Proper Function and Recent Selection

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"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's (1973, 1976) influential work. Griffiths (1992, 1993) and Godfrey-Smith (1994) have refined this approach by arguing that it must add the claim that the relevant natural selection occurred *recently*, often in the form of maintenance selection. I describe the reasons for this shift to the "Modern History" (MH) view and the resulting theories, in Section 2.

In Section 3, I describe how 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 due to lack of variation or due to selection for other effects.

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In Section 4, I specify some of the problems this causes for the MH account. For example, if the MH theory correctly explicated the concept of proper function, biologists often could not assign proper functions even to prototypically functional traits, since scientists usually do not know that the necessary form of maintenance selection has occurred. This greatly weakens the etiological school's seemingly best attempt to elucidate proper function and thus also weakens the hope of explicating biological teleology in terms of natural selection.

In Section 5, I describe how the etiological approach can survive by adopting a theory I introduce and name the "Continuing Usefulness" (CU) account. According to this account, a trait has the proper function F if and only if, first, the trait was favored by selection for doing F *at some point* (perhaps far in the past), and, second, the trait has *recently* contributed to survival and reproduction by doing F.[1] This separates the requirement involving natural selection from the requirement involving recent activity; on my view, the MH account conflated these. I explain and defend the CU account, especially the weak adaptationism assumed by the first condition and the causal notions invoked by the second.

2. Modern History Views. Both Modern History (MH) theories accept that multiple 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, were correctly analyzed by Cummins (1975) and have no such implications. Millikan (1989b) 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 dysfunctional.[2] Neander presents 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

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[1] Here and elsewhere in the paper, "trait" refers to a *type* of trait, unless otherwise noted. A trait-type contributes to survival and reproduction only if tokens of the trait do so in individual organisms.

[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.

> the phenotypic expression, to be selected by natural selection. (1991, 174)

This account and Millikan's (1984, 1989b) 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; for the purposes of this paper, both will count as MH accounts even though there are slight differences between them (which I will discuss below). They present three reasons to add the MH requirement. The first, stressed by Godfrey-Smith (1994), stems from the fact that the original selection for any trait may have favored an entirely different effect than the one that counts as the trait's current proper function. For example, theorists have suggested that feathers first became widespread because they allowed thermoregulation, only later being utilized for flight (Ostrom 1979). 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 do not 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 (cf. Mayr 1961, Sherman 1988), and, according to it, explanations involve claims about *either* 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 an 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 the action of such non-selective processes as genetic drift, functional explanations involve only recent natural selection, according to the MH account, and thus form a narrow "subset of evolutionary explanation" (Godfrey-Smith 1994, 356). This sort of distinction isn't a particularly impressive one, but it's not clear that biology needs the distinction to be any more robust than this. 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 any trait became 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 theory. 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).

As mentioned above, Godfrey-Smith's (1994) and Griffiths' (1992, 1993) theories are slightly different, and I will describe each more precisely here. Following Millikan (1984, 1989b), Godfrey-Smith 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:

(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. (1994, 359, my italics)

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 terms. The important sort of selection for him is that which blocks "regressive evolution," i.e., changes that result when a trait no longer plays a key adaptive role, such as when a cave-dwelling species becomes sightless. He 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. (1993, 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" (417–418). 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. (1993, 418)

Griffiths' definition is slightly more liberal than Godfrey-Smith's since it does not 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.

3. Maintenance of Useful Traits without Natural Selection for the Useful Effect. A basic problem, however, confronts the Modern History view: 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 exist[3]: either a) there may not have been suitable variation in X for natural selection to have occurred at all, or b) selection that maintained X in the population may have favored some effect other than F. Although Griffiths (1992) and Godfrey-Smith

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

(1994) recognize these possibilities (as I will discuss below), they do not 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 functional classification depends on a judgment about the recent action of natural selection, biologists cannot be confident about the proper functions of traits. In fact, I will argue, 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 recent maintenance selection.

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 is 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 that reduce the risk of the trait's failing to be expressed, in a process called "canalisation" (Waddington 1959). Given a trait X that 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. (1996, 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 trait.

Admittedly, it is 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 the large amount of genetic code required for 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 that are born with heritably worse feathers for flying may have died or failed to reproduce for reasons that 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 cannot produce as efficient flight as feathers of type p1 (in this species). But p2 feathers may make their bearers more susceptible to hypothermia, or less efficient at eliciting 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. Imagine now that p2 feathers carry no unfortunate side-effects such as hypothermia or starvation; the feathers are just relatively inefficient for flight. But it is possible that the genetic mutation (let's call it g2) that would lead to feathers of type p2 has effects on other traits—i.e., pleiotropic effects—that are maladaptive. For example, perhaps g2 causes a malformation of some other ectodermal tissue: once again, if individuals with g2 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 a gene that they think plays a certain role, they often find that it plays other roles that 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 (homozygous 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 by selection because of its effects during development, rather than its effects in the immune system.

4. Consequences for the Modern History View. So a trait with an effect that is crucial to survival and reproduction, the sort of effect biologists are eager to consider a proper function, may be maintained in the population for reasons other than natural selection's favoring its accomplishing this useful effect. I will call this the possibility of "Non-Selective Maintenance" (NSM), even though it includes situations where selection favors some effect. As mentioned above, both Griffiths (1992) and Godfrey-Smith (1994) recognize this possibility but downplay it. Godfrey-Smith 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." (1994, 356–357, my italics)

In some sense, he is correct to say that any etiological theory takes "risks of this sort," but he ignores how drastically magnified they are after the addition of the MH requirement. It's much rarer that there has not been *any* selection, *ever*, for the effect that we consider the trait's proper function than just that there has not been any such selection *recently*.

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 that 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 a heart since they could almost never be confident that it was recently favored by natural selection for pumping blood.

Griffiths (1992) also recognizes the possibility of NSM and also discounts it in formulating his definition of proper function. He repeatedly acknowledges that a trait that 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 reveal the prevalence of NSM—it is unclear why this helps his account: it seems that a philosophical explication of a concept purportedly *currently* at work in biology should not depict biologists as relying on assumptions that they do not and cannot *currently* make.

An MH proponent could argue that although NSM *is* a real possibility, biologists ignore it (*assume* that it is not a possibility) when assigning proper functions, and thus the MH view correctly characterizes the concept of proper function they are using (albeit relying on a flawed assumption).[4] This response would be worthy of more consideration if there were independent evidence that biologists ignore the possibility of NSM whenever they assign proper functions and use functional language: the MH theorists have not presented such evidence, and biologists do discuss the possibility of NSM in many specific cases, often in conjunction with the use of functional language (cf. Emlen et al. 1991, Jamieson 1991). In addition, the Continuing Usefulness (CU) account I introduce in the next section sanctions proper function assignments that match those of biologists, without depicting them as relying on any erroneous assumptions. Without some more direct evidence that biologists ignore the possibility of NSM when assigning proper functions, the CU theory must count as superior to the MH account as conceptual analysis.

5. The Continuing Usefulness (CU) View. In this section, I present and discuss a theory that handles the problems Griffiths (1992, 1993) and Godfrey-Smith (1994) raised for previous etiological theories, as well

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[4] David Magnus and Ruth Millikan have mentioned this possible defense for the MH theorists to me.

as the ones I raised above for their theories. I call it the Continuing Usefulness (CU) account:

> A trait-type X has the proper function F (at time t) if and only if
> C1) X has arisen, been modified, or been maintained by natural selection at some point (prior to t) because its doing F contributed to the fitness of individuals with X, and
> C2) X's doing F has recently (prior to t) and importantly contributed to the survival and reproduction of organisms in this species with this trait.

The idea of "contributed" in (C2) is meant in a causal sense: X has contributed to survival and reproduction if its trait-tokens have helped individuals with these tokens survive and reproduce. 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. The theory stands firmly within the etiological school because of condition (C1). This condition also preserves the explanatory implications of proper function ascription, widely prized by etiological theorists since Wright (1973, 1976), because 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.[5]

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 exaptations (Gould and Vrba 1982). 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 (cf. 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 that are so efficient at supporting animals and serving as levers must have been favored by natural selection at some point 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

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[5] Condition (C2) resembles a proposal Neander (1991a, 182–183, fn. 12) reports she received in personal communication from Christopher Boorse and William Lycan, but neither she nor they consider combining this condition with an etiological requirement, as I do here.

account: functional explanations are a subset of evolutionary explanations since they concentrate on traits that still perform (or have performed until recently) the roles that 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 have not allowed sight recently.

The CU view raises two prima facie questions. 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 fitness" by allowing flight if the feathers are not currently being maintained for aiding flight (Millikan 1989a, 174; 1993, 39–40; Godfrey-Smith 1994, 352). Without delving too deeply into these worries, let me dispel them. We can take "X's doing F contributes to survival and reproduction in individuals with X" as meaning that tokens of X play a causal role function 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. And although many effects (other than aiding flight) may count as causal role functions of feathers, only ones that have also been favored by selection at some point will count as proper functions, according to the CU account.

The second problematic issue stems from the suggestion of adaptationism reflected by any etiological condition like (C1). Other etiological theorists have by-passed this issue (e.g., Godfrey-Smith 1994, 344), and space limits me to saying very little, but I will say this: the CU theory relies on only a *weak* adaptationism that is quite tenable. It is weak since it does not claim that *all* traits with a useful effect count as an adaptation for producing that effect, only that *some* do. Dawkins (1986) presents a compelling discussion of many such traits. For example, we require some explanation for the many facets of feathers—from the high strength to weight ratio, to the microscopic hooklets and barbules which link feathers together to form an airfoil (Feduccia 1996, 130)—that make them such efficient facilitators of flight. Although any one of these facets may be a non-selected by-product of other selected parts or of an immutable aspect of development, it is completely beyond reasonable biological thought to claim that *no aspect of feathers was ever favored by natural selection for contributing to flight.* If this were true, we would have no explanation how such an apparently well-designed object could have come into existence. Even if biologists cannot be confident that selection has recently maintained feathers because of their effect on flight, they can be confident that at least some of the features of this incredibly efficient item were selected at some point for their contribution to flight.

Admittedly, the CU view (like many accounts of function) must rely on a prior division of animals into parts, in ways that cannot be cashed out in terms of evolution alone. 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. Millikan (1993) has discussed cases of this type. These will be cases where a standoff may develop 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 that cannot be formalized, depending as it does on perceptions of parts and wholes.

In summary, the CU account presents a viable form of the etiological approach to proper function, which handles the problems that motivated the Modern History account and those that weaken it. Also, 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 is forgotten at key places in philosophy of biology.

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