14. Real Traits, Real Functions?

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ABSTRACT

Discussions of the functions of biological traits generally take the notion of a trait for granted. Defining this notion is a non-trivial problem. Different approaches to function place different constraints on adequate accounts of the notion of a trait. Accounts of function based on engineering-style analyses allow trait boundaries to be a matter of human interest. Accounts of function based on natural selection have typically been taken to require trait boundaries that are objectively real. After canvassing problems raised by each approach, I conclude with some facts that satisfactory notions of trait must respect.

In the extensive literature on what it means for a biological trait to have a function, philosophers and biologists have given the notion of function star billing. They have paid little attention to the notion of trait appearing in the supporting role. My goal in this chapter is to turn the spotlight onto this fundamental notion and demonstrate that we lack and need an analysis of trait. I use 'analysis' here with a broad meaning that encompasses traditional conceptual analysis, theoretical definition, and other ways of specifying meaning.

Before embarking, it is useful to address another terminological point. Many biologists prefer the term 'character' to 'trait'. There are a couple of reasons for this. First, it appears that Darwin himself did not use the term 'trait' to refer to the properties of organisms, writing instead of characters. Secondly, 'character' has found favor with systematists, who have introduced a technical distinction between characters and character-states (explained below). Thus provenance and technique combine to invest 'character' with a cachet that the more homely 'trait' lacks. Nevertheless, 'trait' is ubiquitous and I, like many

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others, will use the term freely and interchangeably with ‘character’ to refer to properties of organisms that interest biologists.

Although my route to the topic of traits goes through theories of function, questions about the delineation of traits have broad significance for biology and the philosophy of biology. For example, the boundaries of the traits or structures identified by morphologists and paleontologists are important for phylogenetic inference. Questions of whether to lump or split behavioral patterns into one action or two for the purpose of developing an ethogram play a similar role in ethology. The question of how much precision is to be expected or desired in the notion of a trait is as fundamental to the philosophy of biology as related questions about notions such as *species* (see contributions to Ereshefsky 1992), *environment* (Brandon 1990), and *niche* (Smith and Varzi 1999). Of course, much useful biological research has proceeded in the absence of completely satisfactory analyses of key terms. Darwin himself wrote on the origin of species, without settling the question ‘what is a species?’ Likewise, Mendel investigated the inheritance of sweet pea traits without settling the obvious question ‘what is a trait?’ Scientific success is obviously possible in the absence of answers to such questions, but it does not follow that there is nothing to be gained by raising such questions, and it would be fatuous to suppose that those who raise such questions are dismissing the science as hopeless.

This chapter has the nature of preliminary work. I do not intend to offer a definitive answer to the question ‘what is a trait?’, for I am skeptical that any single answer will be satisfactory, any more than any single analysis of *species* has proven satisfactory for all biological purposes. It is an important task for the future to try to specify what answers suit which purposes, but that is a much larger project than can be accomplished here. The more restricted project in this chapter is to identify roles that different notions of trait might play in the debate about biological functions.

The chapter is divided into five sections. In the first section I describe the two major approaches to understanding functions that have emerged in both the biological and the philosophical literatures. In the second section I survey the relatively scarce amount that has been written about the notion of trait. The third section introduces a distinction between effectively nominalist approaches to identifying the traits of organisms, which make trait selection a matter of human interest, and effectively realist approaches, which attempt to provide more objective criteria for traithood. In the third and fourth sections I describe some apparent shortcomings in the effectively nominalist approach to traits implied by Cummins’s account of functions and some problems with an effectively realist proposal derived from the work of Godfrey-Smith. In the fifth, final section I conclude with some facts that satisfactory notions of trait must respect.

1. Two Accounts of Function

To set the stage for understanding the role of the notion of trait in the analysis of functions, this section contains an overview of the two major approaches to the notion of function. While biologists have tended to focus more narrowly on attributions of function within their science, philosophers have often had an eye on the broader applications of the term beyond biology. Nonetheless, the same two classes of approach have come to dominate both the biological and the philosophical literatures.

- *Etiological* approaches to function look to a causal-historical process of selection; functions are identified with those past effects that explain the current presence of a thing by means of a historical selection process (typically natural selection in the case of biological function).
- *Systems-analysis* approaches invoke an ahistorical, engineering style of analysis of a complex system into its components. Functions of components are identified with their causal contributions to broader capacities of the system.

There are variant views within these two classes, and there are accounts of function that attempt to meld them. There are also many accounts of function that fall outside these general approaches. These details are amply illustrated in the other contributions to this volume so they need not detain us here.

Philosophers have tended (perhaps somewhat parochially) to identify the two kinds of approach with the philosophers who first articulated them in the philosophical literature. Etiological approaches are associated with Wright (1973) and engineering-analysis approaches are associated with Cummins (1975). Indeed it is quite common to see the labels 'Wright functions' and 'Cummins functions' used by philosophers to identify the two approaches. Precedents for each kind of approach can, however, be found independently in the biological literature. (This is not to deny that Wright and Cummins significantly advanced the development and understanding of the respective approaches. But see Pittendrigh 1958, Tinbergen 1963, Williams 1966, Ayala 1970, and Hinde 1975 for examples of the historical approach; Rudwick 1964, and Bock and von Wahlert 1965 for the systems-analysis approach; and see Allen *et al.* 1998 for an overview and representative papers.)

As the preceding citations indicate, much of this work on the notion of function was done during the third quarter of the twentieth century. During the latter part of the century, particularly since the mid-1980s, there has been a resurgence of philosophical interest in analyses of function, driven largely by the development of evolutionary approaches to the phenomena of mind and language. Most prominently, proponents of 'teleosemantics' have constructed naturalistic accounts of the phenomena of meaning and mental content in terms of proper function, while offering solutions to puzzles about cognitive error and misrepresentation by assimilating them to typical cases of biological malfunction. The notion of biological function has, consequently, occupied a central position in the debate about teleosemantics.

Evolutionary approaches to the phenomena of mind and language have borrowed extensively from the pre-existing literature on functions and teleology (with the possible exception of Millikan 1984, who seems to have constructed her theory of proper function *ab initio*—see Millikan 1989 for comparisons). The earlier work was not directly concerned with questions about the functions of mind or language. Indeed (rightly or wrongly) many of the biologists responsible for this early work would be more than a little skeptical of the possibility of justifying claims made about the evolution of such traits. Whether or not such skepticism is justified, it behoves those who would make claims about the functions of mind, language, beliefs, or sentences to say something about the identification of such traits within their preferred approaches to function.

Different accounts of function place different theoretical and practical constraints on an adequate notion of trait. For instance, etiological accounts that center on natural selection require an account of trait that allows the reidentification of traits across generations while providing a suitable framework for the causal requirements of natural selection. Furthermore, the comparative method required to establish hypotheses about etiological function mandates, if the approach is practicable, the identification of traits across taxonomic groups. Systems analyses, as well as being expected to support the comparative method, require that traits be identifiable as components that make a distinctive causal contribution to the system capacity in question.

Criteria for trait identity are important to arguments about human evolution. Some arguments about the uniqueness of the human mind, human language, and human culture depend on the refusal to identify a human trait with certain traits of non-humans or of our ancestors (see Allen and Saidel 1998). Other claims about the evolutionary function of complex features of organisms presuppose that it is proper to classify these complex features as single, real traits. None of these claims or arguments can be properly investigated without a clear conception of what we mean by ‘trait’. We cannot persuasively argue that human language is a different trait from vervet monkey communication, or even that it is a trait at all, without first having specified what we mean by ‘trait’ and whether that meaning is suitable to the task at hand. The next section surveys some attempts to define the notion of trait.

2. Definitions of Trait

Although ubiquitous, the notion of trait is rarely introduced explicitly. Authors typically help themselves to it without comment. There are a few exceptions, but these are typically less than enlightening. For example, in their exposition of evolutionary theory, von Schilcher and Tennant (1984: 31) explicitly introduce 'trait' alongside 'characteristic' as a stylistic variant of 'property', but they remark that the notion of property has itself 'eluded satisfactory analysis by philosophers'. Aside from a remark about Wittgenstein to illustrate their point, they leave it at that.

As mentioned above, biologists typically link the notion of trait to that of character. For example, the entry for 'character' in the glossary of Futuyma's widely used textbook (1998) on evolutionary biology makes this connection. 'Character' is itself defined in conjunction with 'character-state'. The distinction between characters and character-states is explained by Eldredge & Cracraft, who write (1980: 30 n.):

> The terms 'character' and 'character-state' merely refer to similarities at two different hierarchical levels. Thus the character 'feathers' is a common similarity of all birds, although specific character-states of the character 'feathers' (e.g., variation in color, texture, and pattern) would be similarities common to various groups of birds. At the same time, it is apparent that even the character 'feathers' could be considered a character-state, say within the vertebrates, if the systematist were considering the 'character' to be the vertebrate integument.

In this passage, Eldredge and Cracraft note that the distinction between character and character-state is relative to the level of phylogenetic analysis. Sober (1988) describes the character/character-state distinction as a special case of the determinable/determinate hierarchy familiar to philosophers. Roughly, a determinable is a more general property (for example, color) that can be specified more determinately (for example, red, green). Typically, the more determinate categories are themselves determinable by yet more determinate properties (scarlet, crimson, . . .), leading to a hierarchy of determinable/determinate relations. This is illustrated by Sober (1988: 35) with the example of bipedalism and quadripedalism as character-states of walking, which is in turn a character-state of locomotion.

Phylogenists are faced with the problem of how to enumerate characters. Cladists, who base their systematics on counting shared characters among members of different species, must be especially careful not to double count by treating two dependent characters as if they were independent, for this can lead to mistaken inferences about the relationship between species. The number of digits on the left forelimb should not, for example, be treated as an independent character from the number of digits on the right (indicating that the relevant notion of independence is not merely logical or nomological). Whether double counting matters for other purposes to which the notion of trait might be put is an open question.

On the same page as the passage quoted above, Eldredge and Cracraft express some embarrassment about their appeal to perceptual similarity as a basis for judgments of shared character. Specifically, they make a remark about the 'infinite regress' in the idea that what is similar is what is judged similar by biologists. Here, perhaps without realizing it, they have hit upon a special case of a difficulty facing any effectively nominalist understanding of properties that is based on a primitive, unanalyzed notion of similarity.

Some explanation of this last remark is in order. Eldredge and Cracraft do not provide a theoretically motivated set of criteria for, nor even constraints upon, the classification of characters or traits. If such criteria or constraints existed and were formulated to be independent of human choice, they would provide a framework for a 'realist' account of characters: that is, an account that provided for the existence of characters delineated by natural processes independent of human theorizing. In metaphysics, nominalism is the view that abstract categories have no real existence. While we should not infer that Eldredge and Cracraft are committed to metaphysical nominalism—for their failure to provide independent criteria or constraints might simply be a symptom of a gap in knowledge rather than a sign of a particular philosophical disposition—nevertheless, their account of characters is *effectively nominalist* (or *effectively non-realist*) because the account itself provides no criteria for character differentiation that would support a realist account.

Bock and von Wahlert (1965: 272) also give an effectively non-realist account of trait—although their preferred term is 'feature', characterized as 'any part, trait, or character of that organism, be it a morphological feature, a physiological one, behavioral, biochemical, and so forth'. They offer a definition of 'feature' as follows: 'Any part or attribute of an organism will be referred to as a feature if it stands as a subject in a sentence descriptive of that organism.' (It is clear from the context that they mean to exclude relational properties by the terms 'part' and 'attribute'.) In contrast to Eldredge and Cracraft, Bock and von Wahlert can be read as endorsing a more explicitly nominalist theory of traits when they embrace the implication that their broad definition commits them to, that there is no privileged way of dividing an organism into features (traits). As they put it: 'The limits of a feature are generally set arbitrarily.' Using the notion of a morphological feature to illustrate, they continue, 'the limits of a feature defined in morphological terms are almost always set in an arbitrary fashion with regard to its development, genetics, and evolution. Hence morphological units should not necessarily be considered as real or absolute units of an organism for other biological studies.'

One might wonder whether effectively nominalist or non-realist conceptions of traits are too shifty to serve as bedrock for function attributions. An alternative, self-avowedly realist conception of trait is suggested by Godfrey-Smith in his book *Complexity and the Function of Mind in Nature.* He writes (1996: 2–23):

> [my] thesis refers simply to 'cognition' as if this was a single thing, a single trait. However, the generalized category of 'cognition', even if it picks out a single kind relevant to everyday discussion, may not reflect a single evolutionary reality. 'Cognition' may well be a collection of disparate capacities and traits, each with a different evolutionary history. . . . we will focus on a small and allegedly fundamental set of mental phenomena. We are concerned with a basic apparatus that makes possible perception, the formation of belief-like states, the interaction of these states with motivational states such as needs and desires, and the production of behavior. Even this contracted set may not constitute anything like a single trait, for evolutionary purposes, but we will proceed on the assumption that it does.

Godfrey-Smith does not fully articulate what he means by 'single trait' or 'single evolutionary reality'. Nor is it exactly clear from his discussion whether his intention to apply both the etiological and analytical notions of function requires the assumption that he makes. Nonetheless, this is one of the few intimations in the literature on evolutionary approaches to function that the notion of a trait needs to be analyzed and that a realist analysis might be provided.

3. Nominalism and Realism

Before proceeding to discuss the relationship between the two major approaches to functions and the positions I have labeled 'realism' and 'nominalism', it is important to note that these terms as I have been using them must be treated with care because ultimately there are metaphysical issues that remain after the more empirical issues facing biologists and philosophers of biology are addressed. It is possible to maintain that scientific theories are ultimately neutral on the traditional metaphysical dispute between realists and nominalists. Hence, even if one were to accept something like Godfrey-Smith's construal of a single trait, a philosophical issue of whether to treat any such property as metaphysically real remains. Where appropriate, I use the qualifier 'effective' (or 'effectively') to indicate the more limited distinction between, on the one hand, effectively realist accounts that place relatively strong constraints on the individuation of traits, and, on the other hand, effectively nominalist accounts that do not provide strong constraints.

There is a correlation between positions taken on this more restricted version of the realism/nominalism debate and the two main approaches to functions. Effectively realist views appear more often among those sympathetic to etiological theories of function, while effective nominalism is more common among supporters of ahistorical systems-analysis approaches. Although both approaches appeal to causal mechanisms in their accounts of function, the type of causal processes consistent with etiological accounts, because based on natural selection, is more circumscribed and arguably less relative to researchers' interests. This idea that etiologically characterized functions are objectively real appears to be a factor in the claim represented by Millikan's subtitle (1984): 'New foundations for realism'.

Although different conceptions of trait have different consequences for accounts of function, it is not my objective here to argue for or against any particular approach to function. I hold a pluralistic view about the notion of function in biology, according to which both etiological and systems-analysis notions of function have roles to play (Bekoff and Allen 1995). On such a view, one would not expect to find decisive arguments favoring one type of approach over the other for all biological purposes. Nonetheless, it is quite compatible with such a view that there are reasons for preferring one approach over another for specific purposes. The next two sections are concerned with pointing out some consequences of adopting effectively nominalist and effectively realist accounts of function.

4. Nominal Functions

I shall use Cummins's account of functions to illustrate the consequences of an effectively nominalist approach to traits. Cummins's account notoriously places only very weak constraints on the choice of components and capacities selected for analysis. The account is also explicit about the relativity of function attributions to specific explanatory contexts. Different explanatory aims will yield different function attributions, and, although only some of these will be of interest to biologists, all are examples of the same pattern of explanation. Thus, for example, the beating sound of a heart may have a function relative to the capacity of the body to indicate the presence of heart disease to a physician, but not with respect to the capacity of the body to move around in the world. Again, I emphasize that *the account* is *effectively nominalist* in the sense intended—namely, that the account itself specifies functions only with respect to systems and capacities delineated according to the pragmatic interests of those who employ it. (Of course, if one latches onto systems and capacities deemed real by objective standards, then the functions of system components that explain those capacities may also be real, so those who follow Cummins's account need not be committed to metaphysical nominalism.)

Cummins's formulation of the definition of function employs the phrase 'appropriately and adequately' to characterize the connection between the explaining effect of a component and the explained capacity of a system. This phrase is intended to mark a graded distinction between cases where the systems-analysis approach has a high degree of 'explanatory interest' because the explaining capacity is markedly simpler than the explained capacity and cases where there is little explanatory interest because the two capacities are relatively similar in sophistication or complexity. The question of how to measure relative complexity must be set aside here. But assuming a common-sense notion of relative complexity, it follows from Cummins's account that there would be little explanatory interest in, for example, accounting for an organism's capacity for selecting a fit mate by postulating a cognitive module that detects fitness—the capacity of the postulated detector is no less sophisticated than the analyzed capacity of the whole organism.

One might argue about the extent to which biologists are constrained in their identifications of the components and capacities of the systems they study, but the point here is that any so-called realist conception of those components is external to Cummins's account of function itself and, indeed, to any engineering-style analysis of a biological system into its components. The notion of 'appropriate and adequate' explanation that is at work in Cummins's account provides constraints on the kinds of traits and capacities involved insofar as completely invented traits may not feature appropriately or adequately in causal explanations of system capacities, whether or not those capacities are themselves construed realistically. But, if one uses Cummins's account of functions and chooses to limit one's attention to particular components or capacities, it is not because the account of functions requires one to do so. This is in contrast to etiological accounts of function, which, by appealing to specific historically causal events of natural selection, place stronger constraints on the traits to which one may attribute functions. For example, to be assigned etiological functions the traits must be heritable.

It is worth noting some consequences of Cummins's approach for two current debates. One consequence is for Godfrey-Smith's project of identifying the function of mind. Even given Godfrey-Smith's stripped-down characterization of mind as a perception–belief–desire–action device, the device thus characterized seems complex enough that one might question the explanatory interest in assigning this 'component' of an organism the function to 'enable the agent to deal with environmental complexity' (1996: 3) In fact, Godfrey-Smith seems to recognize this as he moves (1996: 16) 'to drop the requirement that the capacity explained by a function is more complex than the function itself'. This move leaves Godfrey-Smith free to attribute a complex function to the mind in order to explain a similarly complex capacity of the organism, but the result is a notion of function that arguably has lesser explanatory power.

A second debate is over whether human language and primate communication are comparable traits (Pinker 1994; Allen and Saidel 1998). Linguists are fond of pointing out ways in which human language differs from the signalling systems of other species. Ethologists are fond of pointing out the ways in which they are similar. If, given what I am calling an effectively nominalist view of traits, any perceived similarity is a good enough basis for trait identification and if the identified set of communicative behaviors in human and non-humans can be used to account for the same capacity (also, presumably, determined by perceived similarity), then both human and non-human forms of communication will be attributed the same function relative to that capacity. It is a feature of Cummins's account, about which I make no judgement, that it is neutral with respect to different stances on these issues. Either the traits are identified as similar or not, and either the explained capacities are similar or not. From one perspective, relative to the goal of explaining a given capacity, the functions of human language and another communication system are the same. From other perspectives, relative to other explanatory aims, they are not. Whether this should count as a 'bug' or a 'feature' of Cummins's account is an open question.

Finally in this section, I turn to the issue of matching systems analysis with the hierarchical conception of character and character-state. Systems analyses are based on the identification of concrete parts of a concrete particular system and figuring out the ways in which the operation of the parts contribute to the operation of the whole. It is an oft-mentioned criticism of Cummins's account that a component that fails to contribute to a capacity lacks a corresponding function. Thus, in his account, a severely deformed heart that cannot pump blood therefore does not have pumping blood as its function. Yet, if it does not have this function, it cannot be said to be malfunctioning. This objection could be escaped if the analysis of function allowed a comparison to hearts of other organisms in the same taxonomic group to determine a function for the malformed particular. But Cummins does not take this route, preferring instead to downplay (indeed deny) the significance of a notion of malfunction for scientific purposes.

Taxonomic groupings play no explicit role in Cummins's account of function. Nevertheless, it is an important part of biological practice to explain homoplasy—the existence of non-homologous common features in different taxonomic groups—in terms of common function. In Cummins's account, function attributions are relative to the identified capacity. It may, then, be possible to accommodate the biological practice by identifying capacities at different levels of abstraction corresponding to different taxonomic levels. For example, to return to Sober's examples from the character–character-state hierarchy, bipedal walking and locomotion are both capacities of mine. The contribution made by my legs to my locomotion might be described abstractly enough to match the contribution made by a parrot's wings to his locomotion. So, among the vertebrates for example, one could perhaps end up with the same function relative to the same capacity attributed to different traits.

There are difficulties, however. The level of generality that is required to identify a common function with respect to locomotion for my legs and the parrot's wings seems unlikely to meet Cummins's condition that the explained capacity be of significantly greater complexity than the explaining function. The challenge is to complete the statement that legs and wings both contribute to the capacity for locomotion by ——, where the blank is filled by something that is of considerably less complexity than locomotion while being of sufficient generality to cover the roles of both perambulation and flight in producing movement. As before, I am relying on an intuitive notion of complexity to make this point. It remains to be seen whether this notion can be spelled out adequately. Problems doing this might provide a reason to drop Cummins's greater-complexity requirement on the explained capacity (Godfrey-Smith, pers. comm.).

This is not the only difficulty facing attempts to fill in the blank at such a high degree of abstraction as the walking/flying example entails. The identified function must also be appropriate to feature in a causal explanation. Perhaps, in this case, the blank could be filled by stating that legs and wings both produce forces in the environment that, through the 'mechanism' of equal and opposite reaction, cause an acceleration of the organism. But, even if this 'function' is of sufficiently lower complexity than the capacity it is supposed to explain, it is not clear that it is adequate for a causal explanation of the capacity for locomotion, for it looks much more like a statement of Newton's law rather than a description that specifies actual causes. The more abstractly one describes a capacity, the less likely one is to be able to find a non-trivial analysis of it into components that have the right kind of causal features. What, for instance, do feathers, skin, and scales all do that makes these character-states of the vertebrate integument good candidates for the attribution of function? On a strict application of Cummins's account, Godfrey-Smith's notion that 'response to environmental complexity' is a function of mind would arguably be a victim of this difficulty. This further motivates his dropping the greater-complexity requirement so as to deploy Cummins's definition of function alongside the etiological account.

4. Real Traits, Real Problems

Let us turn now to considering consequences of an effectively realist account of traits for discussions of biological function. The reader will recall that from Godfrey-Smith's brief remarks on the matter we derived the effectively realist suggestion that a single trait is any (possibly complex) feature of an organism whose components have a common evolutionary history (CEH). Under the CEH notion of a trait, the phenotypic expression of a single allele will constitute a single trait as a limiting case, for there can be no parts with different evolutionary histories. Of more interest are traits that are polygenic in origin. If a heart is to count as a single trait, it is because its various parts (chambers, valves, and so on) have a common evolutionary history. If there are to be non-adaptive or maladaptive traits, CEH should be allowed to encompass non-adaptive mechanisms as well as the history of natural selection. The CEH approach can be considered successful insofar as it allows parts of the organism or its behavior to be carved out objectively from a phenotype. I believe, however, that the CEH approach is not adequate to the task. One problem is due to the fact that the extent to which parts of an organism's phenotype share a common history is almost always guaranteed to be a matter of degree. The evolutionary history of a finger is linked to that of other fingers, which in turn linked to the rest of the hand, the hand to the arm, the arm to the torso, and all of it to the circulatory and nervous systems, and so on. It is this holism that underlies the skepticism of Gould and Lewontin (1979) about dividing an organism into traits for separate analysis.

Gould and Lewontin attack the idea that organisms are composed of isolable traits on the grounds that organisms are tightly integrated systems whose parts cannot be antecedently identified. They write (1979: 217), 'The dissection of an organism into parts, each of which is regarded as a specific adaptation, requires two sets of a priori decisions. First, one must decide on the appropriate way to divide the organism and then one must describe what problem each part solves.' They argue that such decisions cannot be justified aprioristically. Sanford (1997) attempts to undermine their critique, arguing in contrast that a posteriori methods of trait identification are available, based on an understanding of the operative causal mechanisms. I believe that the best way to understand the notions of 'a priori' and 'a posteriori' at work in this debate is not in the traditional epistemologist's sense of prior or subsequent to experience. Rather, at issue is whether biological theory provides any way of making the divisions. In the absence of reasons for dividing up the organism in a particular way that are based on an empirically derived theory, the division is empirically and theoretically arbitrary and in that sense aprioristic.

Even if Gould and Lewontin's charge that such divisions are unacceptably aprioristic can be avoided, I would argue that CEH is problematic in failing to provide a non-arbitrary way of isolating single traits. CEH is a matter of degree, and there is no non-arbitrary way to set a threshold on how much shared history is enough shared history to identify a single real trait, except by requiring complete linkage of the genes responsible for the expression of the phenotypic character. If that threshold is adopted, then there will be relatively few complex single traits, and those that would pass the test are unlikely to correspond to our common (albeit pre-theoretical) ideas about what is to count as a single trait. There is a growing recognition that genes are shared by different systems (Piatigorsky 1998). For example, squid maintain symbiotic, bioluminescent bacteria in structures designated as 'light organs'. Enzymatic assays reveal that these organs contain high densities of proteins that are found in both ocular lenses and ordinary muscle tissue (Montgomery and McFall-Ngai 1992), indicating that lenses and muscle have a common evolutionary history. Yet it is counter-intuitive that they should be counted as the same trait.

It might be argued that such an outcome is the cost of progress—that our intuitions should not count for much and that such a thorough revision of our conception of trait is required—but that is a discussion I do not intend to pursue here. My purpose is served if this gives one more reason to agree that the notion of trait requires further investigation.

If the collection of capacities that constitute cognition, or a mind, is not a single trait by the CEH standard, is this fatal to Godfrey-Smith's project of finding the function of mind? Godfrey-Smith explicitly makes the assumption that mind is a single trait, but need he make this assumption? If the mind fails to count as a single trait, containing parts with separate evolutionary histories, then one might worry that functions grounded etiologically in natural selection could be attributed only to the parts and not to the whole. But is this worry justified? If the worry has purchase anywhere, it would be most acute in what I will call 'gerrymandered' traits: pairings or larger groupings of features that seem entirely *ad hoc*. Consider, for instance, the combination of toes and nose. Does toes + nose have any functions of its own, beyond the functions of toes and the functions of noses?

It is my view that functions of a gerrymandered trait might be objectively attributable and distinct from the simple summation of the functions of each part considered separately. Take objectivity first. Gerrymandered entities or properties can generally be accommodated within an objective framework. For instance, consider the gerrymandered entity consisting of myself (CA) and the Statue of Liberty (SOL). Call it 'CA–SOL'. The combined mass of CA–SOL is an objectively measurable property derived from the masses of each component of CA–SOL. Furthermore, we might define some other quantity, call it 'cohesion', which is a function of the gravitational attraction between CA and SOL. 'Cohesion' is not a property of either part alone, but it is a perfectly objective property of the whole that could, in principle, be measured or calculated at any moment. In a corresponding fashion, then, if toes have a function via their contributions to ancestral fitness, and noses have a function via their contributions to ancestral fitness, the gerrymandered 'trait' of toes + nose has, minimally, the combined functions. But because the toes + nose complex may have had synergistic effects for which there has been selection—in locomoting towards good smelling food, for instance—it may be possible to assign a function objectively to toes + nose that does not belong to either toes or nose alone.

Put differently, the contribution to ancestral fitness made by the complex toes + nose may have been greater than the contributions of each separately. Thus there may have been selection for the complex over and above selection for each component. (Something like an iteration of this argument may provide additional support for Gould and Lewontin's holism about selection on phenotypes.)

Of course the mere fact of objectivity does not entail that these objects or properties are of any scientific or intellectual interest. The 'cohesion' of CA–SOL is hardly of any fundamental interest to physicists, and unlikely even to be of any practical interest to anyone—not even its sentient component. It is perhaps here that Godfrey-Smith's worries about the biological reality of the traits he labels 'mind' and 'cognition' have some purchase. It can reasonably be maintained that 'mind' is not as gerrymandered as toes + nose. But the notion of mind is gerrymandered nevertheless. To see this, consider the role of learning in cognition. Classical conditioning, operant conditioning, and observational learning all have different evolutionary histories. The capacity for classical conditioning is, for instance, sensitive to the kinds of correlations between stimuli that have been salient in the natural environments of the particular species. In other words, the capacity to form a given connection between a given unconditioned stimulus (US)—for example, food—and a given conditioned stimulus (CS)—for example, bell—varies from species to species depending on the evolutionary history of that species. The capacity for operant conditioning is also affected, but by different facts about the evolutionary history. For instance, it is much easier to get pigeons to tap a stimulus with their beaks for a food reward than it is to get them to press a bar with a foot for that same reward, whereas for rats the opposite (*mutatis mutandis*) is true. These differences presumably can be explained in terms of the different natural feeding strategies (for example, pecking versus digging) in each species. Furthermore, within a given species, the capacity for classical conditioning will have been shaped by different selection pressures than the capacity for operant conditioning.

Hence, learning is not a single trait according to the CEH criterion. Since cognition subsumes learning neither is it a single trait. Even so, there may be biological functions that arise from the interactions between the various components that cannot easily be reduced to the functions of the individual system components. And, if so, it may be possible to conduct an inquiry into the biological functions of cognition without Godfrey-Smith's assumption that mind is a single trait.

The possibility remains that a trait such as 'cognition' is too gerrymandered to be of interest to biologists. Without a non-arbitrary way to say how much gerrymandering is too much, we have only a vague conception of trait. Determining the boundaries of this conception is presently a matter of interests and expedience. Consequently, etiological functions are perhaps less sparse and more interest relative than the realists have suggested.

5. What is a Trait?

In this chapter I have raised some questions about how well we understand the notion of trait. I suspect that different notions of trait are needed to serve different purposes for biologists, but here our focus has been on how these questions bear on the accounts of biological function. Even in this narrower context, it may well be that no single definition of trait will be forthcoming.

No matter what account of function biologists explicitly endorse, their approach to function attribution depends, as a matter of practical necessity, upon the comparative method that utilizes comparison of similar structures or behaviors within and outside a taxonomic group. Etiological accounts explicitly identify the functions of trait T in organism O by looking to O's ancestors to find the effects of ancestral versions of T (T*) relevant to the survival and reproduction of O's ancestors. In practice, of course, one cannot literally look to O's ancestors, who are long since deceased. Rather, one usually must apply the comparative method to the traits (T*) of related species to try to draw inferences about the functions of ancestral traits. The issue of cross-taxonomic trait identifications must also be faced by proponents of systems accounts of function if they are to provide an adequate framework for the application of the comparative method.

Attempts to deal with these cross-generational and cross-taxonomic issues must respect the following facts:

(*a*) *Phenotypic variation.* T and T* will typically be distinguishable. My nose need not be identical in shape to any of my ancestors' noses (for which I am extremely grateful in several cases). Nor need it be identical in form to a chimpanzee's nose for the comparative method to be applied.

(*b*) *Genetic variation.* The genetic causes of T will not be identical to T*. Typically, T and T* will be polygenic. The exact set of alleles responsible for my nose need not be the same as those responsible for my ancestors' noses or a chimpanzee's nose. The further back in history or across taxa we go, the less correspondence there will be of alleles, or even of loci on chromosomes.

Consequently the notion of tokens of the same trait cannot be based on genes or phenotype alone. Given the complexity of genotypic and environmental causes of phenotypes, it seems to me that any definition of 'trait' based on these notions will result in a notion of 'same trait' that is inherently vague. (See also Millikan's definition (1984) of 'higher-order reproductively established family' wherein it is a proper function of reproduced genes to produce 'similar' structures. This melding of phenotypic and genetic aspects still relies upon a potentially troubling, unanalyzed notion of similarity. For example, for some purposes squid muscles and the covers of their light organs are similar, as well as having a common genetic cause.)

Of course, biology does not and should not grind to a halt without an answer to the question 'what is a trait?' But one who has physics as a model for scientific inquiry might see the vagueness apparently inherent in the notion of trait as a reason to think that scientific biology cannot preserve such a notion as a basis for its future development. Others might see such vagueness as quintessentially biological. Just as there are no clear boundaries between species, why should there be a clear boundary between traits? Perhaps a hierarchy of trait-types can be mapped onto the taxonomic hierarchy. I argued above that, as traits are identified across broader and broader taxonomic groups, they become less suited for the kinds of causal explanations that are supposed to ground function attributions, especially in systems-analysis approaches. But perhaps this counts in favor of the proposal, for it seems rightly to capture the difference between the rather minimal informativeness of answering the question 'why do vertebrates have limbs?' with 'for locomotion' and the somewhat greater informativeness of answering 'why do cheetahs have long legs?' with 'for speed in catching antelope' without appealing to an unanalyzed notion of complexity.

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