

Proper Function and Recent Selection

Peter Schwartz

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Abstract:

"Modern History" versions of the etiological theory claim that in order for a trait X to have the proper function F, individuals with X must have been recently favored by natural selection for doing F (Godfrey-Smith 1994, Griffiths 1992, 1993). For many traits with prototypical proper functions, however, such recent selection may not have occurred: traits may have been maintained due to lack of variation or due to selection for other effects. I examine this flaw in Modern History accounts and offer an alternative etiological theory, the Continuing Usefulness account, which appears to avoid such problems.

1. Introduction.

Etiological accounts of the notion of proper function in biology, which say that a trait can only have a proper function F if it has been favored by natural selection for doing F, have dominated much of the philosophical debate after Wright (1973). Even critics of this approach admit it is needed to describe one of the concepts at work in biology (Amundson and Lauder 1994, Walsh 1996). One of the most important developments within the etiological school has been to claim that the relevant natural selection must have occurred recently, often in the form of maintenance selection (Griffiths 1992, 1993, Godfrey-Smith 1994). I describe the reasons for this shift to the "modern history" (MH) view, and the resulting theories, in section 2.

However, a simple yet important problem arises for such accounts: for many traits with prototypical proper functions, such recent selection may not have occurred. Traits may have been maintained in the population due to lack of variation or due to selection for other effects. In section 3, I describe how this may happen. Thus if the MH theory correctly explicated the concept of proper function, biologists could not assign proper functions to even prototypically functional traits, since scientists (usually) don't know that the necessary form of maintenance selection has occurred. I elucidate this fatal flaw for the MH account in section 4.

But the difficulty does not necessarily sink the etiological approach in general, since etiological theories can avoid the problem by dropping the Modern History requirement. In section 5 I propose an alternative called the Continuing Usefulness (CU) theory, and describe its advantages.

Independently of the success of this theory, the lesson is clear: an explication of the concept of proper function in biology should not require recent selection to have occurred. In general, philosophers and biologists need to pay careful attention to the distinction between a trait's contributing to survival and reproduction by doing F and its being favored by natural selection for doing F¹.

2. Modern History Views and Reasons to Accept Them.

I will concentrate on two views that require selection to have acted recently (or to have been expected to have done so (Griffiths 1992, 1993)) in order for a trait to have a proper function. Both theories accept that multiple

¹ Here and elsewhere in the paper, "trait" refers to a type of trait. A trait type contributes to survival and reproduction only if instances of the trait do so regularly in individual organisms.

ideas of function are at work in biology and concentrate on the concept of proper function, i.e. the concept that carries the implication that there is an available evolutionary explanation for the trait (Griffiths 1992, 1993; Godfrey-Smith 1994). "Causal role functions," in contrast, many agree, were correctly explicated by Cummins (1975) and have no such implications. Millikan (1989) and Neander (1991) emphasize that the proper function of a trait, unlike its causal role function, plays a key role in determining whether the trait falls under biological categories like "heart" and in determining what states of the trait count as dysfunctional². Neander (1991) presented an influential explication of proper function in terms of natural selection:

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.
(174)

This account and Millikan's (1984, 1989) similar one place no restriction on when the relevant action of natural selection occurred.

In contrast, Godfrey-Smith (1994) and Griffiths (1992, 1993) require the action of recent selection for a trait to have a proper function, and I'll consider their accounts here. Following Millikan (1984, 1989), Godfrey-Smith (1994) treats human hearts as a "family" of "members" whose properties are the result of "copying," and he presents the following definition of proper function:

(F3) The function of m is to F iff:

² Recent critiques have argued that many biological categories organize traits by causal role function or homology (Amundson and Lauder 1994), but it is still relatively uncontroversial that ones like "heart" are based on proper function.

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

Godfrey-Smith's two main novelties are his requirement in (ii) that the members of the family T "are components of biologically real systems" and in (iv) that they have been selected "in the recent past."

Griffiths (1992, 1993) states his version of the Modern History requirement in slightly different terminology. The important sort of selection for him is that which blocks "regressive evolution," i.e. changes which result when a trait no longer plays a key adaptive role, such as when a cave-dwelling species becomes sightless. He (1993) defines the notion of "an evolutionarily significant time period" for a trait as

... a period such that, given the mutation rate at the loci controlling T and the population size, we would expect sufficient variants for T to have occurred to allow significant regressive evolution if the trait was making no contribution to fitness.

(417)

A "proximal selective explanation" is "one that involves the action of selective forces during the last evolutionarily significant period, or would

have involved such action during that period had the mutation rate not fallen below expectation" (417-8). Using these terms, he states his formal account of proper function:

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

Griffiths' definition is slightly more liberal than Godfrey-Smith's since it doesn't require actual recent activity by natural selection: it is enough that natural selection "would have" acted if the mutation rate had not dropped "below expectation." The crucial fact for both theorists is that the selection was recent, and Griffiths (1992, 1993) emphasizes that such selection usually acts to maintain the trait in the population.

Godfrey-Smith (1994) and Griffiths (1993) present three reasons to move from an account like Neander's to an MH view. The first, and probably most prominent, stems from the fact that the original selection for any trait may have favored an entirely different effect than the one which counts as the trait's current proper function. For example, theorists have suggested that feathers first became widespread because they allowed thermoregulation (Ostrom 1979), only later being utilized for flight. Gould and Vrba (1982) treat feathers as a prototypical example of an "exaptation." Although other biologists cling to the theory that feathers originally arose under selection pressure for flight (e.g. Feduccia 1996), we must at least admit uncertainty over what role feathers originally played.

The original selection for almost any trait may be similarly obscure, and Godfrey-Smith (1994, 358) gives a number of examples: a) bones may have first arisen as a way of storing phosphates; b) electrical prey-stunning

systems in some eels may have first been organs for just sensing prey; c) neurotransmitters in our brains may have first been chemicals for communicating between individuals. These examples suggest that making proper functions rest on facts about long-ago natural selection is unwise, for two reasons: first, we don't know much about such selection, and, second, even if we did, it might well sanction the wrong proper functions. In contrast, recent selection looks much more appropriate for both purposes: biologists can make more confident inferences about what recent selection has favored, and such natural selection has a higher likelihood of favoring the "right" effects.

The second motivation for concentrating on recent selection comes from a distinction that biologists make between types of explanations. As Godfrey-Smith (1994, 351) notes, Tinbergen (1963) classically separated four ways that we can mean the question "why does this behavior occur?" We can be asking about a) the mechanisms that cause it, b) its current functions, c) its evolutionary history, or d) its development. This division has been accepted as something like dogma in behavioral ecology and other areas of evolutionary theory (c.f. Mayr 1961; Sherman 1988), and, according to it, explanations involve either claims about a trait's function or its evolutionary history. Thus an account that makes function depend on evolutionary history seems to ignore a distinction that biologists accept.

The shift to a MH account recreates a distinction, though, without dropping the reference to natural selection in the definition of function. While evolutionary explanations may involve natural selection acting at any time, or even such processes as genetic drift, functional explanations (according to the MH account) involve only recent natural selection. Although both evolutionary and functional explanations involve natural

selection, they do so in different ways, and are different kinds of explanations. This formulation leaves the distinction weak, but perhaps strong enough to make sense of the practice of biologists. Functional explanations will understandably emphasize effects with current survival value, since these effects will often be the ones that were recently favored by natural selection.

Third, Griffiths (1992, 1993) stresses the MH theory's correct classification of vestigial traits, which biologists consider to be prototypically functionless. Griffiths points out that before a trait becomes vestigial, it carried out an important role and was probably favored by natural selection for doing so. If an account of proper function only requires that the trait was favored for having the effect at some point, then these vestigial traits still have their proper functions, in violation of biological practice. The MH account blocks this problem: as long as the trait has not recently been favored for doing F, it does not have F as its proper function, and thus soon becomes vestigial relative to F. If a trait has lost all its proper functions, it is a "vestige simpliciter" (1993, 417).

3. Maintenance of Useful Traits without Natural Selection.

Despite these three good reasons to shift to the MH theory, a basic problem interferes: many traits with prototypical proper functions may not have been recently favored by natural selection for carrying them out. Even if X contributes to survival and reproduction of individuals with this trait by doing F, two possibilities exist³: either a) there may not have been suitable variation in X for natural selection to have occurred at all, or b) selection which maintained X in the population may have favored some effect other than F. Although Griffiths (1992) and Godfrey-Smith (1994) recognize these

³ "X" refers to a type of trait, like Godfrey-Smith's "T" and Griffiths' "i".

possibilities (as I will discuss below), they don't delve into the biological details or discuss the grave consequences for their theories, as I do here. The most serious problem is that in most cases biologists do not have sufficient data to rule out these circumstances. So, if their classification depends on a judgment about the recent action of natural selection, they can not be confident about the proper function of traits. In fact, I will argue below, biologists may have grounds to be much more confident about the action of natural selection in the distant past -- especially when the trait was being modified rather than just maintained -- than about its current action.

Natural selection only acts when there is "heritable variation in fitness" (Lewontin 1970; Endler 1986, 4; Sober 1993, 9). For natural selection to occur at some time, three conditions must hold:

- S1) there is variation in the trait in question,
- S2) the variation is heritable, and
- S3) the variation in the trait results in a difference in fitness.

Requirements (S1) - (S3) serve most importantly to remind us that it's not so easy to know when selection is occurring. There are many obstacles to directly showing the existence of such heritable variation and fitness differences, and studies doing so are few and far between (Endler 1986). For most traits in most populations biologists simply do not have this data.

In addition, there are reasons why natural selection may decrease variation in useful traits. Beyond directly eliminating maladaptive genes, selection may favor genetic arrangements which reduce the risk of the trait's failing to be expressed, in a process called "canalisation" (Waddington 1959). Given a trait X which makes a crucial contribution to survival and reproduction by doing F, natural selection will favor individuals with the lowest percentage of offspring and grandoffspring lacking the trait. Wagner

(1996) presents computer models of evolution where genomes evolve to suppress the phenotypic effects of mutations. Calling this effect "epigenetic stability," he writes,

... a quite indirect process is at work, in which genotypes with low epigenetic stability are eliminated from a population due to the large fraction of maladapted offspring they produce. A reorganization of the epigenetic system towards high stability to mutations takes place. (1018)

There is even some empirical support for the idea that a trait's importance to fitness is correlated with resistance to changes. Stearns and Kawecki (1994) estimated the importance of various traits to fitness in drosophila, and then introduced a cause of random genetic change (a "P-element plasmid insert"). They found that the importance of a trait to fitness -- the amount of expected change in fitness due to the trait's changing by 10% -- was negatively correlated with the amount of variation seen in the offspring.

Admittedly, it's not clear how often such a process can completely eliminate heritable variation. And a more optimistic assessment of our knowledge may reason as follows: given a complex trait such as feathers and the ubiquitous occurrence of mutation and recombination, some individuals must have arisen recently with heritably inefficient feathers. But even with some heritable variation in a useful trait, another major problem arises: the trait may not be maintained for the right reasons. For example, individuals which are born with heritably worse feathers for flying may have died or failed to reproduce for reasons which have nothing to do with natural selection for efficient flight. Imagine that feathers of type p1 are ubiquitous in some species, and that, due to a mutation, individuals with feathers of type p2 arise, where from an engineering standpoint feathers of type p2 are worse

than feathers of type p1 at producing efficient flight (in this species). But p2 feathers may make their bearers more susceptible to hypothermia, or may less efficiently elicit feeding from parents, and these effects could kill off such individuals before they even have a chance to fly. Under these scenarios, the elimination of p2 feathers from the population would be due to their other effects, rather than their failure to allow efficient flight.

Similarly, pleiotropic effects of genetic changes may cause the elimination of some heritable variation. Consider genetic change g2 which would lead to feathers of type p2 in individuals surviving to adulthood: other effects of g2 may mean that individuals with feathers of type p2 will also have other maladaptive traits. Perhaps all individuals with p2 feathers can be expected to have malformations of some other ectodermal tissue. Once again, if these individuals die before they have a chance to attempt (inefficient) flight, phenotype p1 would be maintained because of these other effects of g2, not because of the inefficiency of p2 feathers for flight.

This may sound like a far-fetched example, but when biologists investigate genes which they think play certain roles, they often find that they play other roles which are even more crucial. Cheng et al. (1995) and Turner et al. (1995) began their investigations of the Syk gene's function in mice to investigate the apparently crucial role it plays in the development of B cells. They attempted to confirm this with a standard "knockout" experiment, i.e. producing mice lacking the gene (homozygotes for a "knockout" mutation) and looking for defects in B-cell development. The only problem was that most "knockout" mice died during development or just after birth, apparently because of the knockout allele's failing to carry out a role Syk usually plays in the development of blood vessels. Thus, Syk may be maintained because of its effects during development, rather than its effects

in the immune system.

4. Consequences for the Modern History View.

As mentioned above, both Griffiths (1992) and Godfrey-Smith (1994) recognize the possibility described in Section 3 but downplay it.

Godfrey-Smith (1994) writes:

The modern history view does, we must recognize, involve substantial biological commitments. Perhaps traits are, as a matter of biological fact, retained largely through various kinds of inertia. Perhaps there is not constant phenotypic variation in many characters, or new variants are eliminated primarily for non-selective reasons. That is, perhaps many traits around now are not around because of things they have been doing. Then many modern-historical function statements will be false. If functions are to be understood as explanatory, in Wright's sense, there is no avoiding risks of this sort." (356-7, my underlining)

Godfrey-Smith (1994) is willing to stick with the MH view despite these counterintuitive possibilities because he thinks that only such an account can solve the problems discussed in Section 2. I hope I have shown in Section 3 that the problem facing the MH view is more dire than Godfrey-Smith realizes: for even the most prototypical traits with proper functions, biologists cannot be confident in the action of recent natural selection.

And the existence of this uncertainty really does mean that his theory cannot fulfill the goal he sets for it. Godfrey-Smith (1994) says that he wants to provide a conceptual analysis of proper function which is "... guided more by the demands imposed by the role the concept of function plays in science, the real weight it bears, than by informal intuitions about the term's

application" (345). As mentioned above, one of proper function's key roles is justifying placing objects into categories like "heart," and a concept whose explication includes the Modern History requirement cannot play such a role: biologists could almost never be confident that an organ should count as heart since they could almost never be confident that it was recently favored by natural selection for pumping blood.

Griffiths (1992) also recognizes the danger I have described, and also discounts it in formulating his definition of proper function. He repeatedly acknowledges that a trait which stops contributing to survival and reproduction may be maintained due to its performing some other function, such as playing some key role in embryology, or because "there is no genetic variation" (1992, 127; also see 122, 123, 125, 129). But although he recognizes the problem, he provides little response; for example, he concludes his initial acknowledgment of the difficulty by writing, "How common this phenomena is must be determined by empirical research, rather than philosophical speculation" (123). While this is certainly true -- only biological research can tell us the prevalence of non-selective maintenance of useful traits -- it's unclear why this helps his account: it seems that a philosophical explication of a concept purportedly currently at work in biology shouldn't depict biologists as relying on assumptions which they don't and can't currently make.

Thus, the most that the MH account can claim is to have identified a sufficient condition for a trait's having a proper function F, a condition which it may turn out most such traits satisfy. The MH account could only claim to provide a conceptual analysis of proper function if biologists knew that they lived in the sort of world which would be produced if each trait had only one effect and each varied independently from all others. As Griffiths (1992)

writes about the assumption that any trait undergoes regressive evolution if it stops performing its proper function, "It is a neat picture. It would be nice if it were true" (129). But since the real world may deviate from this picture, the MH account falls seriously short as conceptual analysis.

5. The Continuing Usefulness (CU) View.

Both Griffiths and Godfrey-Smith cling to their MH accounts despite these difficulties because they see no other way that the etiological approach can handle the problems discussed in Section 2. But there may well be such a theory, which I will introduce here and call the Continuing Usefulness (CU) account. According to this view, a trait type X has the proper function F if and only if

- C1) X has arisen, been modified, or been maintained by natural selection at some point because its doing F contributed to the fitness of individuals with X, and
- C2) X's doing F has recently contributed to the survival and reproduction of organisms in this population (or species) with this trait.⁴

Like Godfrey-Smith's version of the modern history account, and unlike Griffiths', the CU account makes no attempt to define "recently"; despite arguable borderline cases, presumably most will be clearly recent or not.

We can quickly see that the CU account can handle the three problems that motivated the MH account. First, the CU theory assigns the correct proper function to traits, like feathers, that may have first arisen as

⁴ Condition (C2) most closely resembles the theory Neander (1991, 182-3, Fn. 12) mentions as a suggestion received in personal communication from both Christopher Boorse and William Lycan.

exaptations. Although feathers may have arisen for reasons unrelated to flying, they must have been favored for carrying out this role at some point: they are just too perfectly suited for flying for any reasonable biologist to see all of their facets as the result of drift or the lucky side-effects of other selected traits (c.f. Feduccia 1996, Norberg 1990). Similarly for other prototypical traits with proper functions, such as bones: although bones may have first arisen as phosphate storage devices, the many aspects of their structure which are so efficient at supporting animals and serving as levers must have been fashioned at some point by natural selection for us to have any explanation for their existence at all.

Second, the CU account describes a distinction between functional and evolutionary explanations much like the one described by the MH account: functional explanations are a subset of evolutionary explanations since they concentrate on traits which still perform (or have performed until recently) the roles which were favored by natural selection. Third, the CU account clearly withholds proper functions from vestigial traits: although the eyes of naked mole rats were once favored for allowing sight, they haven't allowed sight recently. Finally, the CU account preserves the explanatory implications of proper function ascription: saying that X has the proper function F implies that a complete explanation of X's prevalence or form must mention X's being selected at some point for doing F.

Before presenting the formal version of his theory, Griffiths writes, "A trait is a vestige relative to some past function F if it has not contributed to fitness by performing F for an evolutionarily significant period" (1992, 128; 1993, 417; my underlining). If we take "evolutionarily significant period" as meaning (roughly) "recently," then the CU account's condition (C2) rules vestiges functionless for the same reason. But Griffiths' (1992, 1993) formal

account of proper function requires not just that functional traits have contributed to fitness recently by doing F, but also that they were avored by natural selection recently for doing F; thus a trait which continues to contribute to fitness by doing F can be vestigial (in respect to F) if there was no selection for its doing F. The (CU) account avoids the problems this raises by separating the requirement that selection occurred (in (C1)) from the requirement of recentness (in (C2)).

Admittedly, the CU theory faces problems of its own, but none as dire as the ones facing the MH view. One problematic notion is the idea of a trait's "contributing" to survival and reproduction, in condition C2. A number of theorists have questioned how we can judge that, for example, feathers contribute to flight if they are not currently being maintained for aiding flight (Millikan 1993, 40; Godfrey-Smith 1994, 352). Without delving too deeply into these worries, let me dissipate them. First, we can take "X's doing F contributes to survival and reproduction in individuals with X" as meaning that instances of X play a causal role function in individuals with X in generating the capacity to survive and reproduce. Both Millikan and Godfrey-Smith accept our ability to judge causal role functions independently of natural selection's occurring, so they shouldn't question our judging that traits have causal role functions of this sort in situations where maintenance selection is not occurring. Second, we often formulate hypotheses about the evolution of traits by first judging how they contribute to survival and reproduction in currently living individuals. Saying that we can't judge the former without judging the latter reverses the epistemological order.

An advocate of the CU view must admit that it relies on a prior distinction of parts of animals into traits, which cannot be cashed out in terms of evolution. For example, cases could arise where an evolutionary change

could be described as either the modification of an existing structure X -- sanctioning attributing X the proper function F -- or the creation of a second structure Y while leaving X unchanged, giving proper function F to Y, not X. These will be cases where there can be a continued standoff over whether or not to attribute the proper function F to X. This possibility for ambiguity, though, may not arise that often: for example, in almost all cases it is clear whether to count a morphological change as a modification of the feather or a change in another part of the body. Splitting the animal up into traits may always remain a basic aspect of biological theorizing which cannot be formalized, depending as it does on perceptions of parts and wholes.

Space limitations preclude further analysis or defense of the proposition that the CU account correctly explicates the biological concept of proper function, but at least this theory shows the possibility of continuing to analyze proper function etiologically after the demise of the Modern History requirement. In addition, the difference between the MH and the CU theories should emphasize a general lesson. When thinking carefully about evolutionary theory and the notions related to it, we must keep distinct in our minds the distinction between a trait's contributing to survival and reproduction of bearers by doing F, and a trait's being favored by natural selection for doing F. Despite seminal attempts to prioritize this distinction (as in Williams 1966), it's forgotten at key places in philosophy of biology. For example, Walsh (1996) writes, "The positive casual contribution that a trait makes to average individual fitness within a regime is just the property that the trait is (or was) being selected for in that regime" (565, my underlining). Without a peculiar understanding of the terms "causal contribution" or "fitness," this is not strictly true.

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