

A Taxonomy of Functions¹

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I Introduction

There are two general approaches to characterising biological functions. One originates with Cummins.² According to this approach, the function of a part of a system is just its causal contribution to some specified activity of the system. Call this the 'C-function' (or 'Cummins function') concept. The other approach ties the function of a trait to some aspect of its evolutionary significance. Call this the 'E-function' (or 'evolutionary function') concept. According to the latter view, a trait's function is determined by the forces of natural selection. The C-function and E-function concepts are clearly quite different, but there is an important relation between them which heretofore has gone unnoticed. The purpose of this paper is to outline that relation.

1 We wish to thank the following people for comments: Henry Byerly, Robert Cummins, Berent Enç, D.D. Kohn, Joel Pust, Larry Shapiro, Elliott Sober, Chris Stephens, and two anonymous referees. This work was funded in part by SSHRC Postdoctoral fellowship 756-94-0750 to DMW.

2 R. Cummins, 'Functional Analysis,' *Journal of Philosophy* 72 (1975) 741-65. Reprinted in E. Sober, ed., *Conceptual Issues in Evolutionary Biology* 2nd ed. (Cambridge, MA: The MIT Press 1994). All quotations from this paper will be taken from the Sober reprint.

This is not the first paper to discuss the relation of C-function and E-function. Previous attempts all follow either one of two strategies. The first proposes that the two concepts are 'unified.'³ The other proposes that they are radically distinct and apply to wholly different fields within biology.⁴ Although each has its merits, neither strategy fully captures what we see as the important relations between C-function and E-function. The reason, we believe, is that previous discussions have relied upon a faulty notion of E-function. When evolutionary function is correctly characterised, the relation and its significance become readily apparent.

II C-function and E-function

We proceed in the following way. First, we present the Cummins account of functions and functional explanations. Then we survey three theories of the nature of evolutionary functions, and endorse only one. Finally, in light of this theory, we present a taxonomy of C-functions and E-functions, discussing the relation between their respective extensions, the means by which they are discovered and, most importantly, the relation between their respective explanatory roles within biology.

1. Cummins Function

Cummins argues that philosophers have misrepresented the role of functional explanation in science. Traditional approaches to function, he says, have proceeded under the unwarranted assumption that 'the point of functional characterization in science is to explain *the presence* of the item (organ, mechanism, process, or whatever) that is functionally characterized' ('Functional Analysis,' 49; emphasis added). Such explanations are teleological, but, Cummins argues, teleology should be no part of functional explanation; you cannot appeal to the function of a naturally occurring phenomenon to explain what it is for or why it is there.

³ P. Kitcher, 'Function and Design,' in P.A. French, T.E. Uehling, and H.K. Wettstein, eds., *Midwest Studies in Philosophy XVIII* (Minneapolis: University of Minnesota 1993) 379-97

⁴ R. Amundson and G. Lauder, 'Function without Purpose: The Uses of Causal Role Function in Evolutionary Biology,' *Biology and Philosophy* 9 (1994) 443-69; P. Godfrey-Smith, 'Functions: Consensus Without Unity,' *Pacific Philosophical Quarterly* 74 (1993) 196-208

Instead, the point of ascribing a function to an object is to explain how it contributes to some overall capacity of the system of which it is a part.

A function ascription, for Cummins, takes place in the context of an analysis of how a particular system (a containing system) performs a particular task. The analysis proceeds by breaking down the containing system into its component parts. The function of a given component is the property (or disposition) it has which causally contributes to the activities of the containing system as a whole. More specifically,

x functions as a ϕ in *s* (or: the function of *x* in *s* is to ϕ) relative to an analytical account *A* of *s*'s capacity to ψ just in case *x* is capable of ϕ -ing in *s* and *A* appropriately and adequately accounts for *s*'s capacity to ψ by, in part, appealing to the capacity of *x* to ϕ in *s*. (Cummins, 'Functional Analysis,' 64)

Taken out of its context the definition of Cummins-style function is fairly inscrutable. Let's see if we can clear it up: *s* ranges over structures whose parts work together in some way; *x* takes as its values the parts of *s*.⁵ *A* ranges over analyses of *s*'s capacities. ψ is an activity of *s* of some interest; ϕ is *x*'s causal contribution to that activity. For example, against the background of explaining the detoxification of blood (*A*), we may wish to analyze the function (ϕ) of the loop of Henle (*x*) with respect to the capacity of the kidney (*s*) to excrete wastes (ψ). The function of the loop of Henle, in this context, is the passive reabsorption of plasma, which concentrates the urea.

The choice of the explanatory analysis, *A*, and the characteristic activity, ψ , is constrained only by interest. A functional analysis (*A*) is interesting to the extent that it explains complex capacities of a system in terms of distinct, less complicated components. There is no requirement that within biology *A* or ψ should be restricted to explanatory contexts or processes of *evolutionary* significance. As Cummins says, 'functional analysis can properly be carried on in biology quite independently of evolutionary considerations' ('Functional Analysis,' 60). The function of the heart, against the background of the circulatory system's capacity to exchange gas and nourishment with the tissues of the body, is to pump blood. Similarly, the function of the heart, against the background of the capacity of an electrocardiogram machine to make traces upon a piece

⁵ In *The Nature of Psychological Explanation* (Cambridge, MA: The MIT Press 1983), Cummins amends his account of function to allow that *s* and *x* may also range over processes themselves (e.g. multiplying 27 by 32) and their component processes (e.g. multiplying 2 by 7, adding 5 and 1), irrespective of how these capacities are instantiated.

of paper, is to produce electrical pulses. Although one of these capacities of the heart has an evolutionarily privileged place, neither constitutes a more correct, or explanatorily privileged, account of the heart's function. We may be more inclined to ask for one function rather than the other, but this is purely a matter of our research concerns.

2. Evolutionary Function

The Cummins conception of function has been criticised for misrepresenting the nature and explanatory purpose of function ascriptions. Detractors say that function is a much richer notion than the Cummins view allows. To ascribe a function to a feature is to say what it is *for*, where not just anything it might do counts as being what it is for. Contrary to the Cummins conception of function, to ascribe a particular function to a feature entails an explanation of why that feature is present (or prevalent).⁶ In further contrast to the Cummins conception, function, thus conceived, has normative import. The normativity of functions induces the distinctions between function and accident and between function and malfunction in a way that Cummins's account cannot.⁷ To return to a previous example, hearts pump blood and also cause traces on a cardiogram: these are both C-functions with respect to some analysis of an individual's activities; but as function is usually understood, only the former of these is the heart's function, while the latter is a mere accident. A heart which (in propitious conditions) cannot pump blood still has the function of doing so; it merely malfunctions.

The richer, normative notion of function is clearly in use within evolutionary biology. There has been considerable energy expended recently on cobbling together a definition of function, understood in this way, from the concepts belonging to evolutionary biology. To our knowledge, there are three general approaches; call them the 'historical

theory' (or the 'aetiological theory'), the 'forward looking theory,' and the 'relational theory.' They share one central idea: that a trait's function — its *evolutionary* function — is determined by its contribution to fitness. Fitness, as we shall use that notion, is a property of an individual, its propensity to survive and/or reproduce.⁸ It is the fitness differences between individuals that natural selection works upon. Thus, in all three theories, evolutionary function is tied in some way to natural selection. Though the central idea is the same in all three, it is the nuances that make the difference. We offer a survey of the salient features of each which, we hope, is sufficiently detailed to justify our claim that one, the relational theory, is clearly superior.

The received view of evolutionary functions originated with Millikan and has since been embellished by Neander and Godfrey-Smith.⁹ The biological function of a trait, *x*, is to do *m* just in case individuals possessing *X* have been favoured by natural selection *in the past* because their *x*s have *med*.¹⁰ The crux of this account is that the function of a trait is the way it has contributed to fitness *in the past*. This is known as the aetiological, or historical, theory of evolutionary functions.

A number of advantages have been claimed for this theory. First, it captures the sense of utility inherent in a function attribution; the historical function of a trait explains what that trait is *for*, by invoking the benefit to its possessors in past environments. Second, by appeal to selection in the past, historical function also explains a trait type's current presence or prevalence in a population.¹¹ Third, function attributions on the aetiological account appear to be normative. They tell us what a trait ought to be able to do. Hearts ought to pump blood because that is what hearts have been selected for in the past. Because historical function in biology is normative in this way, it supports the distinctions between function and accident and between function and malfunction. Traits

6 It will become apparent that there is some dispute over how to interpret the question of why a feature is present. Some (B. Enc, 'Function Attributions and Functional Explanation,' *Philosophy of Science* 46 [1979] 343-65; and we) believe that function ascription yields genuinely teleological explanations of the presence of a feature (i.e. it explains why a feature persists by citing its effects); others (K. Neander, 'The Teleological Notion of "Function,"' *Australasian Journal of Philosophy* 69 [1991] 454-68; P. Kitcher, 'Function and Design'; P. Godfrey-Smith, 'A Modern History Theory of Functions,' *Nous* 28 [1994] 344-62; R.G. Millikan 'In Defense of Proper Functions,' *Philosophy of Science* 56 [1994] 288-302) believe that function ascriptions merely explain the current presence of a trait by citing its causal history.

7 L. Wright, 'Functions,' *Philosophical Review* 82 (1973) 139-68

8 S. Mills and J. Beatty, 'The Propensity Interpretation of Fitness,' *Philosophy of Science* 46 (1979) 263-86; see also Sober's *Conceptual Issues in Evolutionary Biology*.

9 R.G. Millikan, *Language, Thought, and other Biological Categories* (Cambridge, MA: The MIT Press 1984) and 'In Defense of Proper Functions'; K. Neander, 'Functions as Selected Effects: The Conceptual Analyst's Defense,' *Philosophy of Science* 58 (1991) 168-84 and 'The Teleological Notion of "Function"'; P. Godfrey-Smith, 'A Modern History Theory of Functions'

10 We shall use the following convention to distinguish trait types from tokens. Upper case italics '*X*' are variables ranging over trait types; lower case italics '*x*' are variables ranging over tokens, such that *x* is a token of *X*.

11 This is the reason for the 'aetiological' epithet.

generally do more than they have been selected to do, but not everything a trait does is a function. For instance, hearts have been selected in the past for their blood pumping capacities, so pumping blood is a heart's function. Some of the things hearts do, like cause traces on cardiograms, are mere accidents. If a heart fails to pump blood (in propitious conditions), it is malfunctioning.

The aetiological theory is undoubtedly powerful, but we contend that it captures only part of the concept of evolutionary function. Not only do we think it is incomplete, we also think that the prevalent, yet mistaken thought that all biological functions are historical has prevented a clear picture of the relation between C-functions and E-functions from emerging. As we see it, there are three problems with the historical theory. One concerns the notion of utility inherent in a function ascription. The second concerns the explanatory role function attribution plays in biology. The third involves normativity.

First, the aetiological account doesn't always properly capture the notion of utility inherent in the concept of function. Consider that the contribution a trait has made to fitness in the past may in some cases diverge from its current contribution to fitness. That is to say the utility of a trait in the past does not determine its current utility. In such cases it is often customary in biology to associate function with current utility. For example, Liem demonstrates how novel uses of the pharyngeal jaw apparatus of cichlid fishes have contributed to their subsequent adaptive radiation.¹² He calls these innovations 'novel functions' (432f.). There is a common intuition among physiologists and functional anatomists, for example, that if a trait type generally contributes to fitness in a novel way within a population, then the novel way may well constitute a function.¹³ For the same reason, we ought to be able to ascribe functions to novel characters which generally benefit their bearers.¹⁴ The aetiological theory explicitly withholds function ascriptions in such cases.

A second problem concerns the presumed explanatory role of function attributions in evolutionary biology. Aetiological functions explain why

a particular biological character is currently prevalent in a population.¹⁵ This is an important application of E-function ascriptions, but there are others. Explaining a trait's expected persistence or maintenance in future populations by describing what it is for is another. For example, we may want to explain why we would expect melanic moths (of the species *Biston betularia*) to replace light morph individuals in a newly polluted forest. The dark colouration happens to camouflage the moths against soot-encrusted trees. Dark moths are less visible to predators in the newly polluted forests and consequently have a greater expected number of offspring than their lighter conspecifics. Camouflage, it appears, ought to be considered the (or a) function of melanic colouration in the newly polluted environment. In this case the function, camouflage, explains why we should *expect* the persistence or maintenance of melanism in *future* populations, but doesn't explain its aetiology.¹⁶ Alternatively, the current function of melanism may be invoked to explain perceived fitness differences between light and dark morph moths. The ascription of merely aetiological E-functions does not have these explanatory consequences.¹⁷

Third, the historical theory does not account for the normativity of function attributions as it claims to do. The historical theory tells us, for instance, that vertebrate hearts ought to pump blood because that is what hearts have been selected for in the past.¹⁸ We take it that this is intended to imply that vertebrate hearts ought to pump blood *now* for the same reason. But that seems wrong. An individual's heart ought to be able to pump blood *now* (in part) because if it cannot she'll die. That is not a fact about hearts' contribution to fitness in the past, it's a fact about the way

12 K. Liem, 'Evolutionary Strategies and Morphological Innovations: Cichlid Pharyngeal Jaws,' *Systematic Zoology* 22 (1973) 425-41

13 We thank Farish A. Jenkins Jr. of the Museum of Comparative Zoology and Harvard Medical School for corroborating this.

14 See J. Bigelow and R. Pargetter, 'Functions,' *Journal of Philosophy* 84 (1987) 181-97; B. Enç and F. Adams, 'Functions and Goal Directedness,' *Philosophy of Science* 59 (1992) 636-54; E. Sober, *Philosophy of Biology* (Boulder, CO: Westview 1993).

15 S. Mitchell, 'Dispositions or Etiologies? A Comment on Bigelow and Pargetter,' *Journal of Philosophy* 90 (1993) 249-59 and 'Function, Fitness, and Disposition,' *Biology and Philosophy* 10 (1995) 39-54; P. Godfrey-Smith, 'A Modern History Theory of Functions'

16 Enç and Adams ('Functions and Goal Directedness') also point out that functional explanations may be either forward-looking or aetiological, *pace* Mitchell, who contends that aetiology is the only explanatory project for which functions are invoked.

17 This is something that advocates of the historical theory readily admit (see especially Mitchell, 'Dispositions or Etiologies?'). They tend to deny that *expected* persistence, or current fitness differences are any part of the explanatory applications of function in evolutionary biology.

18 See R.G. Millikan, 'Truth Rules, Hoverflies, and the Kripke-Wittgenstein Paradox,' in *White Queen Psychology and other Essays for Alice* (Cambridge, MA: The MIT Press 1993), esp. n. 10; and K. Neander, 'Functions as Selected Effects.'

hearts generally contribute to fitness *now*. Hearts generally contribute to fitness now by pumping blood. Those individuals whose hearts can't pump blood suffer a fitness decrement on average on account of it. More abstractly, a token of a trait ought to be able to contribute to fitness in the way that tokens of their type generally do *now*. Current contribution to fitness determines what a trait ought to do *now*, but current contribution to fitness is no part of the aetiological theory of E-functions.

A common thread runs through each of the above three criticisms of the historical theory: that the general contribution that a trait type has made to fitness in the past does not determine its current contribution to fitness and that current contribution to fitness ought to be at least *part* of the concept of evolutionary function. Because the aetiological theory ties function exclusively to past contribution to fitness, it fails to encompass what might be called 'current function.'

This brings us to the second theory of evolutionary function. Bigelow and Pargetter have proposed the propensity theory, often called the 'forward looking theory.' The gist of the forward looking thesis is that the function of a trait is what traits of its type do to contribute to fitness *currently*. Function, according to this view, is not a historical notion; it has to do with the way a trait benefits its possessors now, irrespective of what it has done in the past. To its credit, the forward looking theory permits the ascription of strictly current functions, as we have suggested an adequate theory of E-function should.¹⁹ But, like the historical theory, it is incomplete. It fails to recognise historical functions. As a result, it fails to account for an important class of explanations for which functions are invoked in biology. Forward looking functions explain the future persistence of a trait, but not its aetiology.

We have canvassed two theories of evolutionary function: the historical and the forward looking. Each captures what the other misses, but neither is complete. There is a need for *both* historical and current evolutionary functions in biology, and a need for the distinctive kinds of explanations that each issues in. The requirement for both current and historical functions brings us to our third theory, relational function.

The relational theory, like its predecessors, ties function to fitness contribution, but in a novel way. It has been developed, and explained in detail, by Walsh ('Fitness and Function'). The leading idea is that the way a trait contributes to fitness may vary wildly according to the

¹⁹ Although there are some problems with the formulation that Bigelow and Pargetter give to novel functions. See D.M. Walsh, 'Fitness and Function,' *The British Journal for the Philosophy of Science* (forthcoming) for a discussion.

environment.²⁰ Thus one cannot specify the contribution that a trait makes to fitness *simpliciter*. Instead, one must specify the contribution to fitness *with respect to a selective regime*.²¹ Consequently, one may not specify the function of a trait *simpliciter*; instead one may only specify the function of a trait *with respect to* some selective regime or other. We give the definition of relational function first and then take a moment to discuss how it yields a satisfactory theory of E-function.

Relational function is defined in the following way:

RF: The/an evolutionary function of a token of type X with respect to selective regime R is to m if and only if X 's doing m positively (and significantly) contributes to the average fitness of individuals possessing X in R .²²

The function of a trait token (x) with respect to R is the way traits of its type (X) positively contribute to average fitness of individuals in R . That is equivalent to saying that the function of (trait token) x in R is just what (trait type) X is being selected *for* in R .²³ This is of the utmost importance. If there is selection (in R) for trait type X in virtue of its (tokens') capacity to do m , then the capacity to do m explains the general utility to an individual of having a trait of type X . It also explains the persistence of X under natural selection. Furthermore, what a trait type is being selected for in R determines conditions of proper functioning for tokens of the trait's type. Tokens of X are working properly when they are capable of doing what X is being selected for. Within the definition RF, we have the basis of all we require of a theory of E-function. Because of its relational nature, RF can recognise both current and historical functions. Because the function of a trait is tied to selection *for* that trait (in a regime), relational function preserves both the explanatory consequences and the normativity inherent in ascriptions of evolutionary function. We take these points in turn.

Relational function, as defined by RF, is neither strictly historical nor strictly current but instances of relational function may be either. When the selective regime, R , is a past regime, the function will be historical.

²⁰ R. Brandon, *Adaptation and Environment* (Princeton: Princeton University Press 1990); R.C. Richardson and R.M. Burian, 'A Defense of the Propensity Interpretations of Fitness,' *Philosophy of Science Association* 1 (1992) 349-62

²¹ By 'selective regime' of a trait we mean the total set of abiological and biological (including social, developmental, and physiological) factors in the environment of the trait which potentially affect the fitness of individuals with that trait.

²² Walsh, 'Fitness and Function'

²³ See E. Sober, *The Nature of Selection* (Cambridge, MA: The MIT Press 1984) and *Philosophy of Biology* for the significance of selection *for* a trait.

When the relevant regime, R , is the current regime, the function is current.²⁴ RF also does justice to the variety of explanations for which evolutionary functions are invoked. A relational function explains the persistence of a trait type from one time t_1 to a later time t_2 within a regime R . When t_2 is the present, the attribution of a function to a trait tells us why that trait type is prevalent in the current population, that is, the function ascription provides us with an aetiological explanation for the trait in question. When t_1 is the present, the attribution of a function to a trait tells us why we should expect traits of that type to be prevalent at t_2 . In addition, invoking function with respect to the current regime allows a biologist to explain observed fitness differences between individuals. Finally, relational function is fully normative. If the function of x (in R) is to do m , then X is being selected for in R because of its (tokens') capacity to do m . That just means that individuals whose x 's are capable of doing m are, on average, favoured by selection. Individuals whose x 's cannot do m , on average, suffer a fitness decrement as a result. From the perspective of the individual, all in all, it's a good thing if its x can do what X is being selected to do. If a token x is incapable of doing m , (in propitious conditions) it is malfunctioning. Traits (tokens and types) have many effects which do not dispose the trait to be selected for in R . These effects are accidents. Thus the function/malfunction distinction and the function/accident distinctions are preserved intact under the relational account of E-function.

The difference between the aetiological theory and the relational theory of E-functions can be thought of as follows. According to the aetiological theory, the function of a trait is not a causal power or a disposition of the trait. It is the product of a past process. Consider Millikan's claim that the 'basic form' of the definition of evolutionary function, 'looks to the *history* of an item to determine its function rather than to the item's present properties or dispositions'.²⁵ In contrast, according to the relational theory, the E-function of a trait is a property or disposition which has some causal role within a selection process. The difference manifests itself in the following way. Suppose that we ascribe to x the function m with respect to R . By the relational theory, this entails that in any regime matching the description of R , tokens of x would

causally contribute to the average fitness of their bearer's by doing m . There is no such implication under the historical theory. It is because RF casts evolutionary function as a causal power or disposition of a trait to contribute to fitness that it allows us to elucidate the relation between evolutionary function and Cummins function.

3. Relation of C-Function to E-Function

A number of recent works have attempted to determine the relation between C-function and E-function within biology.²⁶ There are two general approaches. One is to minimise, or deny, the apparent differences between the C-function and E-function concepts (P.E. Griffiths, 'Functional Analysis and Proper Functions'; P. Kitcher, 'Function and Design'). The other is to acknowledge that C-function and E-function are distinct concepts suited to disparate, more or less discrete domains of biology (Godfrey-Smith, 'Function'; Amundson and Lauder, 'Function without Purpose'). Each of these approaches makes an interesting and important claim, but neither, we believe, fully captures the important relation between C-functions and E-functions. We discuss these proposals in turn before moving on to our own account.

Kitcher proposes the unification of evolutionary and causal role functions, stressing the overlap of their respective extensions. He claims that whenever one ascribes a function of either sort there is a source of design in the background. It is, presumably, design which suits systems to functional analysis in the first place. In biology, the source of design is natural selection in the past:

I claim that Cummins has captured an important part of the notion of biological function, but that his ideas need to be integrated with those of the etiological approach, not set up in opposition to it. When we attribute functions to entities that make a causal contribution to processes, there is, I suggest, always a source of design in the background.... [Where organisms are involved] ... selection lurks in the background as the ultimate source of design, generating a hierarchy of ever more selection pressures, and the structures, traits and behaviours of organisms have functions in virtue of their making causal contribution to responses to those pressures. (P. Kitcher, 'Function and Design,' 390)

24 A single regime, R , may be both historical and current; when that is so, the function is both historical and current.

25 R.G. Millikan, 'Propensities, Exaptations and the Brain,' in *White Queen Psychology and other Essays for Alice* (Cambridge, MA: The MIT Press 1993), 13; emphasis in original

26 Including K. Neander, 'The Teleological Notion of "Function"'; P. Kitcher, 'Function and Design'; P. Godfrey-Smith, 'Functions: Consensus without Unity'; R.G. Millikan, *White Queen Psychology*; P.E. Griffiths, 'Functional Analysis and Proper Functions,' *British Journal for the Philosophy of Science* 44 (1993) 409-22; and R. Amundson and G. Lauder, 'Function Without Purpose.'

The Kitcher proposal recognises that *m's* being the C-function of a feature does not preclude its also being an E-function. We advocate this much of his view. However, it is worthwhile noting that if functions, either C-functions or E-functions, are as we have described them, then 'design by natural selection' is a part of neither concept. 'Design by natural selection' is an inherently historical notion. To say that a system exhibits a given design because of natural selection is to say that there has been natural selection *in the past* for the structure of the system.²⁷ Cummins is quite explicit that his conception of function is wholly independent of design by natural selection.²⁸ We have urged that selection in the past is not integral to E-functions. Kitcher's proposal for unity fails because of its reliance upon natural selection in the past to ground both C-functions and E-functions.

Amundson and Lauder ('Function without Purpose') effectively make the point that there are many applications of function in biology which do not presuppose natural selection in the past. They acknowledge aetiological evolutionary functions as usually understood, but argue that they are of limited use in many fields of comparative biology. They discuss how functional anatomists and physiologists often ascribe a function to a feature without any concern for, or knowledge of, its selectional history. They argue that the concept of evolutionary function is often not applicable to these subject areas. The kind of function deployed in them is causal role function, or what we have called 'C-function.' There is much to applaud in Amundson and Lauder's discussion. However, as they do not recognise a category of non-historical E-functions, the question is left open whether the functions ascribed by physiologists and anatomists fall within this category.²⁹

So, we have two proposals for relating C-function to E-function. One (Kitcher, 'Function and Design'; Griffiths, 'Functional Analysis and Proper Functions') stresses their similarity. Kitcher explicitly advocates the reduction of C-function to E-function. The other (Amundson and Lauder, 'Function without Purpose'; Godfrey-Smith, 'Functions') argues that C-function and E-function are very different concepts with different domains. Both approaches are predicated upon a strictly historical

²⁷ See C. Allen and M. Bekoff, 'Biological Function, Adaptation, and Natural Design,' *Philosophy of Science* 62 (1995) 609-22. There may well be an ahistorical sense of 'design,' but there is no ahistorical sense of 'design by natural selection.'

²⁸ This point is stressed by Godfrey-Smith in 'Functions.'

²⁹ We return to this question once we have developed our account of the C-function/E-function relation.

account of evolutionary functions. We believe that when E-function is construed in accordance with RF, the relation between C-function and E-function becomes clearer and much more interesting than either of these proposals suggests.

It is quite evident that there are significant differences between the C-function and E-function concepts as we have presented them, so there is little hope of a straight reduction of one kind of function to the other. A synopsis of the differences is instructive.

First, the causal role (or disposition) of a *token x* in a particular system determines its C-function. The causal role (or disposition) of *token x* in a system is neither necessary nor sufficient to determine its E-function.³⁰ Take the example of poor Sally's heart. EKG traces inform us that her heart fails to pump blood (efficiently). It is still the E-function of her heart to pump blood, despite the fact that it is incapable of doing so. Sally's problem is precisely that her heart does not have the C-function of pumping blood with respect to her circulatory system. Her heart does cause traces (albeit aberrant ones) to appear on a paper when hooked up to a cardiogram machine. This is the C-function of Sally's heart with respect to *that* system; but it is no E-function of the heart to cause traces of any sort to appear on a paper.

Second, C-functions and E-functions differ significantly over what they entail about tokens and types. A feature has an E-function (with respect to a selective regime) only if it is a member of a type, each member of which has the same E-function. A trait token *x*'s membership in trait type X determines its conditions of proper functioning. It is this feature of E-functions that underwrites the function/malfunction and function/accident distinctions. Considerations of type membership are irrelevant to the ascription of C-functions.

Third, E-functions and C-functions play different explanatory roles. C-functions explain the capacities of *token* systems by citing the causal powers of their components; they are causal explanations. The capacity of Sally's heart to produce electrical pulses explains how the (token) cardiogram machine produces traces on a piece of paper. E-functions, in contrast, explain the presence or persistence of trait *types* by citing some typical effect; they are teleological. Vertebrates have hearts and will continue to have hearts because hearts contribute to average individual fitness by pumping blood.³¹

³⁰ See R.G. Millikan, *Language, Thought, and other Biological Categories* ch. 1 and 'In Defense of Proper Functions'; K. Neander, 'Functions as Selected Effects.'

³¹ Cummins (in a personal communication) made this point to us quite vividly.

Not only are the C-function and E-function *concepts* quite different, so are their extensions. There are many applications of C-function in biology for which E-functions are inappropriate. We can ascribe a function, a C-function, to a biological entity or process even when it makes no contribution to the *fitness* of the system under analysis (in any regime). Many of the systems to which C-function analysis is applied in biology are not units of selection. For instance, one may do a C-function analysis of the role of krill (*Euphausia sp.*) in marine food webs and find that krill fix energy from plankton, and feed baleine whales. This is the causal contribution of krill to the flux of energy in marine ecosystems; it is their C-function with respect to an analysis of that system. There needs to be no assumption that natural selection has designed the ecosystem in this way. A function ascription of this type would not have the explanatory consequences usually associated with E-function ascriptions; it simply explains how energy flows through one trophic level of the marine ecosystem. It does not explain how krill came to be present in marine environments, or their prospects for future success, nor should we require it to. Nor would this ascription of function have the normative import associated with E-functions. We would not be entitled (or inclined) to say of an individual krill which happened to avoid being eaten by a whale, that it had malfunctioned.

C-functions may be ascribed even when the system of which the feature is a part *is* a unit of selection. This may occur when the feature doesn't *positively contribute* to the system's fitness. In some cases the fitness contribution may be negative. Such ascriptions are important in pathology for example. In certain auto-immune diseases, such as rheumatoid arthritis and multiple sclerosis, the immune system reacts to parts of the body as though they were antigens. We may ask for the function of, say, B-cells of the immune system in the production of the symptoms of arthritis. The answer is that B-cells attack the hyaline cartilage of synovial joints, causing swelling, deformation and pain. This is most definitely a C-function of the B-cells of an individual against the background of the symptoms of arthritis, but it is no evolutionary function. It does not explain what B-cells are *for*. Even though this may be considered a *malfunction* of B-cells, it is nevertheless an important contribution to the production of the symptoms of arthritis. In other

According to his (C-function) conception, 'the function of hearts explains circulation, not hearts.' E-function explanations, in contrast, are natural selection explanations. On what natural selection explains, see E. Sober, 'Natural Selection and Distributive Explanation: A Reply to Neander,' *British Journal for the Philosophy of Science* 46 (1995) 384-97.

cases the fitness effect may be neutral. Consider the case of junk DNA. Junk DNA replicates itself just like normal DNA. It plays a causal role in replication comparable to any other region of the DNA molecule. Thus it has a C-function within an individual, to contribute to the replication of the genome. However, junk DNA does not contribute to an individual's fitness. Junk DNA has a C-function within an individual, to replicate itself, but it has no E-function for the individual.³²

To say that C-function and E-function are different concepts (with different extensions) is not to say that there isn't an important relation between them; there is. One way to demonstrate this relation is to investigate how, typically, E-functions are discovered. It is fairly uncontroversial that the E-function of the heart is to pump blood. Enç (1979) outlines the procedure by which Harvey's discovery of the heart's function was made.

The search for the function of the heart is carried out relative to some property of the blood ... the property in question here is a *capacity* (or dispositional property), and the search consists in finding out how what the heart does *contributes to the exercise of this capacity*. Thus discovering the function of a part at least involves discovering some capacity or property (often dispositional) and showing (a) how the physical movements of that part bring about the production of some effect ... and (b) how *the production of that effect is causally necessary for the exercise of the discovered capacity*. (Enç, 'Function Attributions and Functional Explanation, 347; emphasis added)

It is clear from Enç's account that Harvey discovered the E-function of the heart by conducting a Cummins-style analysis.³³ The analytic strategy, *A*, was to consider the heart, *x*, as part of a system, *s*, (the circulatory system), with respect its capacity, *y*, to nourish the body's tissues. In the context of this analysis, the function, *φ*, of the vertebrate heart is to circulate blood. Enç's account is intentionally reminiscent of Cummins's description of the heart's C-function:

32 Junk DNA has an evolutionary function at the level of the gene. The E-function of junk DNA is to replicate itself. Replicating itself and having no fitness consequences for the individual has high fitness consequences for the junk DNA. Doing just that explains why junk DNA is present. These are the E-functions of junk DNA at the level of the gene.

33 Harvey may not have *known* he was discovering the E-function of the heart. Presumably he possessed neither the concept of fitness nor that of a selective regime. Nevertheless, he discovered (*de re*, so to speak) the E-function of the heart because he performed the kind of functional analysis by which E-functions are revealed.

It is appropriate to say that the heart functions as a pump against the background of an analysis of the circulatory system's capacity to transport food, oxygen, wastes, and so on, which appeals to the fact that the heart is capable of pumping. ('Functional Analysis,' 64)

We clearly have a case where the E-function of a trait and its C-function, with respect to an analytical account, coincide.

The point here is a methodological one; evolutionary functions are discovered by conducting C-function analysis.³⁴ It seems quite evident that *m* could not be designated the evolutionary function of a trait token, *x*, unless there were a Cummins-style functional analysis which established that it is (or was) the C-function of *some token* of *x*'s type to do *m*.³⁵ This is a necessary condition for a C-function analysis to reveal an E-function, but it is not sufficient; something more is needed to make a C-function an E-function. Recall that the E-function of a trait token is determined by the contribution to the *average fitness* of *individuals* possessing tokens of its type. So, in addition the C-function analysis would have to be such that:

- (i) the most inclusive system under analysis, *s*, is the *individual* (or the relevant unit of selection),
- (ii) the capacity of *s*, ψ , to which *x* contributes is survival or reproduction or both: i.e. the contribution of *x* is to *s*'s *fitness*, and that,
- (iii) doing ψ significantly contributes to the *average fitness* of those individuals possessing the trait type to which *x* belongs.

Conditions (i)-(iii) are intended to stipulate that the causal role revealed by the C-function analysis is also the (or a) contribution of that trait type to *average individual fitness*. Not every C-function analysis of fitness contribution reveals this *typical* contribution to fitness. Consider a C-function analysis of poor Sally's heart. Sally's heart does not make the same causal contribution to her fitness that *properly* functioning vertebrate hearts make to the average fitnesses of their bearers. Hence whatever contribution Sally's heart makes to her survival cannot be its

³⁴ A similar point is made by P.E. Griffiths in 'Functional Analysis and Proper Functions.' For a superb example of how E-function is revealed by C-function analysis, see Kingsolver and Koehl's discussion of the function and evolution of insect wings: J.G. Kingsolver and M.A.R. Koehl, 'Aerodynamics, Thermoregulation, and the Evolution of Insect Wings: Differential Scaling and Evolutionary Change,' *Evolution* 39 (1985) 488-504.

³⁵ The functional analysis need not involve the token *x* itself.

E-function. A Cummins-style analysis of her heart would not reveal the E-function of vertebrate hearts.

So what is the relation between the C-function concept and the E-function concept? As we mentioned, there is no straight reduction of one concept to the other. However, conditions (i)-(iii) above suggest that we can reduce E-function to C-function *plus* the concept of *contribution to average individual fitness* (with respect to a selective regime) employed in the definition of relational function, RF. The following relation holds:

The E-function of a trait token (with respect to a regime) is that C-function which constitutes the (positive) contribution to average individual fitness for tokens of the trait's type (with respect to that regime).

Notice that this reduction of E-function to a kind of *typical* C-function does not entail that if it is the E-function of (token) *x* to do *m*, then *x* actually performs *m* in the economy of the individual. All it entails is that traits of *x*'s *type* significantly and positively contribute to the average fitness of individuals by doing *m*.

One might be tempted to object that if there is to be any reduction of one kind of function to the other it should go the other way, because, to quote Dennett, '... [t]he biologist who helps himself even to such an obviously safe functional category as *eye*, *leg*, or *lung* is already committed to assumptions about what is good.'³⁶ Evidently, one cannot ascribe a C-function to a lung without recognising it as a lung, and *lung* is an E-functional category. So, E-function ascription is prior to C-function ascription. The objection fails to heed one of the salient differences between C-functions and E-functions made above. C-functional analyses hold over trait tokens without any regard to the types of which they partake. Thus, unlike E-function ascriptions, C-function *ascriptions* are made to a trait irrespective its type membership. Consequently, one may perform a C-function analysis on a token *lung* without first recognising it as falling under the E-functional category *lung*. While it may well be true that trait types in biology, such *eye*, *leg*, or *lung*, are defined according to their E-function, that does not entail that the E-function of a trait token must be recognised prior to an analysis of any of its C-functions.³⁷

³⁶ D.C. Dennett, 'Intentional Systems in Cognitive Ethology: The "Panglossian Paradigm" Defended, in *The Intentional Stance* (Cambridge, MA: The MIT Press 1987) 237-86, at 278; *italics in original*. We thank an anonymous referee from this journal for raising this challenge.

³⁷ We happen to think, contra Millikan and Neander, that traits are not individuated by their E-functions. For biologists, trait types are defined by relations of homology.

We may now turn briefly to Amundson and Lauder's claim that physiologists and functional anatomists generally attribute C-functions which are not evolutionary functions.³⁸ We agree that physiologists and anatomists attribute C-functions to traits, on the basis of Cummins-style functional analyses. But they don't attribute just any C-functions. The important questions are: 'which C-functions are these sciences interested in?' and 'why these rather than others?' Amundson and Lauder's response is correct as far as it goes; they state that 'functional anatomists typically choose to analyze integrated character complexes which have significant biological roles' (450). But what constitutes a 'significant biological role'? It seems to us that a trait has a significant biological role when it contributes to the survival and (or) reproduction of individuals, and that this role is typical for the trait type. That is to say that typically a C-function has a significant biological role insofar as it meets the conditions (i)-(iii) above. When that occurs, the C-function is also an E-function. We claim that the C-functions most commonly ascribed by anatomists and physiologists are also E-functions and are interesting because they are E-functions.³⁹

The above discussion suggests that every E-function is a C-function. More precisely, if m is the E-function of trait x , then m is a C-function of a significant proportion of (most of?) the tokens of x 's type. This tells us the relation between the respective extensions of the C-function and E-function concepts. Consider the matrix on page 511; it encompasses the full range of function ascriptions in biology.

Each of the cells represents a legitimate kind of C-function in biology. We have argued, contrary to the historical theory of evolutionary function, that the concept of E-function comprises cells 1 and 2. When the

Lauder, for example, discusses the use of functions in cladogram construction (G.V. Lauder, 'Homology, Form, and Function,' in B.K. Hall, ed., *Homology: The Hierarchical Basis of Comparative Biology* (San Diego: Academic Press 1994) 151-96). He concludes that sameness of function is evidence for — albeit defeasible evidence for — sameness of biological trait type. If sameness of function is defeasible evidence for sameness of biological trait type, then functions cannot be the criterion for individuating biological traits.

³⁸ See also Cummins's *The Nature of Psychological Explanation*, 29.

³⁹ Our claim here is reminiscent of a point made by Cummins. Arguing against a definition of function proposed by Nagel, Cummins says 'it would at most tell us which effects are picked out as functions; it would provide no hint as to why these effects are picked out as functions' ('Functional Analysis,' 60; emphasis in original). This echoes our criticism of Amundson and Lauder's view quite nicely. They correctly identify which C-functions are attributed by anatomists and physiologists, but do not answer the question why these effects are picked out as functions.

Selective Salience for s		
Explanatory Role	Enhances average fitness of s	Does not enhance average fitness of s
aetiological	1	3
non-aetiological	2	4

selective regime is set as a past regime, and conditions (i)-(iii) (above) hold, the result of a Cummins-style functional analysis will be an historical E-function (cell 1). It will entail an explanation of the aetiology of the trait. When the selective regime is current, and conditions (i)-(iii) hold, the result will be an ahistorical E-function (cell 2). It will entail an explanation of what a trait is for, but may or may not entail an explanation of its aetiology.⁴⁰ C-functions may fail to be evolutionary functions and yet may entail an explanation of a trait's prevalence (cell 3). The example of junk DNA belongs here.⁴¹ Some cases falling within cell 4 have already been discussed: the function of krill in a marine ecosystem and the function of B-cells in the production of the symptoms of rheumatoid arthritis. These are non-aetiological non-E-functions. All four kinds of C-function ascriptions are important in biology. Only two of these, 1 and 2, are E-functions.

III Aetiological, Teleological, and Causal Explanation

The relation between E-function and C-function is mirrored by the relation between their respective explanatory roles. As we discussed, the Cummins approach to functions and the evolutionary approach are motivated by sharply divergent opinions on the explanatory role that functions ought to play. The theory of evolutionary functions we present is motivated by the view that E-function ascriptions are teleological and sometimes aetiological. For Cummins, functional explanations are

⁴⁰ These, we believe, are the functions most commonly ascribed in comparative anatomy and physiology, those functions discussed at length by Amundson and Lauder in 'Function without Purpose.'

⁴¹ We expect examples of this sort to be rare.

strictly causal, and neither teleological nor aetiological. It would seem that Cummins functions and evolutionary functions are appropriate to different kinds of questions. Cummins functions answer how-questions, e.g. 'how do hearts contribute to the activities of the circulatory system?' Evolutionary functions answer why-questions, e.g. 'why do vertebrates have hearts?' or 'why will vertebrates continue to have hearts?' E-functions explain the (prevalence or) persistence of trait types. C-functions explain the effects of tokens.

Within evolutionary biology, however, the distinction between why-questions and how-questions is not so trenchant: why-questions just are a certain kind of how-question and certain answers to how-questions constitute answers to why-questions. To explain what a trait is *for* (i.e. to give a teleological explanation) in evolutionary biology is to explain *why* that trait type persists from one time to the next under natural selection. In turn, *why* a trait persists is explained by citing *how* the trait type contributes in general to the fitnesses of its bearers (with respect to some selective regime). Teleological explanation in biology is a special case of causal explanation which invokes contribution to fitness. E-function attribution has teleological import precisely because it identifies a certain *typical causal role* (i.e. a typical C-function) in the determination of individual fitness. When that causal role has occurred in *past regimes*, the teleological explanation that function attribution issues in is also aetiological. Thus, within evolutionary biology, aetiological functional explanation is a special kind of teleological explanation, which, in turn, is a special kind of causal explanation. The relation between causal, teleological and aetiological explanations reflects the relation between Cummins-style, evolutionary and historical functions. The subsumption of teleological explanation under causal explanation, *via* E-function, requires that E-function is a causal power or disposition. It is one of the virtues of the relational theory that it identifies E-function as a causal power or disposition.

IV A Taxonomy Of Functions

We propose a taxonomy of functions as depicted in Figure 1.

Figure 1 is to be interpreted in the following way. We recognise three 'nested' categories of function, each is distinguished by its explanatory role. The end of each branch represents a category of function (from left to right: causal, non-teleological C-functions; current E-functions and historical E-functions). Each is marked by the authorities who have proposed it as a more or less complete account of biological function. Our conception of the relation of C-function and E-function is represented by the square brackets along the top of the diagram (labelled

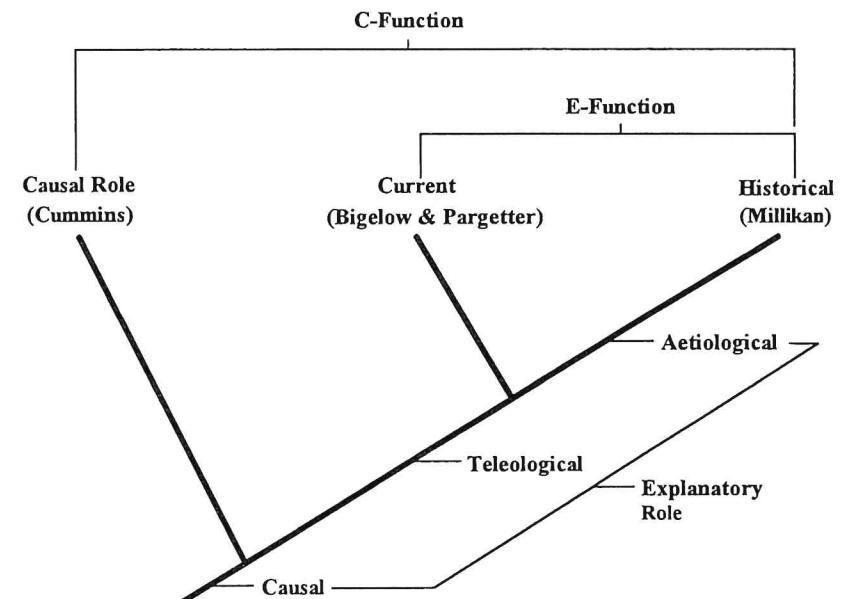


Figure 1. A proposed taxonomy of functions. See text for details.

'C-function' and 'E-function'). Historical E-functions (The 'Millikan' functions) constitute a proper subclass of E-functions, as do current E-functions (the 'Bigelow and Pargetter' functions). E-functions as a whole constitute a proper subclass of C-functions (the 'Cummins' functions). The characteristic explanatory roles which distinguish the various types of function are shown along the main branch of the diagram (labelled 'Causal,' 'Teleological,' and 'Aetiological'). As discussed in the previous section, all function ascriptions explain (a certain kind of) causal role. A subset of these, E-functions, further explain the prevalence and (or) persistence of trait types by citing their causal contribution to average fitness of individuals. Such explanations are teleological. A more exclusive subset of evolutionary functions, historical E-functions, are aetiological. They explain the current presence of a trait by advertizing to the causal contribution to average fitness within the history of the lineage.

V Conclusion

We endorse the relational theory of evolutionary function. Doing so permits us to elucidate the relation between the two concepts of function employed within biology. E-functions are a kind of C-function typical for traits of a type where the causal contribution is to fitness. Consequently, the E-function of a trait is discovered by conducting a C-function analysis of its trait's typical contribution to the survival and reproduction of the individuals possessing it. Finally, the explanatory roles played by E-functions are special cases of the explanatory role of C-functions. The presence and maintenance of traits is explained by citing that trait's causal role in the survival and reproduction of individuals within a selective regime.

Received: August, 1995

Revised: April, 1996

Consistency Among Intentions and the 'Simple View'

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What is the relation between the intention to A and doing A intentionally? It is natural to suppose that the latter entails the former. That is, it is natural to accept what Michael Bratman has called the 'Simple View' of the relation between acting intentionally and having an intention. Bratman is one noteworthy writer who has denied that the Simple View is true. In the present paper I do not defend this view. I contend that one well-known argument that Bratman offers for thinking that the Simple View is false fails, in fact, to disprove it. If there are reasons for thinking that the Simple View is false, as I believe there are, they are not the ones that Bratman has offered. My discussion of Bratman also raises some more general questions about the principles governing the rational formation of intentions. I suggest that a special sort of example casts doubt on the tenability of a commonly accepted principle that Bratman, among others, utilizes.

Bratman holds that an agent may A intentionally without having (or having had) the intention to A. One of his two lines of argument for this contention rests on a certain kind of case. He gives an ingenious example meant to show that the alleged connection between intentional action and intention fails to hold. This involves someone playing a set of connected video games. The player is very skillful at guiding 'missiles' at video targets. Each game has one target, and hitting the target gives the player a score. The games are connected in such a way that both