Function Without Purpose:

The Uses of Causal Role Function in Evolutionary Biology

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ABSTRACT: Philosophers of evolutionary biology favor the so-called "etiological concept" of function according to which the function of a trait is its evolutionary purpose, defined as the effect for which that trait was favored by natural selection. We term this the selected effect (SE) analysis of function. An alternative account of function was introduced by Robert Cummins in a non-evolutionary and non-purposive context. Cummins's account has received attention but little support from philosophers of biology. This paper will show that a similar non-purposive concept of function, which we term causal role (CR) function, is crucial to certain research programs in evolutionary biology, and that philosophical criticisms of Cummins's concept are ineffective in this scientific context. Specifically, we demonstrate that CR functions are a vital and ineliminable part of research in comparative and functional anatomy, and that biological categories used by anatomists are not defined by the application of SE functional analysis. Causal role functions are non-historically defined, but may themselves be used in an historical analysis. Furthermore, we show that a philosophical insistence on the primary of SE functions places practicing biologists in an untenable position, as such functions can rarely be demonstrated (in contrast to CR functions). Biologists who study the form and function of organismal design recognize that it is virtually impossible to identify the past action of selection on any particular structure retrospectively, a requirement for recognizing SE functions.

KEY WORDS: Function, natural selection, anatomy, homology.

1. INTRODUCTION

Philosophical analyses of the concept of biological function come in three kinds. One kind defines the function of a given trait of an organism in terms of the history of natural selection which ancestors of the organism have undergone. In this account the function of a trait can be seen as its evolutionary purpose, with

Biology and Philosophy 9: 443–469, 1994.

purpose being imbued by selective history. A second approach is non-historical, and identifies the function of a trait as certain of its current causal properties. The relevant properties are seen either as those which contribute to organism's current needs, purposes, and goals (Boorse 1976) or those which have evolutionary significance to the organism's survival and reproduction (Ruse 1971; Bigelow and Pargetter 1987). A third approach has been articulated and defended by Robert Cummins (1975, 1983), mostly in application to psychological theory. Cummins's view is unique in that neither evolutionary nor contemporary purposes or goals play a role in the analysis of function. It has received little support in the philosophy of biology, even from Cummins himself. Nevertheless, we will show that the concept is central to certain ongoing research programs in biology, and that it is not threatened by the philosophical criticisms usually raised against it. Philosophers' special interests in purposive concepts can lead to the neglect of many crucial but non-purposive concepts in the science of biology.

Karen Neander recently and correctly reported that the selective view of function is "fast becoming the consensus" (Neander 1991, p. 168). Larry Wright showed in his canonical (1973) paper on selective function that an intuitively pleasing feature of the view is that citing a trait's function would play a role in explaining how the trait came to exist. Concepts of function similar to Wright's were hinted at by the biologists Francisco Ayala (1970) and G.C. Williams (1966), and later endorsed by the philosophers Robert Brandon (1981; 1990), Elliott Sober (1984), Ruth Millikan (1989), and Karen Neander (1991), among others. (For a good review of the history of philosophical discussions of function see Kenneth Schaffner, 1993, chapter 8.)

The evolutionary, selective account of function is commonly termed the "etiological concept" since functions are individuated by a trait's causal history. In the present context the term "etiological" may lead to confusion, so we will refer rather to the *selected effect* (SE) account of function. The Cummins style of account will be designated the *causal role* (CR) account (following Neander 1991, p. 181).

Given the consensus in favor of SE function among philosophers of biology, it is surprisingly difficult to find an unequivocal rejection of Cummins's alternative. This may stem from a recognition that some areas of science (medicine, physiology, and perhaps psychology) require other kinds of function concepts. It does seem generally accepted, however, that SE function is the concept uniquely appropriate *to evolutionary biology*. It is this position which we will attempt to refute.

Ruth Millikan (1989) and Karen Neander (1991) have recently presented arguments in favor of selected effect concepts of biological function. We will pay special attention to these papers for two reasons. First, they express positions on the nature of philosophical analysis which we find valuable, and which we will use in defending CR function. Second, they examine Cummins's account of function in detail. Some of the ideas they develop are shared with other advocates of SE function, and many are novel; all are worthy of analysis.

(Unless otherwise stated, all references to Millikan and Neander will be to those papers.)

Millikan examined the source of the criticisms which philosophers had made against the SE theory, and found them to be based in the philosophical practice of conceptual analysis. She declared this practice "a confused program, a philosophical chimera, a squaring of the circle ..." among other crackling critiques (p. 290). The search for necessary and sufficient conditions for the common sense application of terms was not what Millikan was about. Neander similarly rejected conceptual analysis of ordinary language as the goal of the philosophical analysis of function. Indeed, in rereading the debates on function of the 1970s, one is struck by the concern shown by philosophers for consistency with ordinary language. Millikan and Neander replace the old style of ordinary language analysis with somewhat different alternatives. Millikan was interested in a *theoretical definition* of the concept of function, a concept which she labels "proper function". Neander instead focussed on a conceptual analysis, but not the traditional kind based on ordinary language. Rather, Neander intended to analyze *specialists*' language – in this case the usage of the term *function* in the language of evolutionary biology. "What matters is only that biologists implicitly understand 'proper function' to refer to the effects for which traits were selected by natural selection" (p. 176).[1] While each writer intended the analysis of function to be relativized to a theory (rather than to ordinary language), Neander intended the relevant theory to be evolutionary biology, while Millikan located her analysis in the context of her own research project involving the relations among language, thought, and biology (Millikan 1984, 1993).

While the intended status of their resulting analyses differed, Millikan's and Neander's approaches had similar benefits for the SE analysis of function (and also, as we will presently argue, for the CR analysis of function). Both approaches tied function analyses to actual theories, in this way eliminating many ordinary-language based counterexamples to SE function. Theoretical definitions, such as "Gold is the element with atomic number 79," need not match ordinary usage, but instead reflect current scientific knowledge about the true nature of the subject matter. The use of bizarre counterfactuals such as Twin Earth cases and miraculous instantaneous creations of living beings (e.g. lions) were a mainstay of earlier criticisms of SE function. These kinds of cases are irrelevant to evolutionary theory and to the vocabulary of real world evolutionary scientists. Appeals to preDarwinian uses of the term 'function' (e.g. William Harvey said that the function of the heart was to pump blood) are equally irrelevant. After all, Harvey didn't know the atomic number of gold any more than he knew the historical origin of organic design. Nonetheless gold is (and was) the element with atomic number 79, and (by the SE definition) the heart's blood-pumping function is constituted by its natural selective history for that effect.

We fully approve of these moves. Taking the contents of science more seriously than is philosophically customary is exactly what philosophers of science ought to be doing. We will not question the philosophical adequacy of Millikan's or Neander's approaches, nor their defenses of SE theory against its philosophical critics. We will, however, call into question the common SE functionalist's belief that evolutionary biology is univocally committed to SE function. We will show that the rejection of ordinary language conceptual analysis immunizes Cummins-style CR function against some very appealing philosophical critiques – critiques expressed by Millikan and Neander themselves. We will show that a well articulated causal role concept of function is in current use in biology. It is as immune from Millikan's and Neander's critiques of CR function as their own SE accounts are from ordinary language opposition.

The field of biology called functional anatomy or functional morphology explicitly rejects the exclusive use of the SE concept of function. To be sure, there are other biological fields in which the SE concept is the common one – ethology is an example. The most moderate conclusion of this semantic observation is only a plea for conceptual pluralism, for the usefulness of different concepts in different areas of research. But further conclusions will be stronger than mere pluralism. We will defend CR function from philosophical refutation. We will show that a detailed knowledge of the selective history (and so the SE function) of specific anatomical traits is much more difficult to achieve than one would expect from the intuitive ease of its application. Finally, we will demonstrate the ineliminability of CR function from certain key research programs in evolutionary biology.

2. ADAPTATION AND SELECTED EFFECT FUNCTIONS

First, a specification of the selected-effect concept of function:

> The function of *X* is *F means*
> *(a) X* is there because it does *F*,
> *(b) F* is a consequence (or result) of *X*'s being there. (Wright 1973, p. 161. Variables renamed for consistency.)

Wright intended his analysis to apply equally to intentional and natural selection. When the context is restricted to evolution, and natural selection accounts for the "because" in (*a*), something like Neander's definition results.

> 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. (Neander, p. 174. Cf. Millikan, p. 228.)

Not surprisingly, there are very closely related concepts within evolutionary biology, particularly the concept of *adaptation*. During the 20th century there has been some semantic slippage surrounding the term. Describing an organic trait as adaptation has meant either 1) that it benefits the organism in its present environment (whatever the trait's causal origin), or 2) that it arose via natural selection to perform the action which now benefits the organism. That is, the term adaptation has sometimes but sometimes not been given an SE, historical meaning. G.C. Williams gave a trenchant examination to the concept of adaptation, referring to it as "a special and onerous concept that should be used only where it is really necessary" (1966, p. 4). In particular, Williams thought it important to distinguish between an adaptation and a fortuitous benefit. These ideas inspired the "historical concept" of adaptation, according to which the term was restricted to traits which carried selective benefits and which resulted from natural selection for those benefits. Terms such as "adaptedness" or "aptness" came to be used to designate current utility, covering both selected adaptations and fortuitous benefits (Gould and Vrba 1982). The onerous term adaptation was reserved for traits which had evolved by natural selection. Robert Brandon recently declared the historical definition of adaptation "the received view" (1990, p. 186). Elliott Sober described the concept as follows:

> *X* is an adaptation for task *F* in population *P* if and only if *X* became prevalent in *P* because there was selection for *X*, where the selective advantage of *X* was due to the fact that *X* helped perform task *F*. (Sober 1984, p. 208. Variables renamed for consistency.)

Sober's task *F* is precisely what SE theorists would call the function of trait *X*. Moreover, Williams, Sober, and Brandon, like Millikan and Neander, all refer to a benefit produced by *X* as the function of *X* just when that benefit was the cause of selection for *X*. In other words, for a trait to be an adaptation (historically defined) is *precisely* for that trait to have a function (selected-effect defined). A trait *is* an adaptation when and only when it *has* a function. The two terms are interchangeable. If a law were passed against the SE concept of function, its use in biology could be fully served by the historical concept of adaptation.

3. FUNCTIONAL ANATOMY AND CAUSAL ROLE FUNCTIONS

The major philosophical competitors to the SE concept of function refer to contemporary causal powers of a trait rather than the causal origins of that trait. Most of these non-selective analyses also advert to the (contemporary) purposes or goals of a system. The goals are presumed knowable prior to addressing the question of function, so that identifying a trait's function amounts to identifying the causal role played by the trait in the organism's ability to achieve a contemporary goal. Robert Cummins (1975) introduced a novel concept of function in which the specification of a real, objective goal simply dropped out. Since neither current benefits and goals nor evolutionary purposes were relevant, evolutionary history was also irrelevant to the specification of function. Cummins focused on functional analysis, which he took to be a distinctive scientific explanatory strategy. In functional analysis, a scientist intends to explain a *capacity* of a system by appealing to the capacities of the system's component parts. A novel feature of Cummins's analysis is that capacities are not presented as (necessarily) goals or purposes of the system. Scientists choose capacities which they feel are worthy of functional analysis, and then try to devise accounts of how those capacities arise from interactions among (capacities of) the component parts. The functions assigned to each trait (component) are thus relativized both to the overall capacity chosen for analysis and the functional explanation offered by the scientist. Given some functional system *s*:

> *X* functions as an *F* in *s* (or: the function of *X* in *s* is to *F*) relative to an analytical account *A* of *s*'s capacity to *G* just in case *X* is capable of *F*-ing in *s* and *A* appropriately and adequately accounts for s's capacity to G by, in part, appealing to the capacity of *X* to *F* in *s*. (Cummins 1975, p. 762. Variables renamed for consistency.)

Cummins's assessments of function do not depend on prior discoveries of the purposes or goals served by the analyzed capacities, as do other non-SE theories of function.[2] This creates a problem for Cummins. Prior, extrinsic information about system goals would narrow the list of possible functions to those which *can* contribute to the already-known goal. With no extrinsic criteria to delimit the list of relevant causal properties, Cummins needs some other method of constraining the list of causal powers which are to be identified as functions. Indeed, the problem of constraint gives rise to the most frequent challenge to Cummins's approach; examples will be discussed below. Critics find it easy to devise whimsical "functional analyses" which trade on the lack of external constraint, and which appear to show Cummins's definition of function to be too weak to distinguish between functions and mere effects. To make up for the loss of the external constraint of goal-specificity, Cummins offers internal criteria for assessing the scientific significance of a proffered functional analysis. A valuable (as opposed to a trivial) functional analysis is one which adds a great deal to our understanding of the analyzed trait. In particular, the scientific significance or value of a given functional analysis is judged to be high when the analyzing capacities cited are *simpler* and *different in type* from the analyzed capacities. An analysis is also of high value when it reveals a high degree of *complexity of organization* in the system. Functional analyses of very simple systems are judged to be trivial on these criteria. "As the role of organization becomes less and less significant, the [functional] analytical strategy becomes less and less appropriate, and talk of functions makes less and less sense. This may be philosophically disappointing, but there is no help for it" (ibid., p. 764). Philosophical disappointment in this messy outcome could be alleviated by requiring an independent specification of goals and purposes prior to any functional analysis. But, as we shall see, such philosophical serenity would carry a high cost for scientific practice.

Cummins's account is of special interest because of its close match to the concepts of function used within functional anatomy. His emphasis on causal capacities of components and the absence of essential reference to overall systemic goals is shared by the anatomists. This is somewhat surprising, since Cummins's chief interest was in functional analysis in psychology. He did assert (without documentation) that biology fit the model, but has written nothing else on biological function (ibid, p. 760). Other philosophers have recognized non-SE uses of function in biology. Boorse cited physiology and medicine as supporting his goal oriented causal role analysis (Boorse 1976, p. 85). Brandon acknowledged the non-historical use in physiology, but disapproved. "I believe that ahistorical functional ascriptions only invite confusion, and that biologists ought to restrict the concept [to] its evolutionary meaning, but I will not offer further arguments for that here" (Brandon 1990, p. 187 n. 24). The wisdom of this counsel will be assessed below.

The classic account of the vocabulary of functional anatomy was given by Walter Bock and Gerd von Wahlert (1965). These authors referred to "the form-function complex" as an alternative to the customary contrast between the two – form *versus* function. This was not merely an attempt at conciliation between advocates of the primacy of form over function and advocates of the converse. Rather, it was a reconceptualization of the task of anatomists, especially evolutionary anatomists. Bock and von Wahlert stated that the form and the function of anatomical traits were *both* at the methodological base, the lowest level, of the functional anatomist's enterprise. The rejection of the contrast between form and function (its replacement with the form-function complex) amounted to a rejection of the SE concept of function itself. In the functional anatomist's vocabulary, form and function were both observable, experimentally measurable attributes of anatomical items (e.g. bones, muscles, ligaments). Neither form nor function was inferred via hypotheses of evolutionary history. The form of an item was its physical shape and constitution. The function of the same item was "all physical and chemical properties arising from its form ... providing that [predicates describing the function] do not mention any reference to the environment of the organism" (ibid. p. 274). This denial of reference to environment eliminates not only the SE concept of evolutionary function, but also the non-historical notion of function as a contribution to contemporary adaptedness or other goal-achieving properties. These implications were intended. Concepts involving biological importance, selective value, and (especially) selective *history*, (and therefore Darwinian adaptation), are all at higher and more inferential levels of analysis than that of anatomical function. The intention was not to ignore these higher levels, but to provide an adequate functional-anatomic evidentiary base from which the higher levels can be addressed.

The level of organization above the form-function complex is the character complex. A character complex is a group of features (typically anatomical items themselves seen as form-function complexes) which interact functionally to carry out a common *biological role*. When we reach the biological role, we find ourselves in more familiar Darwinian territory. The biological role of a character complex (or of a single trait) is designated by "that class of predicates which includes all actions or uses of the faculties (the form-function complex) of the feature by the organism in the course of its life history, provided that these predicates include reference to the environment of the organism" (ibid. 278). At last we find reference to that organism/environment relation which constitutes adaptedness or fitness. The further inference to the SE advocate's concept of evolutionary function involves an additional assertion that the trait's present existence is not fortuitous, but the result of a history of natural selection controlled by the same benefits which the trait now confers in its biological role.

So a chain of inference from anatomical function to evolutionary function involves several steps and additional (i.e. non-anatomical) kinds of data. An evolutionist may not feel the need to start from the anatomical base, of course. Given a simple trait with a known biological role, the evolutionist might feel justified in ignoring anatomical details. But in highly integrated character complexes with long evolutionary histories (e.g. the vertebrate jaw or limb) it is arguably perilous to ignore anatomical function (Wake and Roth 1989).

In one way, Bock and von Wahlert's concept of function is even more radical than Cummins's. Cummins assigns functions only to those capacities of components which are actually invoked in a functional explanation, those which are believed to contribute to the higher level capacity being analyzed. Bock and von Wahlert include *all possible* capacities (causal powers) of the feature, given its current form. Some of these capacities are utilized and some are not. Both utilized and unutilized capacities are properly called functions. The determination of unutilized functions may require experiments which are ecologically unrealistic, but this is still a part of the functional anatomist's job. Bock and von Wahlert suggest that a functional anatomist might want to experimentally study the functional properties of a muscle at 40 percent of its rest length, even when it is known that the muscle never contracts more than 10 percent during the life history of the organism (1965, p. 274). The relevance of unutilized functions depends on the sort of question being asked. Other anatomists attend primarily to utilized functions. "The study of function is the study of how structures are used, and functional data are those in which the use of structural features has been directly measured. Functions are the actions of phenotypic components" (Lauder 1990, p. 318). Bock's special interest in unutilized functions comes from his interest in the phenomenon of preadaptation (or exaptation) (Bock 1958; Gould and Vrba 1982). It is often the unutilized functional properties of traits which allow them to be "coopted" and put to new uses when the evolutionary opportunity arises.

Apart from the issue of unutilized functions, Cummins's concept of function matches the anatomists'. Functional anatomists typically choose to analyze integrated character complexes which have significant biological roles. An anatomist might choose to analyze the crushing capacity of the jaw of a particular species. Cummins's s is the jaw, and G the capacity to crush things. In the analysis the anatomist might cite the capacity of a particular muscle (component X) to contract, thereby bringing two bones (other components of s) closer together. If the citation of that capacity of X fits together with other citations of component capacities into an "appropriate and adequate" account of the capacity of the jaw to crush things, then it is proper on Cummins's analysis to say that the function (or a function) of that muscle is to bring those two bones closer together.

We can also apply Cummins's evaluative suggestions to such an analysis. In a valuable functional analysis, the analyzing capacities will be simpler and/or different in type from the analyzed, and the system's discovered organization will be complex. Suppose the capacity to crush of the hypothetical jaw derives from the extremely simple fact that objects between the two bones are subjected to the brute force of muscle *X* forcing the bones together. Here the "organization" of the system is almost degeneratively simple, and the force of the muscle hardly simpler or different in kind from the crushing capacity of the jaw. A functional analysis of very low value. On the other hand, suppose that the jaw is a complex of many elements, muscle *X* is much weaker than the observed crushing capacity, the crushing action itself is a complex rolling and grinding, the action of muscle *X* moves one of its attached bones into a position from which the bone can support one of the several directions of motion, and that this action must be coordinated with other muscle actions so that it will occur at a particular time in the crushing cycle. Here *X*'s function is much simpler than the analyzed capacity, is different in kind (moving in one dimension in contrast to the three dimensional motion of the jaw) and the organization of components which explains jaw action is complex indeed. A functional analysis of high value.

As in Cummins's account, functional anatomical analyses make no essential reference to the benefits which the analyzed capacity might have, nor to the capacity's evolutionary goal or purpose. While the decision to analyze the jaw may have been motivated by a knowledge of its biological role (the fish eats snails), that knowledge plays no part in the analysis itself. The biological role of the jaw system does not influence the function which the component muscle is analyzed to have. The discovery of a new biological role (perhaps the jaws are also used in producing mating sounds) may suggest new situations under which to examine the function of muscle *X*, but even such a discovery would not alter the estimated function(s). Even more remote from functional analysis are hypotheses regarding selective pressures, or any other explanations of why the jaw has its present capacities. Neither Cummins nor a functional anatomist intends to explain the origin of a muscle when stating its function in the jaw.

4. CRITICISMS OF CAUSAL ROLE FUNCTION

The purpose of this section is to evaluate some critical commentary on Cummins's concept of causal role function, and to assess the extent to which it might call into question the use of CR function in functional anatomy. In Millikan's case at least, it would be inaccurate to read the comments as a general critique of CR function. She has herself made use of Cummins-like concepts in other contexts (1993, p. 191). In (1989) her intent was to discuss purpose and dysfunction, concepts to which CR function doesn't apply. Nevertheless, in discussing purposive function both Millikan and Neander make claims for its importance which would appear to subordinate CR function to SE function. It is these implications which we must examine.

Millikan and Neander each amply demonstrated that the most common philosophical objections to SE function lost their force when the theory of SE function was understood not as ordinary language conceptual analysis, but as an explication of current scientific theory. Their own criticisms of CR function, however, seem to assume that the opposition theory is exactly what they deny their own theories to be – a good old-fashioned ordinary language conceptual analysis. If CR function theory is treated as an explication of the practices of science, those criticisms fail in exactly the way Millikan and Neander show their own philosophical opponents to fail. In other words, their criticisms of CR function rely on giving SE and CR functions unequal treatment – one as theoretical definition and the other as ordinary language analysis.

First, a minor example of the unequal treatment of the SE and CR theories. Millikan, Neander, and Sober each point out that Cummins's CR theory counterintuitively allows reference to "functions" in non-biological (or biologically uninteresting) systems. These are examples of the whimsical Cummins functions mentioned above, made possible by Cummins's abandonment of goal specification. Millikan offers the "function" of clouds as making rain in the water cycle (p. 294), Neander the "function" of geological plate movements in tectonic systems (p. 181), Sober the "function" of the heart (via its mass) to allow an organism to have a certain weight (1993, p. 86). These are indeed counterintuitive results. But the criticism simply does not apply to the real world of scientific practice. By Cummins's own evaluative criteria (and given the facts of the real world) functional analyses of these systems would have no interest. Analyzing capacities would not be significantly simpler or different in type from analyzed capacities (are plate movements simpler than earthquakes?) nor would the system's organization be notably complex. (The geological structures which result in earthquakes might be complex, but the "organization" of these structures *vis a vis* their explanation of the capacity of the earth to quake is not.) Real world scientists do not perform Cummins-like functional analyses outside the organic and artifactual domains (or on non-organized properties like body weight). Millikan herself elegantly explains why this should be so. In defense of SE function she observed that the only items *in our world* with interesting Cummins functions are items with proper (SE) functions (p. 293). In our world, all of the interesting causal role functions have a history of natural selection. Instant lions would have no such history, but they do not exist in our world. Earthquakes and rainfalls are in our world, but have no such history, and so no complex functional organization. Such imaginative counterexamples might be telling against conceptual analyses of ordinary language function concepts. But they count neither for nor against CR or SE function theories, so long as those theories are *each* seen as science-based rather than conceptual analyses of ordinary language.

A second and more complex criticism involves the so-called "normative" role of function ascriptions and the problem of pathological malformations of functional items. Neander considers it the responsibility of a theory of biological function to categorize organic parts such that the categories are able to "embrace both interspecies and pathological diversity" (Neander p. 181). Millikan endorses at least the latter, and other SE theorists have been concerned with variation and dysfunction as far back as Wright (1973, pp. 146, 151). According to these theorists, only SE function can categorize parts into their proper categories irrespective of variation and malformation. It does so by defining "function categories." CR function (like other non-historical theories) cannot define appropriate function categories, and so is unable both to identify diseased or malformed hearts as hearts, and to identify the same organ under different forms in different species.

On pathology, Millikan points out that diseased, malformed, and otherwise dysfunctional organs are denominated by the function they would serve if normal. "The problem is, how did the atypical members of the category that cannot perform its defining function *get* into the same function category as the things that actually can perform the function?" (Millikan p. 295. *Cf.* Neander p. 180–181.) A CR analysis of a deformed heart which cannot pump blood obviously cannot designate its *function* as pumping blood, since it doesn't have that causal capacity. On the other hand, even the organism with the malformed heart has a selective history of ancestors which survived because *their* hearts pumped blood. So the category "heart" which ranges over both healthy and malformed organs must be defined by SE, not CR, function. On interspecies diversity of form:

> The notion of a 'proper function' is the notion of what a part is *supposed* to do. This fact is crucial to one of the most important theoretical roles of the notion in biology, which is that most biological categories are only definable in functional terms. For instance, 'heart' cannot be defined except by reference to the function of hearts because no description purely in terms of morphological criteria could demarcate hearts from non-hearts. (Neander p. 180)

The claim that biological categories must be defined by SE functional analyses is a significant challenge to CR functional analysis. If SE function is truly the basis of biological classification, then CR functional analyses must either 1) deal with undefined biological categories, or 2) depend on prior SE functional analyses for a classification of biological traits. We will now argue that SE functionalists are simply mistaken in this claim. SE functions are not the foundation for the classification of basic biological traits. To be sure, CR function does not define basic categories either. The classifications come from a third, non-functional source.

Consider Neander's claim that "most biological categories are only definable in functional terms." Hardly a controversial statement, especially in the philosophical literature. Nevertheless it is utterly false. Perhaps most *philosophically interesting* biological categories are functional (depending on the interests of philosophers). But a glance in any comparative anatomy textbook rapidly convinces the reader (and appalls the student) with the ocean of individually classified bones, ligaments, tendons, nerves, etc., etc. We do not mean simply to quibble over a census count of functional versus anatomical terms in biology. Rather, we wish to argue for the importance, often unrecognized by philosophers, of anatomical, morphological, and other non-purposive but theoretically crucial concepts in biology. In this case the relevant conceptual apparatus belongs to the field of comparative anatomy.

Many body parts can be referred to either by anatomical or functional characterizations. The human kneecap is a bone referred to as the patella. 'Kneecap' is a (roughly) functional characterization; a kneecap covers what would otherwise be an exposed joint surface between the femur and the tibia. 'Patella' is an anatomical, not a functional, characterization. The patella in other vertebrates need not "cap" the "knee" (for example, in species in which it is greatly reduced) and some species might conceivably have their knees capped by bones not homologous to the patella. The category *patella* is not a function category but an anatomical category. *Kneecap* is a function category. To call a feature a wing is to characterize it (primarily) functionally. To call it a vertebrate forelimb is to characterize it anatomically. The wings of butterflies and birds have common functions but no common anatomy.

The concept of *homology* is central to the practice of evolutionary biology. It is arguably as important as the concept of *adaptation*. Anatomical features which are known (at their naming) to be homologically corresponding features in related species are given common names. A traditional Darwinian definition of homology refers to the common derivation of body parts: "A feature in two or more taxa is homologous when it is derived from the same (or a corresponding) feature of their common ancestor" (Mayr 1982, p. 45). This definition has recently come under scrutiny, and a more openly phylogenetic definition (most clearly explicated by Patterson 1982) is often preferred. (See Hall 1984 for discussions of homology.) On this concept, homologous traits are those which characterize natural (monophyletic) clades of species. Thus, the wing of a sparrow is homologous to the wing of an owl because the character 'wing' (recognized by a particular structural configuration of bones, muscles, and feathers) characterizes a natural evolutionary clade (birds) to which sparrows and owls belong. Wings of sparrows are not homologous to wings of insects because there is no evidence that a clade consisting of birds + insects constitutes a natural evolutionary unit. This remains true even if 'wing' is characterized functionally, as 'flattened body appendage used in flight.' Whatever the favored definition of homology, one feature of the concept is crucial: *the relation of homology does not derive from the common function of homologous organs*. Organs which are similar in form not by virtue of phylogeny but because of common biological role (or SE function) are said to be *analogous* rather than homologous. The wings of insects and birds are analogous – they have similar SE functions, and so evolved to have similar gross structure. The forelimbs of humans, dogs, bats, moles, and whales, and each of their component parts – humerus, carpals, phalanges – are homologous. Morphologically they are the same feature under different forms. Functionally they are quite distinct.[3]

Comparative anatomy, morphology, and the concept of homology predate evolutionary biology. They provided Darwin with some of the most potent evidence for the fact of descent with modification. (This alone demonstrates the importance of other-than-adaptational factors in evolutionary biology.) So the evolutionary definition of homology mentioned above is a theoretical definition. As with other theoretical definitions, it is subject to sniping from practitioners of conceptual analysis. A philosopher could argue (pointlessly) that "homology" cannot *mean* "traits which characterize monophyletic clades," since many 1840s biologists knew that birds' wings were homologous to human arms but disbelieved in evolution (and so disbelieved that humans and birds shared a clade). SE advocates' usual reply to the William Harvey objection is applicable here. Just as Harvey could see the marks of biological purpose without knowing the origin or true nature of biological purpose, preDarwinian anatomists could see the marks of homology without knowing the cause and true nature of homology itself.

But if anatomical items are not anatomically categorized by function, how are they identified? There are several classical (preDarwinian) ways of postulating homologies. Similarity in structure may suggest homology. Second, the "principle of connectedness" states that items are identical which have identical connections or position within an overall structural pattern. Third, structurally diverse characters may be recognized as homological by their common developmental origin in the embryo. Mammalian inner ear bones and reptile jaw bones can be seen (if you look *very* carefully) to arise out of common embryological elements. If you look closer yet, the reptilian jaw bones can be seen to be homologous to portions of the gill arches of fish. The important point is that if anatomical parts had to be identified by their common biological role or SE function, all interesting homologies would be invisible. Darwin would have lost crucial evidence for descent with modification.

The fact that anatomical or morphological terms typically designate homologies shows that they are not functional categories. There is some casual use of anatomical terms by biologists, especially when formal analogies are striking. Arthropods and vertebrates each have "tibias" and "thoraxes" but the usage is selfconsciously metaphorical between the groups; dictionaries of biology have two separate entries. The anatomical unit is, e.g., the *vertebrate tibia.*

There is indeed a set of important biological categories which group organic traits by their common biological roles or SE functions. The most general of these apply to items which have biological roles so broadly significant in the animal world that they are served by analogous structures in widely divergent taxa. Among such concepts are gut (and mouth and anus), gill, gonad, eye, wing, and head (but not skull, an anatomical feature only of vertebrates). Also in the group is that all-time favorite of philosophical commentators on function – the heart. These are presumably what Neander had in mind as typical "biological categories", and they are reasonably regarded as "function categories" in Millikan's sense. They are analogical (as opposed to homological) in implication. Narrower function categories occur also (e.g. kneecap and ring finger) but are of limited scientific interest.

The importance of the above function categories comes from the fact that they all apply to features which result from evolutionary convergence – the selective shaping of non-homologous parts to common biological roles. It might be argued that homologous organs or body parts can be categorized by function as well. For example, *kidney* is not listed among the above function terms. Kidneys do all perform similar functions, but properly-so-called (i.e. by scientific biological usage) they exist only as homologs in vertebrates. Analogous organs exist in mollusks, but are only informally called kidneys. "The excretory organs are a pair of tubular metanephridia, commonly called kidneys in living species" (Barnes 1991, p. 345). But isn't 'kidney' a function category? Well, kidneys do all perform common functions (in vertebrates). But they are also homologous. This means that we could identify all members of the category 'kidney' by morphological criteria alone (morphological connectedness and developmental origin). So, at least in that sense, 'kidney' is not a function category, or at least not *essentially and necessarily* a function category. Unlike hearts, kidneys can be picked out by anatomical criteria alone. Identifying the function of kidneys amounts to discovering a (universal) functional fact about an anatomically defined category.

Even full-fledged, cross-taxon functional categories like 'heart' can often be given anatomical readings within a taxon. That is, *the vertebrate heart* can be treated as an anatomical category like the kidney. Vertebrate hearts, like kidneys, do have common functions. But they are identifiable within the taxon by their anatomical features alone. For example, mammalian heart muscle (as well as that of many other vertebrates) has a unique structure with individual cardiac muscle cells connected electrically in specialized junctional discs. The histological structure of mammalian cardiac muscle could not be mistaken for any other tissue. Thus, it is incorrect to suggest that hearts that characterize natural evolutionary clades cannot be characterized by anatomical criteria. This situation will obtain just when all of the members of the functional category are homologous within the taxon. Since all *vertebrate* hearts are homologous, they can be identified by anatomical criteria, notwithstanding the name they share with their molluscan analogs. Similarly, tetrapod hearts can be defined by unique anatomical features as can amniote hearts, and mammal hearts. The nested phylogenetic pattern (vertebrates:tetrapods:amniotes:mammals) is thus mirrored in the nested set of anatomical definitions available for vertebrate hearts. This is not surprising as it is nested sets of similarities that provides evidence of phylogeny. On the other hand, *insect wing* cannot be treated as an anatomical category, for the simple reason that the wings of all insect taxa are probably not homologous.

Again, the point is not to quibble over the word-counts of biological concepts which are function categories and those which are not. The question is this: Do the observations of Millikan, Neander, and other SE advocates on function categories imply that CR functional anatomists will be dependent on SE functionalists in order to characterize their subject matter? Does the existence of biological function categories mean that a reliance on causal role function will leave functional anatomists unable to identify dysfunctional hearts as hearts, a malformed tibia as a tibia? Is it true, as Neander reports, that "no description purely in terms of morphological criteria could demarcate hearts from non-hearts"?

These claims, taken as critiques of CR functional anatomy, are almost completely groundless.[4] Morphologists are able to identify anatomical items by anatomical criteria, ignoring SE function, and do so frequently. Are hearts impossible to define by "morphological criteria alone"? It is hard to know what Neander means by this. Criteria actually *used by morphologists*, e.g. connection, microstructure, and developmental origin, certainly *are* capable of discriminating between hearts and non-hearts within vertebrates. Perhaps by "morphological criteria" Neander has in mind the gross physical shapes of organs. To be sure, hearts have quite different shapes and different numbers of chambers in different vertebrate species. But no practicing morphologist uses gross shape as the "morphological criterion" for an organ's identity. Even a severely malformed vertebrate heart, completely incapable of pumping blood (or serving any biological role at all), could be identified as a heart by histological examination.

Complaining about the absence of necessary and sufficient gross physical characteristics for a morphological identification of *vertebrate heart* is surely an unwarranted philosophical intrusion on science. Such an argument should only be offered by someone practicing the "confused program, philosophical chimera" of ordinary language conceptual analysis. Morphologists can get along quite well without providing necessary and sufficient conditions for hearthood which would satisfy conceptual analysts. There is no doubt that the philosophers among us could play the conceptual analyst's game, and dream up a bizarre case in which a miraculously-deformed vertebrate's heart happened to have bizarre embryonic origins and histology, and was located under the poor creature's kneecap. The organism, if real, would baffle the anatomists just as the instant lion would baffle Darwin. But post-ordinary language philosophers do not indulge in that style of philosophy. Anatomy *as it is practiced* requires no input from SE functionalists or from biological students of adaptation in order to adequately classify and identify the structures and traits with which it deals.

SE functionalists are not the only philosophers whose emphasis on purposive function is associated with an underappreciation of anatomical concepts. Daniel Dennett shows the same tendency. Dennett argued for the indeterminacy of (purposive) functional characterizations. He brought up Stephen Jay Gould's famous example of the panda's thumb. Gould (1980) had observed that the body part used as a thumb by the panda was not anatomically a digit at all, but an enlarged radial sesamoid, a bone from the panda's wrist. Dennett's comment: "The panda's thumb was no more *really* a wrist bone than it is a thumb" (Dennett 1987, p. 320). The problem with this claim is that while 'thumb' is a functional category, 'radial sesamoid' (or 'wrist bone') is an anatomical one. Even if Dennett is correct about functional indeterminacy, anatomical indeterminacy would require a separate argument, nowhere offered. Dennett's arguments for functional indeterminacy involved the optimality assumptions he claimed were present in all functional ascriptions. Such arguments carry no weight in anatomical contexts. Such an unsupported application of a point about function to an anatomical category reflects the widespread philosophical presumption that biology is almost entirely the study of purposive function. (See Amundson 1988, 1990 on Dennett's defenses of adaptationism.)

To be fair, we must acknowledge that Millikan and Neander, like other SE functionalists, were primarily interested in *purposive* concepts of function, not in *all possible* function concepts. And it is true that SE function provides an analysis of purpose which is lacking in CR function. But their interests in purpose can lead SE functionalists to overestimate the value of purposive concepts. It is simply false that anatomists require purposive concepts in order to properly categorize body parts. Anatomical categorizations of biological items already embrace interspecies and pathological diversity without any appeal to purposive function. Anatomical distinctions are not normally based on CR function *either*, to be sure. Functional anatomists *per se* do not categorize body parts. Rather they study the capacities of anatomical complexes which have already been categorized by comparative anatomists. Causal role functional anatomy proceeds unencumbered by demands to account either for the categorization or the causal origins of the systems under analysis.

5. THE ELIMINABILITY OF CAUSAL ROLE FUNCTIONS

In this and the following two sections we will consider whether CR functions, as studied in functional anatomy, can be eliminated from evolutionary biology in favor of SE functions. We will find them ineliminable.

First, let us consider the simplest case. Is it possible that there is a one-to-one correspondence between SE functions and CR functions? Perhaps CR functions just *are* SE functions seen through jaundiced non-historical and non-purposive lenses. To examine this possibility let us suppose that we could easily identify which character complexes serve their present biological roles in virtue of having been selected to do so. (Not at all a trivial assumption, as will soon be seen.) What would be the relation between the biological role(s) played by a character complex (e.g. a jaw) and the CR functions which characterize the actions of its component parts? Bock and von Wahlert offer an answer. "Usually … the biological roles of the individual features are the same as those of the character complex" (Bock and von Wahlert 1965, p. 272). Taking the jaw as a character complex which has as one of its biological roles the mastication of food, each component muscle, bone, etc. of the jaw shares in the food mastication biological role.

But if the biological roles, and hence the SE functions, of the components of a character complex are the same as those of the overall complex itself, the CR functions of the components cannot be the same as their SE functions. All components of a complex have the *same* biological role/SE function, but each plays a *different* causal role within the character complex. So on this account SE functions cannot replace CR functions. Perhaps this result is to be expected. Bock and von Wahlert are, after all, functional anatomists. But if advocates of SE function hope to oppose this result, and refute the special significance of CR function, they presumably must argue that the activities of each component of a character complex is individually subject to the SE definition of function.

One consideration which might tempt an SE advocate in this direction is Millikan's observation, mentioned above, that all items in this world with functional complexity have undergone histories of natural selection. (Or, in the case of artifacts, were created by organisms which have such a history.) Notice, however, that the generalization *Functionally complex items have selective histories* does not by itself imply that a positive selective influence was responsible for every causal property of every component of the functional complex. Bock and von Wahlert could accept the generalization but still distinguish biological role from CR function.

Indeed, there are many reasons to reject the identification of CR functions as merely non-historically-viewed SE functions. For example, some functional anatomists wish to examine *unutilized* CR functions; clearly an unutilized function is not one which can be selected for. Further, the identification of CR with SE functions would define preadaptations (or exaptations) out of existence. But the question of the existence of currently utilized but unselected-for preadaptations (exaptations) or other selectively unshaped causal properties must be decided on the basis of evidence, not by definitional fiat.

We will not further belabor this implausible position; perhaps no SE advocate would take it anyhow. The point of this and the previous section is only that CR functions cannot be definitionally or philosophically eliminated. More interesting questions remain. Why do anatomists *need* to deal with causal role functions? Why can't they get along with purposes and selected effects?

6. APPLICABILITY OF SELECTED EFFECT FUNCTION TO RESEARCH IN FUNCTIONAL ANATOMY

A major concern of practicing functional anatomists is the utility of concepts such as function and biological role. In day-to-day research, how are functions to be identified and compared across species, and how, in practice, are we to identify the biological role of a structure? By specifying that function is that effect for which a trait was selected, SE functionalists have placed anatomists in a difficult position. In order to be able to label a structure with a corresponding function, a functional morphologist must be able to demonstrate first, that selection acted on that structure in the population in which it arose historically, and second, that selection acted specifically to increase fitness in the ancestral population by enhancing the one specific effect that we are now to label a function of the structure. There are at least three areas in which practical difficulties arise in meeting these conditions.

First, as biologists have long recognized (e.g., Darwin 1859, chapter 6), structures may have more than one function, and these functions may change in evolution. If such change occurs, are we to identify the function of a structure as the effect for which it was first selected? If selection changes to alter the SE function of a structure through time, how are functional morphologists to identify which SE function should be applied to a structure? A recent example that points out some of the difficulties of an SE concept of function in this regard is the analysis of the origin of insect wings performed by Kingsolver and Koehl (1985). Although efforts to estimate the past action of selection (as discussed below) are fraught with difficulty, Kingsolver and Koehl used aerodynamic modeling experiments in an effort to understand the possible function of early insect wings. Do short-winged insect models obtain any aerodynamic benefit from the short wings? In other words, is it likely that selection acted on very small wings to improve aerodynamic efficiency and enhance the utility of the small wings for flight, eventually producing larger-winged insects? If so, then it would be possible to argue that the SE function of insect wings is flight. However, Kingsolver and Koehl (1985, p. 488) found that short insect wings provided no aerodynamic advantage, and argued that "there could be no effective selection for increasing wing length in wingless or short-winged insects ...". These authors did find, however, that short wings provided a significant advantage for thermoregulation; short wings specifically aided in increasing body temperature, which is important for increasing muscle contraction kinetics and allowing for rapid movements. Based on these data then, one might hypothesize that insect wings originated as a result of selection for improved thermoregulatory ability, and that only subsequently (when wings had reached a certain threshold size) did selection act to improve flight performance.

If we identify the function of insect wings as that effect for which they were *first* selected, then we would say that the function of insect wings is thermoregulation. It might be argued that in fact, the earliest wing-like structures actually are not proper wings, and that modern insect wings really do have the SE function of flight because at some point there was selection for improved flight performance. But this fails to recognize the size continuum of morphological structures that we call insect wings, the fact that large wings even today are used in thermoregulation, the structural homology of large and small wings, and the virtual impossibility of identifying the selection threshold in past evolutionary time. If we cannot identify the threshold, we will not know when to change the SE function of wings from thermoregulation to flight. Examples such as this illustrate the difficulty of assuming that the present day roles or uses of structures are an accurate guide to inferring past selection and hence SE function.

The SE theory of function does not rule out the existence of changing patterns of selection on a given structure nor the existence, in principle, of several SE functions for one structure. However, the complexities of this common biological situation for the association of an SE function with a specific structure have not been adequately addressed or appreciated.

Second, 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? The example of insect wings given above represents a best case scenario in which we are able to make biophysical models and use well-established mathematical theories of fluid flow to estimate the likely action of selection. But many structures (particularly in fossils) are not amenable to such an analysis. Even with modern populations, studies designed to show selection on a given trait are difficult and are subject to numerous alternative interpretations and confounding effects (Endler 1986; Arnold 1986). Functional morphologists do not have the luxury of simply asserting that the SE function of structure X is F (as philosophers so regularly do with the heart): there must be direct evidence that selection acted on structure X for effect F.

Third, there is considerable difficulty in determining that selection is acting (or acted) on *just* the structure of interest, even in extant taxa. Such difficulties are, for all practical purposes, insurmountable when dealing with fossil taxa or ancient structures. For the SE function of a structure to be identified, it is critical to be able to show that selection acted on that particular structure. However, as has been widely documented (e.g., Falconer 1989; Rose 1982), selection on one trait will cause manifold changes in many other traits through pleiotropic effects of the gene(s) under selection. Thus, selection for increased running endurance in a population of lizards may have the concomitant effect of increasing heart mass, muscle enzyme concentrations, body size, and the number of eggs laid, despite the fact that selection was directed only at endurance.

In fact, many phenotypic features are linked via common developmental and genetic controls, and this pattern of phenotypic interconnection makes isolation of any single trait and its selected effect very difficult (Lauder et al. 1993). If biologists had a ready means of locating the specific trait that is (or was) being acted on by selection, then the SE definition of function would be easy to apply. In actuality, due to pleiotropy, one typically sees a response in many traits to any particular selective influence. In laboratory selection experiments, the selected effect is known, and it is relatively easy to separate the selected trait from correlated responses. But in wild populations, one observes changing mean values of numerous traits in response to selection, and it is extremely difficult to separate the individual trait that is responding to selection from those that are exhibiting a correlated response.

It is also important to recognize that in extant species, the selected effect may be easier to identify than the trait acted upon by selection. This might seem counterintuitive at first, since so many studies of adaptation proceed by first identifying a trait, and only then searching for its selective advantage(s). The difficulty of identifying the trait arises because of the correlation of the many biological traits that influence selected effects or organismal performance, and the hierarchical nature of physiological causation. Consider one powerful method for the study of selection in nature: the analysis of cohorts of individuals in a population and their demographic statistics by following individuals through time (Endler 1986). For example, if one marks individual insects in a population and measures their fitness (e.g., mating success) and their performance on an ecologically relevant variable (say, maximum flight duration) one might well find that the mean flight duration increases in the population through time due to selection against individuals that cannot remain aloft long enough to successfully mate. (Such selection might be demonstrated using the statistical methods proposed by Arnold [1983; Arnold and Wade 1984; Lande and Arnold 1983].) Here we have strong evidence that selection is operating, and an identified selected effect (increased flight duration). But what is the trait *X* on which selection is acting? Suppose, as we mark the individual insects, we also take a number of measurements of morphology (such as body size, eye diameter, wing length and area). We can now examine these morphological variables to see if we observe changes in these population means that are correlated with changes in flight duration. If we find that only one variable, wing area, showed an increase in mean value that was correlated with the increase in flight performance through time, then we might we willing to conclude that wing area was trait *X*, the trait for which the SE function is 'increasing flight duration.'

Unfortunately, an example of this type would be truly exceptional. The common result is that *many* variables are usually correlated with changes in performance and fitness. It is almost certain, in fact, that many aspects of muscle physiology, nervous system activity, flight muscle enzyme concentrations and kinetics, and numerous other physiological features would show correlated change in mean values with the increase in flight duration. In addition, body length and mass are likely to show positive correlations, as are wing length, area, and traits that have no obvious functional relevance to flight performance (such as leg length). If we cannot identify the causal relationships among these correlated variables to single out the one that was selected for, we will be unable to assign a trait *X* to the SE function already identified. We have a SE function, but we do not know which trait to hang it on. The fact that pleiotropic effects are so pervasive in biological systems causes severe problems in applying the definition of SE function.

Two issues relate to the analysis of traits that might be selected for in an example such as the one discussed above. First, we might choose only to measure traits on individuals which *a priori* physiological and mechanical considerations suggest should bear a functional relationship to the demonstrated performance change. Thus, we might decide not to measure variables such as leg length since it is difficult to identify a physiological model in which increasing leg length would cause increased flight duration. Choosing variables based on an *a priori* model will certainly help narrow the universe of possible traits, but the remaining number of physiologically and mechanically relevant traits will still be very large. A second complexity in picking the trait that has been selected for arises from the hierarchical nature of physiological processes. A change in a performance characteristic (such as flight duration) may result from changes at many levels of biological design (Lauder 1991): muscle mass and insertions could change, muscle contraction kinetics could change by changing the proportion of different fiber types, enzyme concentrations within fiber types could be altered, and many features of the nervous system could be transformed. These different types of physiological traits have a hierarchical relationship to each other (in addition to a possible pleiotropic relationship) that represents a causal chain: changes at any one or more of these levels of design could account for a performance change at the organismal level. Yet, each of these features must be a distinct trait *X* in the SE definition, and we are unlikely in most cases to be able to identify the particular trait, or particular combination of traits, that was selected for. Of course, flight duration itself might well be considered as a trait, subject to selection and the same hierarchical patterns of underlying physiological variation as any other trait. In this case, the very same difficulties would obtain: we would need to be able to document selection *on that trait* (flight duration) in order to apply the SE concept of function.

These considerations show why anatomists are rarely able to identify which of the causal role functions of a given trait are its SE functions – that is, which (if any) are the effects for which the trait was selectively favored. But, as the next section will show, anatomists can not afford to abandon CR functions simply because SE function assignments are unavailable. Important research programs are at stake.

7. RESEARCH PROGRAMS IN WHICH CAUSAL ROLE FUNCTION IS CENTRAL

Several aspects of current research in functional and evolutionary morphology make crucial and ineliminable use of the concept of CR function. Anatomists often write on 'the evolution of function' in certain organs or mechanical systems, and may do so with no reference to selection or to the effects of selection (e.g., Goslow et al. 1989; Lauder 1991; Liem 1989; Nishikawa et al. 1992). Rather, in these papers functional morphologists mean to consider how CR functions have changed through time, in the same manner that morphologists have traditionally examined structures in a comparative and phylogenetic context to reconstruct their evolutionary history. Indeed, a significant contribution of the field of functional anatomy (which has blossomed in the last twenty years by adopting physiological techniques to measure CR functions in different species) has been to treat functions as conceptually similar to structures. For example, Lauder (1982) and others (e.g., Wake 1991; Lauder and Wainwright 1992) have argued that CR functions may be treated just like any other phenotypic trait, and analyzed in an historical and phylogenetic context to reveal the evolutionary relationship between structure and function.

So, like SE functionalists, CR functional anatomists and morphologists are interested in history. But unlike SE functionalists, anatomists do not *define* a trait's function by its history. CR function is non-historically defined. The historical interests of evolutionary morphologists are not directed towards the evolutionary mechanism of selection or the analysis of adaptation. The relation between the approaches to history taken by SE functionalists and anatomical functionalists parallels the two major explanatory modes used in the analysis of organismal structure and function. These have been termed the *equilibrium* and the *transformational* approaches (Lauder 1981; Lewontin 1969). Studies of organismal design conducted under the equilibrium view study structure in relationship to environmental and ecological variables. Such analyses are appropriate for investigating current patterns of selection and for interpreting biological design in terms of extant environmental influences. The goal of equilibrium studies is to understand extrinsic influences on form (such as temperature, wind velocity, or competition for resources), and these studies are designed to clarify current patterns of selection and hence adaptation (Bock 1980; Gans 1974). Equilibrium studies tell us little about the history of characters, however (Lewontin 1969), as the very nature of the methodology presumes (at least a momentary) equilibrium between organismal design and environmental stresses.

Many studies in functional morphology, especially in the last ten years, have adopted the transformational approach (Lauder 1981) in which historical (phylogenetic) patterns to change in form are explicitly analyzed for the effects of intrinsic design properties. Here, the focus is not on adaptation, selection, or the influence of the environment, but rather on the effect that specific structural configurations might have on directions of evolutionary transformation. For example, a functional morphologist might ask: does the possession of a segmented body plan in a clade have any consequences for subsequent evolutionary transformation in design? Under a transformational research program one might examine a number of lineages, each of which has independently acquired a segmented body plan, to determine if subsequent phylogenetic diversification within each lineage shows any common features attributable to the presence of segmentation (regardless of the different environmental or biophysical influences on each of the species). In fact, segmentation, or more generally, the duplication or repetition of parts, appears to be a significant vehicle for the generation of evolutionary diversity in form and function by allowing independent specialization of structural and functional components (Lauder and Liem 1989). An exemplary transformational study is Emerson's (1988) analysis of frog pectoral girdles in which she showed that the initial starting configuration of the pectoral girdle in several clades was predictive of subsequent changes in shape. This transformational regularity occurred despite the different environments inhabited by the frog species studied. Transformational analyses by functional morphologists are historical in character: they focus on pathways of phylogenetic transformation in design which result from the arrangement of structures and the causal roles of those structures.

Functional morphologists also view organismal design as a complex interacting system of structures and functions (Liem and Wake 1985; Wake and Roth 1989). Indeed, the notion of 'functional integration,' which describes the interconnectedness of structures and their CR functions, is central to discussions of organismal design and its evolution. The extent to which individual components of morphology can be altered independently of other elements without changing the (CR) functioning of the whole is one aspect of this current research (Lauder 1991). Given a structural configuration involving many muscles, bones, nerves, and ligaments, for example, all of which interact to move the jaws in a species, one might ask what effect changing the mass of just one muscle will have on the action (CR function) of the jaws as a whole. Some arrangements of structural components will have limited evolutionary flexibility due to the necessity of performing a given function such as mouth opening: even minor alterations in design may have a deleterious effect on the performance of such a critical function. This implicates CR functions as an agent of evolutionary constraint. We could also inquire about possible components in a functionally integrated system that might theoretically be changed while maintaining the function of the whole system: do predicted permitted changes correspond to patterns of evolutionary transformation actually seen? The comparison of predicted and actual pathways of transformation is but one part of a larger effort to map a theoretical 'morphospace' of *possible* biological designs. By defining basic design parameters for a given complex morphological system, a multidimensional morphospace may be constructed (e.g., Bookstein et al. 1985; Raup and Stanley 1971). Comparing this theoretical construct with the extent to which actual biological forms have filled the theoretically possible space allows the identification of fundamental constraints on the evolution of biological design. A frequent finding is that large areas of the theoretically possible morphospace are unoccupied, and explaining this unoccupied space is a key task of functional and evolutionary morphology.

For these reasons, it is difficult to envision how the concept of a CR function, so integral to both transformational analysis and functional integration, could be eliminated from the conceptual armamentarium of functional morphologists without also eliminating many key research questions.

8. CONCLUSION

Our rejection of some of Millikan's and Neander's conclusions should not disguise our strong agreement with their stance on the relation between the practices of science and philosophy. We heartily agree that conceptual analyses of ordinary language are inappropriately used to critique the concepts of a science. Indeed, most of our defenses of CR function against ordinary language conceptual analysis are versions of the ones used first by Millikan or Neander as they defended SE function against the same opponent. We differ from them not on the proper uses of philosophy, but on the needs and practices of biology.

We are more pluralistic than most philosophical commentators on function. We do not consider the SE concept of function, or its near-synonym the historical concept of adaptation, to be biologically or philosophically illegitimate. Our reservations about the application of purposive concepts in biology are primarily epistemological. As Williams said of adaptation, SE function in biology is "a special and onerous concept that should be used only where it is really necessary." Causal role function in anatomy, if less philosophically fertile than selected-effect function, is on much firmer epistemic footing. It also happens to be ineliminably involved in ongoing research programs. This alone ought to establish its credentials.

Given comparative anatomy to categorize its subject matter, and ecological or ethological studies of biological role to suggest which character complexes to analyze, functional anatomy is subject to none of the conceptual analyst's critiques of CR function. It is just as immune from philosophical refutation as Millikan's and Neander's science-based theory of SE function. The adequacy of each account is to be assessed not by its ability to fend off the facile imaginations of conceptual analysts, but to deal with real world scientific issues.

Finally, a recent recommendation from Elliott Sober.

> If function is understood to mean adaptation, then it is clear enough what the concept means. If a scientist or philosopher uses the concept of function in some other way, we should demand that the concept be clarified. (Sober 1993, p. 86)

We submit that Sober's challenge has now been met.

ACKNOWLEDGEMENTS

We received valuable comments on an earlier version of this paper from Elliott Sober, Ruth Millikan, Robert Brandon, and an anonymous referee. Kenneth Schaffner generously supplied a prepublication copy of the chapter we cited, and helpful observations on various function concepts. The work was supported by NSF grants SBE–9122646 (to RA) and IBN91–19502 (to GVL).

NOTES

[1] We take it that Neander intends her analysis to reflect biologists' use of the term 'function', not necessarily their use of the concept defined by Millikan as 'proper function'. Both Millikan (p. 290, note #1) and Neander (p. 168, note #1) refer to Neander's widely circulated but unpublished "Teleology in Biology." In that paper Neander referred only to the biological concept of 'function' (i.e. not to 'proper function') except when she needed to distinguish between "a part's proper function and things which it just happens to do fortuitously." (Neander manuscript, p. 11)

[2] A minority of commentators interpret Cummins as surreptitiously introducing goals and purposes by choosing for analysis only traits which are already known to be purposive (Rosenberg 1985, p. 68; Schaffner 1993, p. 399 ff.). We interpret Cummins as fully agnostic with regard to purpose, which is why the criticisms being considered are worthy of discussion. Rosenberg appears to be the only philosopher who supports Cummins's account of function for evolutionary biology; he does so partly because of this purposive reading. Whatever Cummins's original intentions, we intend CR function to be both non-historical and non-purposive in its applications.

[3] Note that even extremely similar traits may arise by convergent evolution, and that the final test of homology is not similarity but rather congruent phylogenetic distribution of

the putative homology with other characters providing evidence of monophyly. Thus, the eye of a squid and the eye of vertebrates are very similar in many (but not all) features. The non-homology of squid and vertebrate eyes does not rest on the differences noted between the eyes (virtually all homologous characters have some differences), but rather on the fact that very few other traits support the hypothesis that squids + vertebrates constitute a natural evolutionary lineage. The phylogenetic relationships among species thus provides the basis on which we make decisions about the homology of individual characters. For similar reasons, our statements to the effect that (homologous) traits *characterize* taxa should not be taken to mean that those traits are logically necessary or sufficient conditions for a species's membership in a taxon. Snakes are tetrapods notwithstanding their leglessness. The phylogenetic distribution of other traits than legs makes it clear that snakes are members of the same monophyletic group as more typically-legged tetrapods. See Sober (1993, p. 178) for a caution against appearances of essentialism in discussions of phylogenetic classification.

[4] There is one felicitous application of Neander's claim about the inadequacies of morphological criteria to designate hearts. Since the category 'heart' is used across major taxonomic differences, a vertebrate taxonomist unfamiliar with mollusks might well not be able to use *vertebrate* morphological criteria to identify a *molluscan* heart. And, to get only slightly bizarre, it is possible to imagine discovering a new taxon of animals which has organs functionally identifiable as hearts, but which fit the morphological criteria for hearts of no known taxon. We agree with the SE functionalist's point in this rather limited set of cases.

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