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How to be a function pluralist

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Abstract

I distinguish two forms of pluralism about biological functions, between-discipline pluralism and within-discipline pluralism. Between-discipline pluralism holds that different theories of function are appropriate for different subdisciplines of biology and psychology (for example, that the selected effects theory of function is appropriate for some branches of evolutionary biology, and the causal role theory is appropriate for disciplines such as molecular biology, neuroscience, or psychology). I provide reasons for rejecting this view. Instead, I recommend within-discipline pluralism, which emphasizes the plurality of function concepts at play within any given subdiscipline of biology and psychology.

1 Introduction

2 Different Disciplines, Different Functions

3 Two Arguments for Between-Discipline Pluralism

4 Two Objections Against the Arguments for Between-Discipline Pluralism

5 A Survey of Function-Bestowing Selection Processes

6 Conclusion

1 Introduction

Function pluralism, simply put, is the idea that biologists use the term ‘function’ in different ways on different occasions. A consequence of function pluralism is that there can be more than one correct philosophical theory of biological function. By function pluralism, I do not mean that there is a divergence between biological and artifact functions, but rather, that ‘function’ means different things within biology itself (and perhaps some branches of psychology).¹ Many philosophers of biology have embraced function pluralism, including (Millikan [1989], p. 293; [2002]; Neander [1991], p. 181; Godfrey-Smith [1993], p. 200; Mitchell [1993], p. 259; Amundson and Lauder [1994], p. 446; Allen and Bekoff [1995], p. 612; Griffiths [1993], p. 410; [2006], p. 2; Maclaurin and Sterelny [2008], p. 114; Bouchard [2013], p. 86; and Brandon [2013], p. 98).

Many of those philosophers (with the exception of Mitchell [1993]) endorse a more specific idea that I call ‘selected-effects/causal-role pluralism,’ or ‘SE-CR pluralism’. This view holds that there are two main notions of function in biology. The selected effects theory (SE) holds, very roughly, that the function of a trait is whatever it was (perhaps recently) selected for by natural selection or some more general process of selection (see Section 5). The causal role theory (CR) holds (again, roughly) that the

¹ For an interesting discussion about the relation between biological and artifact functions, see (Preston [1998], [2003]; Millikan [1999]; Vermaas and Houkes [2003]; Lewens [2004]; Nanay [2013]; Piccinini [2015]; Maley and Piccinini [forthcoming]).

function of a trait consists in its contribution to some system capacity, which capacity has been picked out by researchers as especially worthy of attention. Garson ([2016]) gives a recent overview of these and other theories of function.

Why would anyone accept SE-CR pluralism? One plausible argument is the following. Sometimes, when biologists attribute a function to a trait, they purport to give a causal explanation for why that trait exists. That is, sometimes functions purport to answer why-is-it-there questions. Moreover (the argument continues), SE is our best current account of this causal-explanatory sense of function.² Thus, to the extent that biologists attribute functions to answer such questions, they are at least tacitly committed to SE. For example, consider a recent paper by the biologist Tim Caro and his colleagues ([2014]) entitled, ‘The Function of Zebra Stripes’. He thinks stripes have the function of deterring biting flies like Tsetse flies. It is fairly clear from the context that Caro wishes to give a causal explanation for why zebras have stripes, and that he uses the term ‘function’ to signal his intent.³

² But see Buller ([1998]) and Mossio et al. ([2009]) for attempts to construct causal-explanatory senses of function that do not appeal to selection.

³ For example, Caro uses the term ‘function’ interchangeably with what he calls ‘evolutionary drivers’ ([2014], p. 3). Additionally, he describes five different ‘functional hypotheses’ for zebra stripes, and he also refers to these as ‘factors proposed for driving the evolution of zebras’ extraordinary coat coloration’ ([2014], p. 2). Caro and his colleagues were also careful to gather *historical* data about Tsetse fly distributions, which

Sometimes, however (the argument continues), when biologists attribute a function to a trait, they simply wish to show how the trait contributes, in tandem with other traits, to some noteworthy systemic capacity, without taking any stance on its history. In other words, function ascriptions purport to answer what-does-it-do questions (or better, how-does-it-work questions). The biologist Kathleen Prudic and her colleagues ([2015]), for example, recently studied the function of eyespots on butterfly wings, and she emphasized that she merely wished to show how eyespots currently help butterflies survive (namely, by deterring predatory attacks away from vital organs). CR is probably our best current account of this sense of the term ‘function,’ perhaps with the added provision that the high-level capacity in question contribute to the fitness of the organism (or containing system). Of course, one can be a pluralist about functions while rejecting SE-CR pluralism (as in Mitchell [1993].)

Let me clarify my claim that SE is our best account of the explanatory sense of function. To the extent that function ascriptions constitute causal explanations for a trait’s existence (roughly, that they purport to answer why-is-it-there questions), I think SE is the only viable theory we have. That does not mean CR functions do not explain anything. They are explanatory, but they do not constitute causal explanations for the existence of traits. Rather, they purport to explain the system-level effect that they highlight (as in Cummins [1975], p. 748). (If one accepts that some explanations are not

would be strange if their hypothesis about function was not intended as a historical claim.

See Larison et al. ([2015]) for a recent criticism of their study.

causal explanations, then perhaps CR gives non-causal explanations for the existence of traits. Garson [2016], Chapter 5 explores this option in more detail.)

I realize that the foregoing argument for SE-CR pluralism relies on controversial premises. My goal here is not to defend the view at any length. That is because I want to pursue a somewhat different question. Assuming SE-CR pluralism is correct, can we say anything general about when, or in which contexts, biologists use the SE sense of function, and when, or in which contexts, they use the CR sense of function? One pessimistic answer to this question is ‘no’. That is, it is possible that we cannot make any generalizations here, and we just have to examine each instance of ‘function’ on a case-by-case basis to figure out which sense is at play.

A more optimistic answer is given by between-discipline pluralism. Between-discipline pluralism holds that different theories of function are appropriate to different branches of biology (and perhaps psychology as well). For example, a between-discipline pluralist might hold that SE is the most appropriate theory of function for certain branches of evolutionary biology (and perhaps evolutionary psychology), and that CR is the most appropriate theory of function for neuroscience or genetics. Proponents of between-discipline pluralism include (Godfrey-Smith [1993], p. 200; Amundson and Lauder [1994], p. 446; Griffiths [2006], p. 3; Maclaurin and Sterelny [2008], p. 114; and Bouchard [2013], p. 86). Between-discipline pluralists of this stripe can accept that SE functions occasionally crop up in other disciplines like genetics or neuroscience, but only when those disciplines purport to answer evolutionary questions (Griffiths [2006], p. 3).

Between-discipline pluralism is an attractive view. If it is correct, it gives us a way to make strong (though defeasible) inferences about which sense of ‘function’ a biologist is using just by knowing which branch of biology that practitioner belongs to. It would save us from the tedious work of sifting through (often ambiguous) textual evidence to decipher which sense of ‘function’ is at play in any given instance.

Between-discipline pluralism, however, is mistaken. It rests on an overly-narrow construal of what SE really holds. Many SE proponents have emphasized that by ‘selection,’ they do not just mean natural selection in the evolutionary sense (and potentially at multiple levels, such as genes, organisms, and groups – see Lewontin [1970]). Instead, selection captures a whole range of processes in the natural world that share a certain abstract similarity. These processes might include trial-and-error learning, antibody selection in the immune system, and even neural selection (see Wimsatt [1972], p. 13; Millikan [1984], p. 28; Godfrey-Smith [1992], p. 292; Griffiths [1993], p. 419; Papineau [1987], p. 65; Neander [2012]; Garson [2011], [2012], [2015], [2016]).⁴ There is also the sort of selection process that takes place with the differential proliferation and deletion of transposable elements in the genome, which plays an important role in molecular biology (Doolittle [1989]; Elliot et al. [2014]). All of these selection processes occur within the individual during that individual’s lifetime. If this approach to SE is correct, we have no a priori reason to restrict SE functions to the domain of evolutionary

⁴ Wimsatt ([1972]) does not define ‘function’ in terms of selection, but he acknowledges the importance of selection processes in thinking about function.

biology alone, to the exclusion of genetics, immunology, neuroscience, and some bits of psychology.⁵ Of course, it may turn out as an empirical matter that those alternative sorts of selection processes play a negligible role in those fields, but that seems unlikely, and at any rate we should not assume it prior to careful investigation.

Given the diversity of selection processes in nature, we should accept a different sort of pluralism. I call this within-discipline pluralism. Within-discipline pluralism seeks out and emphasizes the plurality of function concepts within any branch of biology. Within-discipline pluralism is the most obvious alternative once we reject between-discipline pluralism. It also has valuable heuristic value because it helps us find SE functions even where we would not have expected them to occur.

I will set out my argument in six sections. Section 2 will explain, in more detail, what between-discipline pluralism is. It will also discuss Neander's ([forthcoming (a)]) argument against this sort of pluralism. Section 3 will present two standard arguments for between-discipline pluralism, the sociolinguistic argument and the ontological argument.

⁵ The question that I am pursuing here is different from, and somewhat independent of, the question of how to define 'natural selection', per se. My claim is that, as far as SE goes, we should interpret selection very liberally to include processes like trial-and-error learning and neural selection, in addition to natural selection. I am not, however, arguing that we should accept a correspondingly liberal definition of 'natural selection' itself; I remain agnostic on that question. See Bouchard ([2008]) and Godfrey-Smith ([2009]) for two contrasting approaches to defining 'natural selection'.

Section 4 will object to those standard arguments. Section 5 surveys the diversity of function-bestowing selection processes in nature, and in particular, trial-and-error learning, antibody selection, and neural selection. Section 6 makes a pitch for within-discipline pluralism.

Function pluralism is not just of interest to philosophers. It has growing scientific significance as well. Debates about the notion of function, and about the coexistence (or lack thereof) of function concepts in biology, are becoming increasingly prominent in molecular biology, with the advent of the ENCODE Project Consortium (‘ENCODE’ stands for ENCYclopedia Of DNA Elements; see ENCODE Project Consortium [2012]). The consortium made headlines in 2012 with its claim that over 80% of the human genome is functional, contrary to the then-popular idea that most human DNA is ‘junk’. In response, philosophically-astute biologists argued that ENCODE relies on an overly-liberal construal of function that runs contrary to standard usage in biology (Graur et al. [2013]; Doolittle [2013]), or even that it conflates SR and CE functions (see Brunet and Doolittle [2014]; Elliott et al. [2014]). Proponents of the consortium recently responded to these attacks by arguing that both SE and CR play important but distinct roles in molecular biology, and that we should recognize both (Kellis et al. [2014]). In other words, the scientists behind ENCODE explicitly embraced function pluralism to defend themselves against the accusation that they were conflating function concepts or using them incoherently. Function pluralism matters outside of philosophy.

2 Different Disciplines, Different Functions

What is between-discipline pluralism? (Recall that when I discuss pluralism here, I am restricting my attention to SE-CR pluralism.) Earlier, I described it as the view that different theories of function are appropriate to different branches of biology, for example, SE goes with evolutionary biology and CR with physiology. But most theorists who endorse between-discipline pluralism probably do not take such a strict stand. Rather, they hold that different branches of biology place overwhelming emphasis on one or the other theory of function. The most attractive feature of this view is that it would provide a convenient way of tracking function concepts in biology, and help to avoid the potential confusion that results from the fact that biology deploys more than one function concept.

Rather than giving a very precise definition of between-discipline pluralism, I will present a series of quotes by its major proponents. This will convey the general idea more effectively than attempting to give a set of necessary and sufficient conditions. (I will also refer back to these passages in the next section when discussing the standard arguments for between-discipline pluralism.)

Godfrey-Smith gave the first clear statement of this sort of pluralism:

Once a modified version of [the selected effect] theory is in place, the explanatory role of many function statements in fields like behavioral ecology is clear. But there remain entire realms of functional discourse, in fields such as biochemistry,

developmental biology, and much of the neurosciences, which are hard to fit into this mold, as functional claims in these fields often appear to make no reference to evolution or selection. These are areas in which the attractive account of functions has always been that of Robert Cummins. (Godfrey-Smith [1993], p. 200)

Godfrey-Smith's view is echoed by Amundson and Lauder, who also assert the 'ineliminability' of CR functions in some branches of evolutionary biology, and in particular, evolutionary morphology:

[...] the field of biology called functional anatomy or functional morphology explicitly rejects the exclusive use of the [selected effects] concept of function. To be sure, there are other biological fields in which the SE concept is the common one – ethology is an example. (Amundson and Lauder [1994], p. 446)

Note that Amundson and Lauder are not saying that SE never appears in evolutionary morphology. Nor do they claim that CR never appears in ethology. Nonetheless, they seem to endorse the view that branches of biology, as a rule, can be sorted into two main categories depending on which theory of function its practitioners typically invoke.

Maclaurin and Sterelny make a similar claim about ecology, where, they hold, CR functions are the norm:

Function in ecology is not like function in evolutionary biology or functional morphology. In those fields, functions derive from selective history [...] It is not likely that we can explain functional roles in local communities in a parallel way [...] as a rule, local assemblages do not have selective histories. (Maclaurin and Sterelny [2008], p. 114)

Bouchard ([2013], p. 86) claims that both SE and CR functions have a role to play in biology, but he emphasizes their divergence between disciplines:

[...] one could say that Amundson and Lauder started by showing that physiology and functional anatomy exclusively use CR functions. Then Griffiths argued that developmental biology was another CR discipline. One of my goals is to add ecology as another functional orphan (relative to SE accounts) [...] (Bouchard [2013], p. 93)

Griffiths ([2006], p. 3), recently summarized the view aptly: ‘unless anatomy, physiology, molecular biology, developmental biology, and so forth turn their attention to specifically evolutionary questions, they investigate function in the causal sense’. One of the anonymous reviewers for this journal pointed out that, in this passage, Griffiths agrees that (say) developmental biology employs both SE and CR functions. That makes it seem as if I should not classify his view as a version of between-discipline pluralism. But note that, for Griffiths, the only time developmental biologists (say) appeal to SE functions is when evolutionary questions happen to intrude into their field. So, I still

think his view should be classified as between-discipline pluralism because he thinks SE functions mainly go with evolutionary biology and CR functions go with all of the other fields; it's just that there is some overlap between those fields.

There are a number of philosophers of biology who think that SE is inapplicable to several branches of biology such as molecular biology, neuroscience, ecology, and psychology (Walsh [1996], p. 558; Sarkar [2005], p. 17; Weber [2005], p. 38; Craver [2013], p. 148; Nunes-Neto [2014], p. 124). Even though they were not discussing the question of pluralism in those contexts, their arguments indirectly support between-discipline pluralism. That is because they agree with the between-discipline pluralist that there is a sizable SE-free zone inside biology.

Before considering arguments for between-discipline pluralism, it is worth considering one notable objection. To my knowledge, Karen Neander, who is a function pluralist, is the only philosopher who has explicitly identified and criticized this approach to pluralism. In her forthcoming book, she calls this view 'popular pluralism' (Chapter 4 of Neander [forthcoming (a)]; also see Neander [forthcoming (b)]). Popular pluralism is the idea that SE is appropriate to evolutionary biology and CR is appropriate to physiology. This sort of view might look like a reasonable 'division of explanatory labor', but it is flawed.

Here is why we should not accept popular pluralism. When physiologists set about studying any given trait, say, the heart, they face a generalization problem. There is an

extraordinary amount of diversity and variation between organisms of the same species. Clearly we do not have the means to carry out a separate functional analysis of every individual's body, one that captures everything unique about them. So we have to make generalizations.

The notion of normal (or proper) functioning helps us solve this generality problem. We can describe a system, real or hypothetical, all of whose parts function normally. 'To solve the generalization problem, physiologists describe systems in which all of the components can perform, in appropriate circumstances, their proper functions ([forthcoming] (a))'. But, she continues, SE is our best way, or at least a very good way, of making sense of this normative notion of function. SE gives us a natural way of understanding biologists' talk about proper function and malfunction. So, to the extent that physiologists rely on a notion of normal (or proper) functioning (which they must because of the generality problem), they are implicitly committed to SE.

I think Neander makes an important point here, and I will come back to it in Section 4, in my critique of the sociolinguistic argument. The crucial point is that just because physiologists (say) do not explicitly appeal to selected effects, they might implicitly do so. So we have no right, as the popular pluralist wants to do, to exclude SE functions from the realm of physiology without further ado.

3 Two Arguments for Between-Discipline Pluralism

Why would anyone accept between-discipline pluralism? There are two arguments that surface in the literature, and both of them are alluded to in the passages given in the last section. I will call these the sociolinguistic argument and the ontological argument.

The sociolinguistic argument rests on an appeal to the way biologists talk and write. It says that, in some branches of biology, when practitioners attribute functions to traits, they make no reference to selection. This argument comes up in the quote from Godfrey-Smith ([1993], p. 200), where he says, ‘functional claims in these fields often appear to make no reference to evolution or selection’. Amundson and Lauder ([1994], p. 463) say, ‘Anatomists often write on “the evolution of function” in certain organs or mechanical systems, and may do so with no reference to selection or to the effects of selection’.

Sarkar ([2005], p. 18) describes the common practice in biology of, ‘making functional attributions from present roles with no reference to evolutionary history’. Walsh ([1996], p. 558), Schlosser ([1998], p. 304), and Wouters ([2003], p. 658) make similar claims. I take it that when these authors say that biologists do not appeal to, cite, or otherwise make reference to selection, they intend to make a sociolinguistic claim, and the basis for that claim is the authors’ own familiarity with relevant scientific literature. I do not dispute their findings. For example, in Section 1, I cited a paper (Prudic et al. [2015]) that discusses the function of eyespots on butterfly wings and which does not explicitly mention selection history.

(As an aside, one might try to give a similar argument from an epistemological stance, rather than a sociolinguistic one. That is, rather than look at how biologists talk, one

might ask about what sorts of evidence they appeal to when they are trying to resolve debates about an item's function. If biologists routinely appeal to historical evidence to solve debates about function, that would suggest they are appealing to SE. If they only appeal to evidence about a trait's current behavior, that would suggest they are appealing to CR, perhaps with the restriction that the relevant system effect has to do with the organism's fitness. The epistemological argument, however, is flawed. The problem is that the link between the evidence that biologists seek to solve questions about function, and the underlying notion of function they are committed to, is a loose one. Even if a biologist is committed to SE, he or she might think the best (the most convenient, the most efficient) way to assess what a trait was selected for is to look at current-day behavior. Maybe Prudic would agree, on reflection, that functions are selected effects, but would also say that the best way to discover functions is by carefully observing current behavior.)

The ontological argument is quite different. Set aside the question of what notion of function biologists appeal to. The fact is that in certain branches of biology, practitioners commonly attribute functions to items that do not have the right sort of selection history. So, SE is not an appropriate theory of function for those disciplines, because it would not license the sorts of function ascriptions that biologists commonly make.

Ecology is a plausible example of such a field. As Maclaurin and Sterelny ([2008], p. 114) point out, ecologists commonly attribute functions to entire groups of organisms, but groups of organisms do not usually have their own selection histories (barring group

selection). Meyer ([1993]), for example, discusses how ecologists assign functions to populations in terms of their roles in trophic structures. Unlike SE, CR would license the function assignments ecologists wish to make, so it is the better theory in that context.

Bouchard ([2013], p. 92) makes a similar point when he says that ecologists assign functions to abiotic parts of ecosystems, like soil types. Since SE typically restricts functions to the parts of living organisms, then SE cannot justify this usage. The ontological argument points to the conclusion that ecology, at least, represents a significant SE-free zone in biology. Maybe a similar argument could be given for other disciplines like genetics or psychology.

4 Two Objections Against the Arguments for Between-Discipline Pluralism

There are two problems with the arguments raised in the last section. The first is more minor and it only affects the sociolinguistic argument. The second is more significant and it affects both arguments equally.

Here is one problem with the sociolinguistic argument. Just because biologists do not always explicitly refer to selection when they are talking about functions, perhaps sometimes they implicitly do. Recall that the whole point of Neander's argument against popular pluralism is that biologists implicitly appeal to selection when they use function in a normative sense. So, proponents of between-discipline pluralism must argue that in these allegedly SE-free fields, such as genetics, biologists neither explicitly, nor

implicitly, appeal to selection. To my knowledge, nobody has made that argument (though Walsh [1996], p. 558 seems to recognize the problem).

The problem can be illustrated by an analogy. Often, when scientists claim that there is a causal connection between two events, they neither explicitly appeal to counterfactual states of affairs, nor to possible worlds. But if the difference-making approach to causation is our best current theory of causation, then it would appear that scientists are, in fact, appealing to counterfactual states of affairs. Moreover, if our best current account of counterfactuals has to do with possible worlds, then they would also be appealing to possible worlds, even if they do not realize that is what they are doing.

Proponents of between-discipline pluralism could respond to this argument by shifting the burden of proof. They could ask, ‘why should we think that biologists in these fields, like genetics or neuroscience, implicitly refer to selection even when they do not explicitly do so?’ My argument has two premises. First, biologists in diverse fields (outside of evolutionary biology) sometimes use ‘function’ with explanatory and normative intent (in a special sense of those terms that I will explain shortly). Second, SE is our best current theory of those explanatory and normative features of functions (when understood in the right way). If those two premises are correct, then it seems to me that biologists in diverse fields sometimes do implicitly appeal to SE, in the sense that they are implicitly committed to SE when they assign functions to things.

Let me clarify: by ‘explanatory,’ I specifically mean that sometimes function statements constitute causal explanations for the existence of traits (for example, as in Caro [2014]). That is, sometimes function statements are meant to answer why-is-it-there questions. As I said earlier, I think SE is our only viable account of this explanatory strand of biological usage. (As I noted in Section 1, there are other ways that functions can be explanatory without constituting causal explanations for traits; I am not interested here in this broader sense of explanation.) By ‘normative,’ all I mean is that it is possible for something to have a function that it cannot perform, that is, something like dysfunction is possible. Note that normative, in this context, has nothing to do with evaluative, a point that Millikan ([2002]) took pains to emphasize.

As I noted above, I realize that those two claims (that SE is our best current account of the explanatory and normative features of function) are quite controversial. Some people think SE functions do not actually explain anything (such as Cummins [1975]). Some think they are not really normative (such as Davies [2001]). Others concede that SE functions are explanatory and normative, but maintain that there are alternative theories of function, like the fitness-contribution account, that do an equally good job of making sense of those features of functions (Bigelow and Pargetter [1987]; Walsh [1996]; Hardcastle [1999]; Mossio et al. [2009]). These issues are somewhat subtle and I do not have the space to enter into them here. I discuss them at length elsewhere (Garson [2016]).

Fortunately, I need not resolve all of these controversies here. My point is just that, if one wants to argue that biologists do not implicitly appeal to selection, one must argue that SE is not our best current account of the explanatory and normative features of function. This argument takes us well beyond sociolinguistic features of biological usage.

Incidentally, I am not claiming that we can never tell, in any given context, which notion of function a biologist is appealing to. In other words, I am not endorsing the skeptical view that says we can never really know what a biologist means by ‘function’ on any given occasion. My own view is that we can. Here is how we decide: when biologists use ‘function’ with explanatory and normative intent, they are implicitly committed to SE; otherwise, they are implicitly committed to CR. (I do think many instances will be ambiguous.) The point of this paper is that we have no reason to think that these two uses will divide up neatly between disciplines.

There is a second problem, and it affects both arguments equally (the sociolinguistic and the ontological). This is a much more significant problem. Both arguments rest on an overly-narrow understanding of what SE holds. SE holds that a function of a trait is, roughly, whatever it was selected for by natural selection or some natural process of selection. But there are many function-bestowing selection processes in nature, other than natural selection in the evolutionary sense. Some of these processes operate over ontogenetic time scales, like trial-and-error learning, antibody selection, neural selection, and the differential replication of transposable elements in the genome. Both of the arguments for between-discipline pluralism assume that the only relevant sort of selection

process is natural selection. If that is the assumption one is working under, it is very natural to infer that SE is only appropriate to evolutionary biology.

5 A Survey of Function-Bestowing Selection Processes

This section surveys some alternative function-bestowing selection processes, and shows how they apply to fields like psychology, immunology, and neuroscience. My goal is to make a case for the ubiquity of SE functions in various branches of science. In particular, SE functions arise in places one would not have expected to find them if one were under the impression that natural selection is the only function-bestowing selection process there is.

The first is trial-and-error learning, or learning by consequences. (I realize we must be cautious with such labels – see below.) I use it first because, since it is familiar, it can help introduce the less-familiar cases like neural selection. By ‘trial-and-error’, I refer not to any specific mechanism of learning, but to any learning process that has the following general form: an organism is in a certain situation; there are a number of behaviors available to that organism; the organism is more-or-less equally disposed to perform any of those behaviors. The organism performs one of those behaviors and it leads to a reward, such as food. As a result, the behavior is reinforced over the other behaviors available to it. That is, the reward boosts the probability that it will perform that behavior in that situation (see McDowell [2009]).

In this circumstance, we should say the behavior in question acquired a new function, namely, whatever it did that caused it to be reinforced over some other behavior. Trial-and-error is a legitimate function-bestowing selection process because it captures the explanatory dimension of function statements. For suppose one were to ask, ‘why does that organism do that?’ An appropriate answer is, ‘because that behavior results in a reward’. In other words, one cites a past effect of the behavior as part of an explanation for the current existence of that very behavior. Such why-is-it-there questions can be answered, correctly, by appealing to a selection process (namely, the reinforcement of one behavior over another). Another way of answering the question is simply to say, ‘the function of the behavior is to produce the reward’.

Many SE theorists have recognized that trial-and-error is a sort of function-bestowing selection process. For example, although Wimsatt ([1972]) never defined ‘function’ in terms of selection, he indicates that selection processes are probably involved in every correct function ascription: ‘the operation of selection processes is not only not special to biology, but appears to be at the core of teleology and purposeful activity wherever they occur (15)’. By ‘selection,’ he explicitly refers to any process that exhibits what Donald Campbell ([1960]) called, ‘blind variation and selective retention’, and he says that trial-and-error learning is an instance of this process.

Millikan ([1984]) and Neander ([1983]) were the first philosophers to explicitly define ‘function’ in terms of selection history; but Millikan also emphasized that ‘selection’ should be defined broadly. As she put it, ‘behaviors that result from training or from trial-

and-error learning involving correlations of a reward with the behavior have as direct proper functions to produce that reward ([1984], p. 28)'. Godfrey-Smith, in an early paper on functions, followed her lead and emphasized that functions can result from the differential reinforcement of cognitive mechanisms: 'It is important that the selective approach [to function] is in no way tied to the genetic kind of biological evolution...A selective basis for functional characterization is available whenever learned characteristics are maintained within the cognitive system because of their consequences' ([1992], p. 292). Papineau ([1987], p. 65) made a similar move when he said that the differential reinforcement of cognitive mechanisms suffices to generate new functions.

Griffiths extended this selectionist picture to capture the process of intelligent deliberation. In his view, whenever an agent is contemplating multiple courses of action, and he or she selects one because of its perceived benefits, that is a kind of function-bestowing selection process. He writes, 'although artifacts are not in actual competition with other artifacts during the design process, they are in hypothetical competition. The designer conceives a range of alternatives and chooses amongst these in virtue of their perceived possession of certain capacities ([1993], p. 419)'. My point is that this broad construal of selection is part of a well-established tradition for thinking about SE functions.

I realize that one must be cautious with labels like 'trial-and-error'. That is because the label is associated with a whole package of behaviorist ideas that has been thoroughly discredited since the 1970s (Roper [1983]; see Kingsbury [2008], which questions the

relevance of trial-and-error for thinking about functions). I wish to distance myself from that package of ideas. First, I am not claiming, as the old-fashioned behaviorists did, that all, or even most, behaviors are acquired through a kind of selection process. Second, I am not claiming that this selection process, where it does occur, must take place gradually over a large number of trials. Third, I am not claiming that there are no innate constraints on the sorts of behaviors that can be acquired in this fashion. One can approach some aspects of learning in a selectionist way without endorsing the whole package of behaviorist ideas (McDowell [2009]).

My second example comes from immunology, though I will not develop it in detail (see Garson [2012] for discussion). The Danish immunologist Niels Jerne ([1955]) formed the selectionist approach to antibody production in the 1950s, and he and others developed it in a series of publications (Lederberg [1959]; Burnet [1959]; Jerne [1967]). Jerne explicitly likened antibody selection to natural selection. He proposed a mechanism of genetic recombination that generates a vast number of different antibodies. When one of those antibodies comes into contact with the antigen specific to it (that shares the same configuration), the antibody is replicated throughout the bloodstream. Jerne contrasted his selectionist view with so-called ‘instructionist’ views, according to which the antigen somehow impresses its form onto a plastic antibody.⁶

⁶ Even in the instructionist views that Jerne dismisses, antibodies could have proper functions. They would have what Millikan calls ‘derived’, rather than ‘direct’, proper functions. See below for more discussion of this distinction.

The standard SE theory should recognize that the differential production of antibodies in the bloodstream is a function-bestowing selection process, because it embodies the same abstract formula: the past effect of the antibody explains its differential reproduction within a population of biological entities (Garson [2012], p. 460; [2016]). In this, I follow Darden and Cain ([1989]), who think antibody selection should be seen as one subtype of a more general, abstract sort of selection process (also see Cziko [1995], Hull et al. [2001]). The difference between my treatment and Darden and Cain's ([1989]) is that they were not concerned about biological functions.⁷

My final example of a function-bestowing selection process is neural selection. Roughly, there are three well-defined sorts of neural selection: synapse selection, whole-neuron selection, and neural group selection, depending on the unit that undergoes competitive interactions (Garson [2015], Chapter 7). One must be cautious here, because neural selection acquired a poor reputation in some circles because of its association with neural *group* selection (Edelman [1987]). Neural group selection is a speculative theory of brain development and cognition. However, the empirical shortcomings associated with the work of Edelman and his colleagues should not tarnish synapse selection and whole-neuron selection, which are empirically well-documented (Wong and Lichtman [2002]).

⁷ I am not claiming that antibody selection is a kind of natural selection. As I emphasized in Footnote 5, I have no desire to engage in debates about the appropriate definition of 'natural selection' itself, except to assert that natural selection is an example of a more general, abstract sort of selection process of which trial-and-error learning and antibody selection are also examples.

To the extent that there is any real controversy here, the controversy has to do with how widespread these phenomena are (see Purves et al. [1996]; Quartz and Sejnowski [1997]; Changeux [1997]; Sporns [1997]).

Roughly, synapse selection takes place under the following conditions. Suppose there are two or more neurons that both form synapses with the same target neuron. Suppose one of those synapses, by virtue of some activity it performs (even if simply its frequent activation) is retained on the target neuron and the other synapses are eliminated. Suppose, moreover, that the retention of the first synapse, and the elimination of the latter, are directly causally related, that is, the activation of the first synapse somehow causes the others to be eliminated (that is, there is something like a zero-sum game taking place between the synapses). In this scenario, I submit, the retained synapse has acquired a novel function by virtue of its role in this competitive interaction.

An example of synapse selection, the formation of abnormal ocular dominance columns in the visual cortex, illustrates the process. Most neurons of layer IV of the visual cortex in a normal mammal are binocularly-driven, that is, they are receptive to information associated with either eye. A small proportion of neurons, however, are monocularly-driven, that is, they are only receptive to information associated with one eye or the other. Experiments carried out in the 1960s showed that, if a kitten is blinded in one eye at birth, then over the next few weeks, most of the neurons in its visual cortex become monocularly-driven, and sensitive only to information associated with the functional eye

(Wiesel and Hubel [1963]). This is beneficial for the kitten because it maximizes visual acuity in the functioning eye.

The underlying mechanism is a competitive one. Each neuron in the visual cortex becomes the site of something like a competition between synapses associated with the functioning eye and those associated with the non-functioning eye (Wiesel and Hubel [1963], p. 1015; also see Rakic [1976]; Antonini and Stryker [1993]; Price et al. [2011], p. 210). Because synapses associated with the functioning eye are activated more frequently than those associated with the non-functioning eye, they tend to be retained over the latter. Crucially, these two processes – the retention of the active synapses, and the elimination of the inactive synapses – are not causally independent of one another. The elimination of the non-active synapses is not just an effect of disuse-related atrophy. Something about the fact that one group of synapses is being activated causes the others to be eliminated. That the elimination of the non-active synapse is a result of a competitive process is shown by the fact that, if the kitten is exclusively dark-reared for the first several months of life, it retains the same degree of binocularity as normal kittens do.

The precise interactions between the pre- and post-synaptic neuron that mediate this competitive process are unclear. Elliott and Shadbolt ([1998]) maintain that synapses associated with the functioning eye are more successful at the uptake of a diffusible trophic substance made available by the target neuron, and this causes them to be differentially retained. More recent work, however, has centered on microglia, which

seem to play a role in synapse selection by ‘pruning’ away (that is, consuming) unused dendritic spines on the post-synaptic neuron (Stephan et al. [2012]).

In my view, if one synapse is retained on a target neuron over some other synapse because of some activity that it performs, it acquires a novel function. For suppose one were to ask, ‘Why is this specific neuron, in the kitten’s visual cortex, monocularly-driven? That is, why does it form a synapse only with neurons associated with the functioning eye, rather than both?’ A correct answer to that question would be, ‘because that synapse transmits visual information to the rest of the brain’. Another way to state the point would just be to say, ‘the function of the synapse is to transmit visual information to the brain’. That is an activity that explains the continued existence of the synapse. It is a correct answer to a why-is-it-there question.

Competitive processes may underlie other sorts of neural plasticity. For example, consider the reorganization of the somatosensory cortex following limb amputation (Pascual-Leone et al. [2005]), or, more generally, the phenomenon of cross-modal projection, where a part of the brain that is specialized for one sort of sensory input becomes recruited (through damage or deprivation) to serve another. Following limb amputation, the neurons that once served the amputated limb can become recruited to serve other capacities, such as the capacity to transmit information about a prosthetic limb. Some researchers believe that this sort of neural plasticity results from a competitive process where preexisting connections are differentially retained because of their ability to serve the novel capacity (see Rauschecker [1995]; Miller [1996]; Ramiro-

Cortés et al. [2014]). If so, it is correct to say that the function of the new configuration of synapses is to serve the prosthetic limb. That capacity explains why that particular configuration of synapses exists, that is, why it was retained over some other configuration.

There are other ways of thinking about how neural structures can acquire new functions over one's lifetime, other than by appeal to neural selection. This is Millikan's distinction between direct and derived proper functions. Suppose one thinks that natural selection in the evolutionary sense is the only process that creates new (direct proper) functions. One could still say that the products of *neural* selection also have functions; they have derived proper functions. In short, a neural structure, *S*, produced by neural selection has a derived proper function because it is produced by a mechanism (neural selection) which has the direct proper function of producing structures like *S* (see Millikan [1989], p. 288). I have no objection to this distinction (see Garson [2012], p. 458). My point here is that we should think of neural selection as a distinctive sort of function-bestowing selection process in its own right, and not just in this derivative way. As such, the products of neural selection also have direct proper functions (in addition, perhaps, to their derived proper functions).

Before continuing, I wish to make one important qualification to deter potential misunderstanding. My argument is not that trial-and-error is a function-bestowing process because it is similar enough to natural selection in the evolutionary sense. Nor do I claim antibody selection and neural selection are function-bestowing processes because

they are just like natural selection. My argument does not hinge on whether there are deep similarities between, say, trial-and-error and natural selection, or merely superficial ones. My point is that a process generates new functions when it fits this abstract description: there is a population of entities that differ from one another in certain ways, and because of those differences, some of the entities reproduce, or are retained, more effectively than others. I have developed this idea into a novel theory of function, the generalized selected effects theory, which I have outlined in other places (Garson [2011], [2012], [2015], [2016]).

In this section, I gave examples of three different sorts of selection processes that take place in various domains of biology and psychology that are very plausibly associated with the production of novel functions. There are other potential function-bestowing selection processes, such as the differential spread and deletion of transposable genetic elements (Elliot et al. [2014]). Together, they make a strong case for the existence of SE functions in several areas of biology and psychology, and the corresponding appropriateness of SE in those disciplines.

6 Conclusion

Between-discipline pluralism is based on a certain idea about what SE holds. According to this interpretation of SE, natural selection in the evolutionary sense is the only sort of selection process in the natural world that can give rise to functions. That narrow interpretation of SE naturally suggests a certain labor-sharing device between different

concepts of function: SE is most appropriate to evolutionary biology (or some sub-branches of evolutionary biology), and CR is most appropriate to other, non-evolutionary contexts like genetics, developmental biology, neuroscience, or ecology (unless evolutionary questions intrude into those disciplines).

I have argued that when we consider the diversity of selection processes in nature, we must shift our viewpoint about how functions should be divided up. In my view, SE functions are appropriate not just when evolutionary questions are being asked, but whenever function statements are used in a causal-explanatory sense, that is, whenever they are meant to answer a why-is-it-there question, in whichever discipline that question arises. CR functions are probably most appropriate as answers to the how-does-it-work question.

A better way to think about function pluralism is within-discipline pluralism. Within-discipline pluralism simply seeks out and emphasizes the plurality of functions inside any branch of biology and psychology. Above, I mainly focused on why we should reject between-discipline pluralism, instead of offering positive reasons for accepting within-discipline pluralism. Yet I have indicated three different arguments for within-discipline pluralism. First, within-discipline pluralism is the most obvious theory once we reject between-discipline pluralism (assuming that we wish to remain pluralists about function at all). Second, there are compelling examples of SE functions in several disciplines outside evolutionary biology, such as neuroscience, psychology, and immunology. Third, within-discipline pluralism has important heuristic value. This is because, if we think SE

functions are appropriate only in the context of evolutionary biology, we may be unable to recognize the existence of selection processes when they crop up in other places.

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