because it is derived from an ancestral heart.

Millikan and Neander take it for granted that biologists categorize items in term of their function. Then they pose a riddle: how could this be since items that belong to a certain category need not perform their function and need not even be able to perform their function. The etiological theory answers this riddle by defining function in historical terms. My answer has been that Millikan and Neander are mistaken in their initial assumption. Biologists classify items primarily in terms of homology. The riddle does not arise. Malformed hearts are hearts because they are homologous to other hearts, not because of their function.

At this point someone might want to interrupt and say “wait a moment, perhaps your appeal to homology shows how malformed hearts can be hearts, but you fail to account for the fact that hearts that are not able to pump blood still have the function to pump blood. In other words how do you account for the biologist’s ability to attribute functions to items that do not perform their function?”. My answer is consist of two parts. First, on my theory function attributions are generalizations about the causal role of the members of a certain homology-category in a certain group of organisms. Vertebrate hearts have the causal role to pump blood because this is how hearts contribute to the maintenance of the organism in those vertebrates that are able to circulate blood. Second, one should not exaggerate the importance of attributing functions to items that are not able to perform their function. The point of a function attribution is to tell us how a certain item or behaviour fits into the organism, not to tell us what malformed items should do.

Both Millikan and Neander tend to distinguish between ‘having a function’ and ‘serving a function’. Statements of the form ‘the function of ... is ....’ are used to express the functions an item or trait has, statements of the form ‘.... functions as ....’ are used to express the functions an item or trait serves. For example, Millikan says:

the definition of “proper function” is intended to explain what it is for an item to *have* a function or purpose, but not what it is for an item to function *as* something. Robert Cummins (1980, 1984) has given us a definition of function that is probably best construed as a theoretical definition [...] of “function as” in some contexts (Millikan 1989b: 293).

She adds:

A diseased heart may not be capable of pumping, of functioning *as* a pump, although it is clearly its function, its biological purpose, *to* pump, and a mating display may fail to attract a mate although it is called a “mating display” because its biological purpose is to attract a mate (Millikan 1989b: 294).

Similarly, Neander maintains that

There is a distinction between a trait *servicing* a function and *having* a function [...] it is the function of all kidneys, diseased or otherwise, to filter the blood, but if they are very diseased they will be incapable of performing, or *servicing*, this function (Neander 1991b: 465).

Such utterances betray a misunderstanding of the role of function attributions in functional biology. The point of a function attribution is not to tell us what a (possibly malformed) item should do,<sup>20</sup> but to tell us how a certain item fits into the organism. On the etiological theory the notion of ‘servicing a certain function’ is dependent on the notion of ‘having a certain function’. If a certain item has a selection history it has a function and it may perform that function or it may fail to perform it.<sup>21</sup> The functions which an item has are in a certain sense intrinsic to that item and this is why they are called *proper* functions.<sup>22</sup> However, in functional biology it is the other way round. A function is not something intrinsic to an item but a position in a system that performs a certain task. Function predicates are position-predicates and function attributions situate an item or behaviour into a system by telling us how that item or behaviour contributes to that system’s tasks by listing the subtasks performed by that item or behaviour. Statements which say that a certain item has a certain function or which say what the functions of a certain item are, are generalizations about the causal roles which the members of a certain category of homologous items perform in a certain group of animals. This means that to say that a certain item is not able to perform a certain function it has, is just another way of saying that that item is not able to perform the causal role performed by homologous items of other

---

<sup>20</sup>Neither are biologists interested in distinguishing functional and accidental *effects* as for instance Larry Wright (1973, Wright 1976) maintains. A function is a position-predicate

<sup>21</sup>Neander (1991b: 465) says that “a trait need not have a function in order to serve it”, but it remains unclear how on the etiological theory one can say that an item serves a function if that item does not have that function.

<sup>22</sup> Millikan (1993a: 31) claims that she has invented the combination “proper function” and that by adding the word “proper” in front of “function” she wanted to “contrast a thing’s ‘proper’ or *own* function with functions imposed on it or accidental to it” (note 1).

animals in the same group. Perhaps there is another item that performs that role or perhaps the position remains empty as a result of which the organism is probably not viable.

Millikan and Neander suggest that function attributions have two normative roles, namely to put items into a cross species category and to tell us what an item should do. I have argued that in functional biology the first role is performed by the notion of ‘homology’ and that the second role is unimportant in functional biology. I have also argued that the point of a function attribution is not to tell us what a (possible malformed) item should do but to situate an item in a system that performs a certain task. Millikan and Neander put the cart before the horse by defining ‘performing a function’ in terms of ‘serving a function’.

#### **7.3.4 Conclusion**

On the etiological account function attributions are normative and teleological. They tell us what an item should do or what it is supposed to do and they do so on the basis of what that item is for (that is why it was brought about—why it was selected). I have argued that this normative and teleological concept of function does not apply to the term ‘function’ as this term is used in functional biology. The point of function attribution in functional biology is to position an item in a system, not to say what it should do.

That the etiological theory does not apply to talk of functions in functional biology is shown by the following considerations. First, when supporting function attributions biologists do not provide the kind of evidence that is needed to draw conclusions about why a certain item, behaviour or trait was selected in the past. Second, the way in which biologists appeal to functions in explanations is quite different from the way in which such appeals should be used according to the etiological theory. On the etiological account function attributions are intrinsically explanatory in that they need not be combined with other statements to tell us why a certain trait is present in the place where it is present. Biologists use function attribution in capacity, design and selection explanations. Both design and selection explanations explain in a certain sense why a trait is present. In both kinds of explanations start by attributing a function to the item concerned. This function attribution is the first step of the explanation, not the complete explanation. In the case of a design explanation the next part says that the character which the item has is useful because that function is better performed if the item is the way it is than in some other conceivable way. In the case of an evolutionary explanation the next part says that the character which the item has evolved because variants having that character performed that function better than competing variants. In both cases the function attribution is not intrinsically explanatory but yields an explanation only when combined with another statement. The function attribution is not dependent on this second statement. Third, the claim of Millikan and Neander that functional biologists need a normative notion of function in order to create interspecies categories that unite items that differ in form and that may contain items that do not per-

form their function or are not able to perform their function turned out to be untrue. Biologists may use the notion of 'homology' to create such interspecies categories.

I draw the conclusion that the notion of proper function as this notion was invented by Neander and Millikan does not apply to the use of the term 'function' in functional biology and is of no help to understand the explanatory practice in that discipline.

