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Address: Department of Philosophy, Hunter College and The Graduate Center, City University of New York, 695 Park Ave., New York, NY 10065.

Email: jgarson@hunter.cuny.edu

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Functions and populations: Sharpening the Generalized Selected Effects Theory of Function

Abstract: The generalized selected effects theory of function (GSE) holds that a trait's proper function is an activity that historically caused its differential persistence or differential reproduction within a population, construed as a collection of individuals that impact each other's persistence or reproduction chances. Several critics have taken aim at GSE on the grounds that its appeal to populations is either unfit for purpose or arbitrary. Here I revise GSE by articulating a notion of population that is fit to purpose and showing that its selection is not arbitrary but flows from the realist commitments of the selected effects theory itself.

1. The Traditional Selected Effects Theory

The traditional selected effects theory (Neander 1983; Millikan 1984; Griffiths 1992; 1993; Godfrey-Smith 1993; 1994) holds, roughly, that the function of a trait is whatever it was selected for – selected for recently – by natural selection or some comparable selection process. The primary virtue of the selected effects theory is that it helps us make sense of what are often called the teleological and normative dimensions of function (to be shortly described) in a naturalistically satisfying way. Another virtue is that it serves as a cornerstone for various fruitful philosophical projects such as naturalizing representation, disease (or disorder), and mechanisms.

"Teleological," "normative," and "proper function," have several meanings in philosophy. Some outright reject that there is any teleology or normativity in nature. It is worth clarifying, then, exactly what I mean by each, so that the explanatory force of the selected effects theory can be properly appraised. By "teleological," I just mean that function statements are often deployed as causal explanations. Specifically, they often purport to explain the existence, form, or distribution of a trait, by pointing to one of that trait's useful effects. As I've sought to document (Garson 2019, Chapter 1), often, when biologists attribute functions to traits, such as the function of deterring biting flies to zebra stripes, they purport to explain why zebras have stripes: zebras have stripes because stripes help deter biting flies. (The reigning theory holds that tsetse flies are averse to landing on striped surfaces, for reasons yet to be fully understood – see Caro et al. 2013).

This explanatory feature of functions raises a serious conceptual puzzle: how can the fact that stripes deter flies explain why zebras have them? How is it possible for an effect of having stripes to somehow turn around and explain its own cause? The selected effects theorist answers that by saying: it does so by virtue of a natural process of selection. The fact that, in the past, stripes deterred flies, and the fact that *that* led to the differential reproduction of striped zebras over stripeless ones, allows the ability to deter biting flies to figure into a causal explanation of the current non-zero frequency of stripes in zebra populations. (To be clear, the fact that a trait was recently selected for performing some activity does not count as a *complete* causal explanation for the current non-zero frequency of that trait; it counts as *part* of that explanation.) By making sense of this puzzling feature of functions, the selected effects theory shows how teleological thinking in biology can be vindicated within a naturalistic and evolutionary worldview (Garson forthcoming).

One might think that the explanandum of the function statement – that function statements are meant to explain the current non-zero frequency of a trait in a population (following Griffiths 1993, 418) – is too tepid. In paradigm cases ("the function of zebra stripes is to deter flies"), aren't function statements supposed to explain why all, or most, members of a population have the trait in question? Not always. In cases such as frequency dependent selection, selection can maintain a trait at a certain stable frequency less than 100%, such as the three different morphs of the male ruff, *Philomachus pugnax*, as described in Zuk and Simmons (2018, 63). Selection might even maintain a trait at a *very* low frequency in a population: consider the "faeder," or female-mimicking ruff, found in a mere one percent of the male ruff population. Still, its unusual features have functions. Some evolutionary theorists even conjecture that psychopathy (or some of its attributes such as lack of empathy) is such a trait, one that is selectively advantageous only when it occurs in an extremely low proportion of the population (for discussion, see Krupp et al. 2012).

Functions are also said to be "normative." They do not necessarily describe what a trait actually does – after all, hearts do not always beat, and zebra stripes do not always deter flies – but in some vague sense of the term they seem to tell us what a trait is "supposed to do." Although the meaning of the term "normative" is contested, I use the term in a fairly deflationary way: all I mean is that if a trait has a function, it is possible for that trait to fail to function (to malfunction, to be dysfunctional) (Neander 2012). If traits could not literally malfunction or dysfunction, then much of biomedicine would be incoherent, as arguably, one of the whole points of biomedicine is to document the ways that bodily parts and processes fail to do what they're supposed to do.

The selected effects theory explains the normativity of function by turning functions into historical properties – similar to the property of being a sibling, an adaptation, an igneous rock, or a volcanic mountain. Whether a trait has a function, and which function it has, depends entirely on its history, not on its current dispositions. Whether a trait is able to perform its function depends on its current dispositions, not its history. On the selected effects theory, then, there is nothing particularly puzzling about how a trait can possess a function it is nonetheless constitutionally unable to perform.

There are three further aspects of the selected effects theory worth mentioning here: pluralism, its meta-analytic (or "metaphilosophical") ambitions, and realism. First, the selected effects theory is compatible with a modest pluralism about functions. What I mean by "pluralism" is the rather unremarkable fact that scientists use the term "function" differently in different contexts. The literature on how, exactly, we should think about pluralism (What are those meanings? In which contexts are those meanings deployed?) has become rather expansive (see Sterner and Cusimano 2019 for a good entry point).

The version of pluralism I adopt here cleaves tightly to Neander (2017a). As she puts it, there are at least two pretheoretical notions of function circulating in the life sciences: the *proper function* sense and the *minimal function* sense. The *proper function* sense admits both a function-side effect distinction and a function-malfunction distinction. The *minimal function* sense does not. If I say, "the function of the heart is to pump blood," I usually imply that many other things it does are *not* functions (such as making beating sounds) and among those other things, some are malfunctions (such as going into cardiac arrest). In contrast, I suspect that the minimal notion of function is at play when the distinction between form and function is invoked: here, “form” is more closely aligned with physical structure, and “function” with something like “activity enabled by that structure” (see Novick 2023 for discussion). In regard to the human patella bone (kneecap), “form” denotes shape and connectivity; “function” an activity it permits (knee extension). Such a notion of function, I believe, is at work in Bock and von Wahlert’s (1965) discussion of function, in which a trait’s functions include “all physical and chemical properties arising from its form.” This minimal notion of function would seem to be ahistorical through and through but also, as Neander (2017a) notes, incapable of supporting a robust notion of malfunction. If one’s patella were crushed so as to no longer permit knee extension, it wouldn’t be “malfunctioning” in the minimal sense of function: it simply would be altered in such a way that it no longer sustains the same profile of activities as before.

The selected effects theory is intended to provide a rigorous articulation of the former, pretheoretical, *proper* sense of function, rather than the *minimal* sense of function. Unfortunately, function theorists are not always clear which of the two pretheoretical senses, if either, they intend to explicate. As a consequence, it is often difficult to decide whether two function theorists are actually disagreeing with one another about what functions are, or whether they are seeking to explicate two different senses. Even biologists sometimes switch back and forth between these two senses or lump them together in ways that are confusing and counterproductive (e.g., Doolittle 2013 demonstrates how this conflation occurs when we’re trying to estimate what proportion of the human genome is “functional”).

Selected effects theorists hold diverse views about its meta-analytic ambitions. The failure to recognize the diversity of those ambitions is another source of potentially fruitless debate. Is the theory meant to be a conceptual analysis of what lay folk "have in mind" when they attribute functions to traits? Or only what modern biologists "have in mind"? Or is it supposed to work as a theoretical definition – that is, is it meant to say what functions are in nature, regardless of what anyone has in mind, as in "aluminum is that element with atomic number 13?" Or is it meant to have a stipulative character, to work as a "Carnapian explication" or an exercise in conceptual engineering? (for discussion, see Millikan 1989a; Neander 1991; Schwartz 2004). These are four quite distinctive projects which will potentially yield four different answers. Sometimes it is not entirely clear which meta-analytic project(s) a philosopher is pursuing. For example, Wakefield has, at times, described his "harmful dysfunction" account of disorder, which prominently involves the selected effects theory, as a conceptual analysis (1992; Wakefield et al. 2006) and at other times as a form of "black box essentialism" (1999) which is usually synonymous with theoretical definition (see Fagerberg 2023 for an exploration of Wakefield's complex meta-analytic goals).

Here, I accept the Millikanian approach which sees the selected effects theory as a theoretical definition ("water is H2O"). Like all theoretical definitions, its articulation should be guided by core features of biological usage – including the explanatory and malfunction-permitting dimensions alluded to above. My view is that selected effects are the only kinds of things in nature that can underwrite the explanatory and malfunction-permitting features of functions while hanging together reasonably well with paradigm biological judgments about what sorts of things have proper functions (hearts, wings), what functions they have, and what sorts of things do not have functions (parts of rocks, hurricanes, and candle flames) (Garson 2019).

The selected effects theory has a final feature that will be central to my argument below. This is its commitment to a realist worldview, in the sense that functions, as a rule, are natural, mind-independent features of reality. Whether something has a function, and what function it has, doesn't depend on how anyone thinks about it or feels about it; it doesn't depend on anyone's values, goals, or research agendas. Whether the activity of a trait represents a function, a side-effect, or a malfunction, depends on the structure of the world, not the structure of the mind. For the selected effects theorist, functions are woven just as tightly into the fabric of nature as causation, gravity, or mass. Of course, some traits acquire a function by virtue of a selection process that involves cognition or consciousness, such as some forms of sexual selection or artifact selection. But even in those cases, the fact that a trait has an effect as its function does not constitutively depend on mental states. For example, perhaps male jealousy has the biological function of helping males to be wary of cuckoldry. But the fact, if it is a fact, that male jealousy has that effect as a function, rather than as an incidental byproduct, or a dysfunction, does not constitutively depend on anyone's current mental states (our current day interests, goals, and values) but its selection history.

Realism about functions is quite critical for the selected effects theorist, for numerous reasons. First, the theory is usually framed within the larger project of naturalism – which is about helping to reveal how puzzling phenomena such as teleology, normativity, and mental representation fit into the natural world, and appeals only to entities and properties that are recognized by contemporary natural sciences. Naturalism is often taken to forbid not only appeals to supernatural entities (intelligent design of nature, say) but also to values (for example, "naturalism" and "normativism" in the philosophy of medicine is a debate about the exact role of values in medical judgment – see Boorse 1975; Bedau 1991; Kingma 2010). Admittedly, the use of "naturalism" to exclude not only supernatural agents but values is strange, as Conley and Glacklin (2021) recently emphasize. It seems to presume that if values exist, they must exist subjectively, a point that, e.g., neo-Aristotelians deny. My point here is merely that if functions depend, constitutively, on goals, interests, or the subjective sort of values, then the naturalistic character of functions would be jeopardized.

This realist or mind-independent character is pivotal for several traditional applications of the functions debate to other areas of philosophy and science, and in particular, for its application to understanding disease and mental representation. Many theorists believe or suggest that diseases (disorders, pathologies) essentially involve dysfunction (or related features like failure of function or loss of function), including Boorse (1975), Neander (1983), Wakefield (1992), Griffiths and Matthewson (2018), and Jefferson (2022). One attractive feature of this view is that whether or not something is a disease (disorder) doesn't merely depend on whether society happens to think it's bad, unusual or weird; it depends on underlying facts about the world. This reigns in the tendency to "overmedicalize" or "overpathologize" conditions that large swaths of society consider to be undesirable or inconvenient. For example, the question of whether ADHD is really a dysfunction, rather than a different mode of cognitive functioning (see Swainpoel et al. 2017 for discussion), depends, for the selected effects theorist, on facts about how it evolved, and not just what society happens to find desirable or convenient.

The realist, mind-independent character of functions is also, quite obviously, pivotal for the project known as teleosemantics, which attempts to illuminate mental representation in terms of function and thereby anchor representation in the natural world. Teleosemanticists hold that what makes a bit of brain activity a representation, and what it is a representation of, depends on functions, which, in turn, depend on non-representational features of the world (e.g., Papineau 1984; Millikan 1989b; Dretske 1986; Schulte 2012; Neander 2017b; Garson 2022a, Chapter 8). If functions depend, constitutively, on values, goals, and interests, then they could not play this role. (Note that I am not making the erroneous claim that the selected effects theory is the only plausible theoretical foundation for teleosemantics: see, e.g., Price 2001; Schroeder 2001; Nanay 2011; see Hundertmark forthcoming for discussion. I am making the trivial claim that whatever theory of function one adopts as the intellectual backbone of teleosemantics, it cannot without circularity be one that depends crucially on intentional mental states.) Moreover, as Neander (2017b, 89-90) points out, all plausible naturalistic approaches to representation, such as Dretske's (1981) informational account, Fodor's (1987) asymmetrical dependence account, and Cummins' (1996) second-order similarity account, seem to lean, at some point or another, on pretheoretical notions like "proper," "normal," or "optimal" functioning, in order to ground representation. So, it's likely that anyone committed to naturalizing representation is also committed to the claim that such functions have a mind-independent existence.

2. The Generalized Selected Effects Theory

I’ve argued that the traditional selected effects theory, despite its numerous virtues, is plagued by an arbitrary restriction, one which demands a significant amendment (e.g., Garson 2011; 2016; 2017; 2019). It restricts functions to things that undergo reproduction or “copying” (e.g., Millikan 1984; 1989b; 1993; Neander 1991, Godfrey-Smith 1993; Neander and Rosenberg 2012). The basic picture of reality which informs the traditional theory is one in which *biological entities form lineages bound by parent-offspring relations*. The members of certain lineages, by virtue of their characteristic features, tend to increase in frequency in a population over others, or at least maintain their frequency (as in polymorphisms). Many selected effects theorists have been quite explicit in this core commitment (Millikan 1993, 34; Godfrey-Smith 1993, 198-199; Neander and Rosenberg 2012, 618; see Kingsbury 2008, 496 for discussion).

I think there are interesting cases in nature of entities that acquire proper functions via a selection process, but one that only involves a history of “differential persistence:” one thing persisting in a population better (that is, longer) than another. Consider a group of neurons in the CA1 area of one’s hippocampus. Neurons don’t reproduce – they do not form parent-offspring lineages – and so they cannot undergo differential reproduction. But they do persist for varying lengths of time, and some persist longer than others on account of their size, shape, or connectivity. I hold that the fact that a token neuron or neural structure (axon, neural group) “out-persists” another by virtue of some characteristic activity is sufficient to give it a new function. I also think trial-and-error learning – say, an infant learning that a particularly piercing cry is more likely to attract the attention of its father than a less piercing one, and that behavioral disposition being differentially reinforced over others on that account – is sufficient to create new functions, too. Nothing like reproduction (copying, lineages of individuals bound by parent-offspring relations, etc.) is needed (see Garson and Papineau 2019 for elaboration). Plausibly, some ecosystem elements (Bouchard 2013; Doolittle 2014), and even some social institutions (Hindriks and Guala 2019), can undergo differential persistence – one “outlasting” another because of some characteristic activity – and hence could come to acquire functions on this liberal view.

Put concisely, the generalized selected effects theory of function (GSE) holds that a function of a trait is an activity that caused its differential reproduction, or its differential retention, in a population (Garson 2017, 524; 2019, 93). By “differential reproduction,” I mean to include all of the entities that the traditional selected effects theory includes. In other words, if the traditional theory gives a function to a trait, GSE gives it the very same function. By “differential retention,” I mean to include entities like neurons (or other neural structures), psychological dispositions, and perhaps some ecosystem elements and social institutions, that don’t reproduce but that undergo differential persistence. By “in a population,” I mean to rule out certain problematic cases, as will be discussed at length below.

There are numerous benefits to GSE. It applies to a large gamut of entities we’d like a theory of function to apply to. It integrates evolutionary and ontogenetic selection processes into a single, streamlined account. It solves the problem of novel functions – how new functions arise over the course of one’s lifetime – and, as applied to teleosemantics, the problem of novel representations. At root, GSE is meant to point to a basic, rather abstract, process, one that is ubiquitous in the natural (and social) world, and to present functions as depending on this process. In that respect, it shares an intellectual affinity with the project sometimes described as “universal selection theory” or “universal Darwinism” while departing from it on key points (e.g., Darden and Cain 1989; Cziko 1995; Dennett 1995; Hull et al. 2001; see Garson 2019, 67-69 for discussion).

The main justification for GSE, however, is not that it has those benefits. After all, a false or groundless theory could have various benefits. At root, my core justification is a parity of reasoning argument (Garson 2017, 533; 2019, 94). The reason for accepting the traditional selected effects theory is that it makes sense of the explanatory and malfunction-permitting features of function in a naturalistically satisfying way, while hanging together well with ordinary biological usage. But GSE does the same, minus an arbitrary restriction ("copying"). Hence, it's the better theory.

3. GSE and the liberality problem

It's natural to wonder whether GSE errs on the side of encompassing too much. This is precisely the point at issue in several of the criticisms lodged against it. Here is an example of "differential retention" that does not create new functions (see Kingsbury 2008, 496). Consider a bunch of rocks scattered on a beach. Some are harder, some are softer, and the softer ones erode more quickly than the harder ones. Eventually, only the harder ones remain. Some rocks, one might say, are "differentially retained" on account of their hardness. But the hardness of a rock doesn't have a proper function: one wouldn't say that the *purpose* of the rock's hardness is to withstand erosion, or that, if the rock erodes anyway, there must have been a *malfunction*.

The fact that GSE appears to give rise to trivializing counterexamples seems to be a non-arbitrary reason to insist that, after all, functions do require something like "copying" or reproduction. As noted above, a germ of this argument is found in Millikan (1993, 34), Godfrey-Smith (1993, 198-199), and Kingsbury (2008, 496). I think we can avoid the counterexamples without rejecting the idea that differential persistence gives rise to new functions. But I've come to realize that the way that I articulated GSE in the past created several new problems and puzzles – problems and puzzles I could have avoided had I elucidated the theory more carefully. This is precisely what I seek to do here.

Initially, I thought that the solution to the puzzle of the rocks, and similar counterexamples, was implicit in the very idea of a selection process (Garson 2017, 536; 2019, 104). Selection, we're often reminded, takes place in a population (Godfrey-Smith 2009; Millstein 2009, 2010; Matthewson 2015). So, what kind of thing is a population? Following recent work in philosophy of biology, I endorsed the following quite minimal criterion: in order for a collection of entities to form a population, those entities must impact one another's absolute fitness (survival or reproduction chances). Having sex, fighting over food, and hunting a wild boar together, are examples of interactions by which we impact each other's fitness. Millstein (2010; also see her 2009, 271) calls such groupings "causal-interactionist populations" and I will follow suit. There is much more to be said by way of fleshing this idea out. The idea of a collection of entities that impact one another's absolute fitness is only meant to be a minimal criterion for populationhood. It is not a complete account. A complete account of populationhood would also have to make reference to features such as the degree of "connectivity" the members of a population must have. It would also have to specify that the members of a population are all of the same "type," rather than different types (for example, that they are all of the same species, rather than different species).

Equipped with this minimal criterion of populationhood, I was able to quickly dispatch problematic cases like rocks on a beach. It's easy to see that a bunch of rocks on a beach don't satisfy this minimal criterion. That is because the rate at which one rock erodes has no impact on the rate at which other rocks erode. Whether a rock erodes quickly or slowly does not affect the erosion rate of others. Of course, this solution forces us to expand what populations are to include things that merely impact one another's *persistence* prospects, rather than their *survival* or *reproductive* prospects, but that struck me as a modest expansion of the idea.

The key virtue of this solution, it seemed to me, was that it solved the problem of liberality without introducing any arbitrary or ad hoc devices that stood in need of further justification. To say that a selection process takes place within a population, i.e., a group of individuals that impact each other's fitness, struck me as bordering on tautology: "restricting functions to the members of populations is not an ad hoc device, but it emerges by reflecting on what natural selection is" (Garson 2019, 104). Therefore, by restricting functions to individuals within populations, I merely purported to clarify something that was already latent in the very idea of a selection process, rather than adding something brand new. (By analogy, to say that a bachelor must not merely be an unmarried male, but an unmarried male that is *eligible to be married* – not an infant, a priest, or a person with advanced dementia – seems to be simply clarifying the standardly-accepted understanding of "bachelor" rather than stipulating some new rules for its application.)

Still, I realized that more needed to be said about the liberality problem. As Neander pointed out to me (cited in Garson 2017, 537), one could modify the rocks example slightly to make the rocks satisfy this minimal criterion. This time, imagine a pile of rocks by the shore. As the waves come crashing in, they rub against each other, and the harder ones contribute to the erosion of the softer. Now we have a collection of entities that impact one another's persistence chances, and hence that satisfies our minimal criterion for populations – so GSE must give functions to them.

To avoid this modified rocks problem, I took the following route. Suppose we analyze, more carefully, the ordinary biological notion of a population. Perhaps we will find other features that populations have that such collections of rocks do not have. In other words, maybe we will find an additional, but still rather minimal, feature of a population that excludes such cases. Then we will not have to resort to any arbitrary or ad hoc restrictions. The solution to the rocks on a beach problem would still, as it were, flow from the very nature of populationhood.

One feature of populations is what we might call their "strong interconnectivity." The idea is that in order for a collection of individuals to form a population, each individual must, on average, have fitness-relevant interactions with many other individuals in the group, not just a few others. Matthewson (2015) has shown how, barring such a condition, we could take two random populations on opposite sides of the world and call the collection consisting of both a "population," too. So, it's plausibly a rather minimal criterion for a population. If we go back to our pile of rocks, it doesn't exhibit strong interconnectivity. Each rock only has persistence-relevant relations with its immediate neighbors. A nice feature of this notion is that it can be measured quite precisely. An intriguing consequence of this for the functions debate is that, if we accept that functions depend on populations, then functions come in degrees, because populationhood comes in degrees (Matthewson 2020).

Unfortunately, critics were quick to point out that one could further modify the rocks example to satisfy this “strong interconnectivity” criterion (Conley 2020; Columbo 2020; Bourrat 2021; Schulte 2021; Dussault 2023; see Matthewson 2020 for discussion). Schulte offers a rockfall example: a bunch of rocks are rolling down a mountain, and smashing into each another as they roll. They could affect each other’s persistence chances and exhibit strong interconnectivity in the process. For that matter, one could put a bunch of rocks in a rock tumbler and leave them for a long time (Conley 2020). Such a group would exhibit strong interconnectivity.

It's worth emphasizing why it’s important to exclude rocks from having proper functions. Why all this fuss over a handful of counterexamples? The issue is not, as one might think, that giving functions to rocks violates my “intuitions.” Many feel, rightly or wrongly, that relying heavily on intuitions to win a philosophical argument is a distasteful activity, and at any rate one that is inappropriate for a theoretical definition, rather than a conceptual analysis. Rather, my view that rocks don’t have proper functions is based on a general methodological principle: a good theoretical definition of function – that is, a definition that seeks to identify a kind of process or pattern underlying ordinary biological usage – should be guided by broad features of that very usage of “function,” in the same way that a good theoretical definition of water should be guided by broad features of ordinary scientific usage of “water” (Garson 2022b). One of these features includes the fact that there are certain sorts of things in the world that biologists do, and other sorts of things they do not, attribute proper functions to. They attribute functions to things like bodily parts and processes (the heart), mental states (male jealousy), and group behaviors (V-formation in birds). They do not generally attribute proper functions to inanimate objects, such as rocks, clouds, hurricanes, clay crystals, and so on – with the exception of artifacts. If my theoretical definition of "function" yields function ascriptions that are at significant odds with the usage that inspires it, that would be evidence that my definition picks out the wrong kind of thing in the world.

Rocks might have "functions" in some other sense of the term, in something like Neander's "minimal" sense. Rocks have various benefits, such as creating soil or containing valuable minerals, and these can correctly be called "functions" of rocks, in the same way that climate change is a "function" of deforestation. But this isn't the proper function sense. If a rock does not contain valuable minerals, it might be disappointing to a prospector, but the rock isn't malfunctioning or dysfunctional. Nothing objectively went wrong with the rock. There seems to be a more-or-less tacit consensus among biologists that rocks, like clouds or hurricanes, aren't the sorts of things that can fail to work the way they're supposed to.

In short, while strong interconnectivity is an important feature of populations, and while pointing to strong interconnectivity probably avoids Neander's specific counterexample, it doesn't do what I meant for it to do – namely, to let us ascribe functions to things (or withhold such ascriptions) in ways that hang together well with the actual biological usage that is intended to guide it.

Before moving on to criticisms pertaining to the rocks example, I should note that some have rejected GSE in favor of the traditional selected effects theory for quite different reasons: not on the grounds that it is overly liberal, but on the alleged ground that it yields conflicting functional norms (Fagerberg 2022). GSE allows for the possibility that one and the same trait can have the function F by virtue of one selection process and the function G (where G is contrary to F) by virtue of another. An antibody might have the evolved function of attacking foreign particles, and the ontogenetically-selected function of attacking healthy tissue. The brain's reward system might have the evolved function of pursuing fitness-relevant goals (like food and sex) and the ontogenetically-derived function of pursuing dangerous substances (like cocaine) to the exclusion of food and sex (see Garson and Papineau 2019 for discussion).

My response to Fagerberg's objection is twofold. First, I accept that GSE allows for conflicts between functions – but that strikes me as an interesting and fruitful implication of it, not an embarrassment (Garson 2019, 73). By the same token, suppose one had a theory of belief formation according to which it is possible for a person to hold two conflicting beliefs. That fact would not be an objection against one's theory of belief formation but an interesting and potentially theoretically fruitful consequence.

Second, even if one thinks that the possibility of function conflict is a serious problem, that problem is inherent in the traditional selected effects theory as well. That is because the traditional theory allows for multiple levels of selection (such as group level, organism level, and chromosome level), and therefore the possibility that a trait can be an adaptation for doing F by virtue of one level but an adaptation for doing G (which is contrary to F) by virtue of another.

For example, D. S. Wilson (2015, Chapter 2) describes how sexual aggression in water striders may be selected for at the individual level and selected against at the group level. Therefore, conflicting functional norms would not supply a reason for preferring the traditional theory to the generalized theory, which was the point of the parity of reasoning argument.

Intriguingly, Millikan (2005, 99-100) has explored the issue of how her version of the selected effects theory allows for such conflicts. One of her examples comes from language. A phrase might have the "direct" proper function of inducing one set of actions in its hearer (e.g., "pass the salt" might have the proper function of inducing its hearer to pass the salt) and a "derived" proper function that is contrary to the first (for example, if the speaker uses the term in a metaphorical, sarcastic, or idiosyncratic way). The fact that there are occasional function conflicts should not, alone, count against any particular theory of function.

4. Three Solutions

I turn now to three critics, Conley, Bourrat, and Schulte (as Dussault 2023 largely reviews these criticisms I will not address that paper here). Each of them takes, as a starting point, the observation that GSE would imply that rocks in a pile can have functions, and each offers a different diagnosis of how GSE errs. Although I think the first two criticisms can be largely handled within the existing framework of GSE, responding adequately to the third demands a substantive revision.

Solution one: Conley

Brandon Conley argues that GSE errs precisely in expanding the traditional theory to entities that don't reproduce. In other words, he thinks the entire theory is a false start. If we don't restrict functions to entities that reproduce, we can't avoid trivializing counterexamples of this sort.

Conley agrees with me that it would be a desirable thing to allow neural selection (say) to give rise to new functions over the lifetime of the individual. But the traditional selected effects theory already lets us do that, thanks to Millikan's (1984; 1989a) well-known distinction between direct and derived proper functions. In short, an entity acquires a "direct" proper function if it undergoes something like differential reproduction on account of that effect. An entity has a "derived" proper function if an entity with a "direct" proper function produces it, in the right way, as a means of satisfying that direct function. A synapse that is differentially retained in the brain cannot acquire a direct proper function, because it doesn't reproduce. But a synapse can acquire a derived proper function on account of being produced in the right way by a mechanism that has the direct proper function of producing entities like that (such as synaptic pruning).

The combination of the traditional selected effects theory, and the distinction between direct and derived proper functions, is a powerful one. But one of the classic problems with the traditional selected effects theory is that it, too, faces trivializing counterexamples. Bedau (1991) argued that, under certain conditions, clay crystals can probably undergo a form of natural selection. But clay crystals don't have proper functions. If a crystal doesn't happen to cleave in two, it's not malfunctioning or disordered. (Of course, nothing prevents them from having functions in the minimal function sense of the term.) Schaffner (1993, 383-4) devised a similar example of a machine that clones ball bearings. Because of some presumably accidental feature of the way the machine is designed, smoother bearings are more likely to fall into gaps, and when they do, they are duplicated. At the end of the process, there is a far greater proportion of smooth bearings than rough ones. He thinks this is a case in which we would not wish to attribute functions to the smoothness of ball bearings. The larger point is that whether one restricts functions to things that undergo differential reproduction, or one expands functions to include things that undergo differential retention, too, one will face the same liberality worries. One of my motivations for restricting functions to populations was to help both GSE *and* the traditional theory, not to avoid alleged counterexamples that are unique to GSE (Garson 2019, 42).

Solution two: Bourrat

Pierrick Bourrat develops a two-part argument against GSE. First, he thinks my appeal to causal-interactionist populations is arbitrary. Furthermore, he thinks the problem I'm struggling with is something of a pseudo-problem. Why the felt need to exclude rocks from having functions? Why not include them and treat them as an uninteresting case? As I have already addressed the latter concern above, I will focus my attention on the former.

Natural selection takes place in a population. That much is generally accepted. But, Bourrat emphasizes, biologists don't entirely agree about how "population" should be defined. Millstein (2010) helpfully documents various ways that biologists have defined populations, such as "a group of individuals of a single species," "groups of organisms of the same species living in a particular geographic region," and groups of conspecific organisms in a region that exhibit "ecological and reproductive interactions." Consider the second of these. Sometimes, biologists use "population" just to *mean* a collection of entities of the same species that occupy the same arbitrarily-delimited region of space and time. For example, an ecologist or conservationist might speak of "the wolf population of Idaho." That is not a causal-interactionist population. Moreover, Lewontin (1970) asks us to imagine two strains of bacteria, A and B, replicating at different rates in a test tube but that have no impact on each other's absolute fitness. He thinks that such a collection undergoes natural selection (in that one strain increases in frequency over the other). The collection of bacteria, however, is not a causal-interactionist population.

With these sorts of examples in mind, Bourrat (2021, 64-5) accuses me of arbitrarily selecting something like Millstein's "causal-interactionist" populations as the correct definition of population – and then presenting this definition as if I'm deducing it from the very concept of natural selection. Aren't I engaging in the same sort of arbitrariness I accuse traditional selected effects theorists of?

I want to ward off a potential and rather subtle misunderstanding of GSE. I did not claim to deduce the *causal-interactionist* notion of a population from the idea of natural selection. Rather, I claimed, more cautiously, that the idea of natural selection depends on a rather vague notion of a population, and that the causal-interactionist conception is one useful way of explicating that notion (Garson 2019, 104). But Bourrat is right that I did not justify why I chose that *particular* construal of populationhood from among the existing biological construals. To that extent it seems arbitrary – precisely the arbitrariness I've accused the traditional selected effects theorist of.

So, I need a different argument for why functions depend constitutively on causal-interactionist populations. Put differently, I need an argument that shows that anyone who is wedded to the selected effects theory (traditional or generalized) must *also* be wedded to the idea that functions require causal-interactionist populations, without suggesting that this appeal to causal-interactionist populations can be deduced from the very definition of a selection process as if it were an analytic truth. Better: it must be shown that the basic package of motivations that drive the selected effects theory (in any form) point, inexorably, to causal-interactionist populations, and therefore that the formulation of the definition ought to embed some reference to such populations (to the extent that it is construed as a theoretical definition rather than, e.g., a conceptual analysis).

There are at least two ways I might attempt to argue that proper functions depend on causal-interactionist populations. The first is to argue that *only the causal-interactionist notion of population can satisfy the explanatory burden that GSE carries*. The second is to argue that *only the causal-interactionist notion of population can satisfy GSE's realist ambitions.* Of these, I'll pick the second.

First, one might argue that, regardless of the plurality of population concepts, it's appropriate to embed causal-interactionist populations within the selected effects theory because doing so satisfies the selected effects theorist's ambition to make sense of the explanatory ("teleological") aspect of functions. One point of the selected effects theory is to show how functions can be explanatory – specifically, to show how, when we attribute a function to a trait, we are, at the same time, offering an explanation of the trait's very existence. But suppose that the selected effects theory could only possess this explanatory power *if* the sorts of populations undergoing selection are causal-interactionist populations. Then we would have a simple, non-arbitrary justification for choosing causal-interactionist populations as the right kind.

I'll break this down a bit more. Some believe there's a deep connection between causal-interactionist populations and "origin explanations" (Nanay 2005; Godfrey-Smith 2009, 50-2). Everyone agrees that natural selection can explain the frequency of a trait in a population. But does it also explain why any particular organism has that trait? Put differently, selection explains why most zebras have stripes. But does it also explain why Amadi the zebra has stripes? Some think it does, but only if the selection process takes place in a population that involves a high level of competition, that is, in a kind of causal-interactionist population. The literature here is large and somewhat unwieldy, and grazes over problems about the nature of explanation, causation, and counterfactuals (see Garson 2019, 32-6).

I have two reasons for rejecting this solution. First, I have doubts about whether natural selection actually *can* explain why a particular organism has a trait, such as why Amadi has stripes. Following Sober (1995), I suspect it can only explain the frequency of stripes in a population. I agree with Neander (1995) and Godfrey-Smith (2009) that selection can make a certain trait more likely to appear within a population by boosting the absolute number of various precursor traits. But that would still constitute an explanation only of why the trait has a non-zero frequency in the population, rather than an explanation of why a particular individual has that trait. The explanation for why any particular zebra has stripes seems to depend entirely on a complex developmental story involving facts about genetic, epigenetic, and environmental interactions, in addition to facts about the mechanisms of inheritance (how it inherited those genes and epigenetic factors from its parents).

Second, and more importantly, I suspect that the debate about origin explanations is somewhat irrelevant to the selected effects theory. When biologists attribute functions to traits – for example, when they say things like, “the function of zebra stripes is to deter biting flies” – they’re generally not trying to explain why this or that zebra has stripes. They wish to explain why zebras, generally, have stripes (or why stripes occur at a non-negligible frequency among zebras). But this is a population-level fact, not an individual-level fact.

There’s a second, far simpler way to respond to Bourrat’s criticism. This has to do with the issue of *realism*. The key attraction of causal-interactionist populations is this: whether a collection of individuals does, or doesn’t, constitute a population, doesn’t depend on the mind. Accounts of population which invoke the mere idea of spatial and temporal boundaries invariably leave the precise choice of boundary-setting up to the investigator. In contrast, causal-interactionist populations give populations a mind-independent character (Millstein 2009; 2010). As noted above, realism about functions is part of the core package of motivations for the traditional selected effects theory, for reasons I’ve outlined.

One might argue that the notion of a causal-interactionist population is equally indeterminate. Its application requires somewhat conventional decisions, for example, decisions about the precise *degree* of interconnectedness a collection needs to exhibit before it counts as a population (Matthewson 2020). Still, this strikes me as the ordinary sort of indeterminacy that afflicts language in general. (When, precisely, is a man bald?) In contrast, the bare idea of "spatial and temporal boundaries" is hopelessly open-ended. (Do all the wolves in Northern Idaho count as a population? Or the entirety of the Northeastern United States? Or North America?) "Causal interaction" is *mildly* indeterminate; "spatial and temporal boundaries" is *wildly* indeterminate. (Of course, given the choice of a particular boundary, there could be an objective fact of the matter as to how many populations of wolves, say, inhabit Northern Idaho, but the conventional character of this decision clashes with the realist ambitions of the theory for reasons I set out in Section 1.)

Solution three. Schulte

Peter Schulte's criticism is the friendliest to GSE. What the rocks example shows, he thinks, is that for a collection to be a population, it's not *enough* that its members impact one another's fitness somehow or other. Rather, they must be bound together by competitive interactions, where "competitive" is understood in a specific way. As Godfrey-Smith (2009, 52) put it, when it comes to constituting populations, "competition is an especially Darwinian glue." This is precisely what the pile of rocks lacks. So, for Schulte, what exactly is a competition?

Consider two hungry mice, Kaila and Freddy, running toward the same food pellet, and suppose Kaila is faster than Freddy. What makes this a competition is not just that Kaila is hurting Freddy's survival chances somehow or another, but that Kaila is hurting Freddy's survival chances by doing just those things that boost her own survival chances. Her gain is his pain. As Schulte puts it, for there to be a competition between A and B, "A exerts a negative influence on B's chances of reproduction or *persistence*, *because* A behaves in a way that enhances its own chances of reproduction or *persistence*" (374).

Compare this scenario with one in which Kaila is resting on a high ledge, falls off the ledge, and injures Freddy in the process. Even though one individual is "doing something or other" that impacts the absolute fitness prospects of another individual, we would hesitate to call this a competition and therefore, for Schulte, it is not the sort of interaction that constitutes populations.

Apply this to the rocks. In order for two rocks in a pile to "compete," it wouldn't be enough for one rock to somehow lower the persistence chances of another rock. Rather, the one rock would have to lower the persistence chances of the other by doing just those things that boost its *own* persistence. But this isn't the case. When a harder rock rubs against a softer rock, and thereby lowers the persistence chances of the softer one, it's no better off for doing so. In fact, the harder rock is hurting its own persistence chances, too.

I think Schulte is onto an important insight, but there are two ways in which I depart from his analysis.

First, while I think the basic intuition motivating his formula is right, I don’t think his definition quite captures it – it errs on the side of over-generality. That’s because it would allow various relationships to count as “competitive” which I don’t think he has in mind, such as when one animal negatively impacts another because of some harmful byproduct it creates in its quest to survive. Suppose an animal, while drinking from a pool of water, routinely but unintentionally defecates in the pool, thus jeopardizing the health of others who drink from it. In this case, it’s hurting others in the course of carrying out those very activities it benefits from, but there’s nothing like a competition taking place.

It seems to me that the basic picture motivating his account, rather, is something like this: for two organisms to compete, there must be something *over which* they compete. There must be a common, limited pool of resources, such that my getting some resources from this pool deprives you of the same. What makes you and I compete with one another isn’t just that I’m negatively impacting your survival, and it’s not just that I’m negatively impacting your survival by virtue of those activities which help me to survive. Rather, it’s that I’m negatively impacting your survival by virtue of depleting some of the resources that you rely on, too.

Here is a second way I depart from Schulte. Why must the sorts of relationships that constitute populations be competitive, rather than competitive *or* cooperative? This becomes easy to see if we imagine a group of animals crowded around a literal pool. One way I impact your survival is by preventing you from getting to the pool. Another way I impact your survival is by making the water more readily available to you, for example, by drinking less than I need to, or by helping you walk to the pool, or by working with you to scare off the members of another species. Sex is trivially a cooperation in which two individuals positively impact each other's access to mating opportunities. The "glue" that binds individuals into populations is this: by using some shared resource, I help or hinder your ability to use the same. It's worth noting that Schulte (2021, 375-6) explicitly points out that if one were to modify his notion of a biological population to include cooperative relations, one would still be able to get the same result: piles of rocks are not populations and therefore the individual rocks that make them up (or their attributes) do not come to have functions. But then it makes it more puzzling to me why he maintains that competitive relations alone are constitutive of populations, rather than that populations are constituted by various fitness-relevant relations, and that competition drives natural selection within any particular population.

Here, I think, is the right way to amend GSE, a way that preserves its core virtues while avoiding trivializing counterexamples:

GSE: A function of a trait is an activity that caused its differential reproduction, or its differential retention, in a population. For the purpose of this definition, a population is a collection of individuals, of the same type, that impact one another's persistence, survival, or reproduction prospects by virtue of the fact that, by using some common resources, they impact each other's ability to use those same resources.

5. Conclusion

My view is that GSE is the best theory of *proper function* on the market: it makes sense of the explanatory and malfunction-permitting character of functions while avoiding the traditional selected effects theorist's rather peculiar insistence that functions attach themselves, first and foremost, to lineages of reproducing entities bound together by parent-offspring relations ("reproduction" or "copying"). This yields a satisfying, and more importantly, a unified theory of proper function. While "function" might be ambiguous in biology, there is only one sort of thing in the world that satisfies the demands of our pretheoretical notion of proper function: namely, selected effects. Selected effects are uniquely summoned, as it were, when biologists call out for proper functions. GSE simply asserts that the sorts of selected effects in question do not rely on reproduction. This conceptual move has important implications for thinking about naturalism, the nature of disease and disorder, mechanisms, and mental representation.

A rather long-standing objection to such a liberal move is that it descends into vacuity, and that it would yield function ascriptions that wantonly violate the very usage it seeks to model itself upon. I initially sought to avoid the liberality problem by leaning on the notion of a (causal-interactionist) population. Yet I erred in two ways. First, I didn't articulate that notion carefully enough, as it let in exactly the sorts of counterexamples I wanted to exclude. Second, I did not show how pointing to causal-interactionist populations represented a natural, and even inevitable, extension of GSE. As a consequence, it had the feel of an inelegant extension designed merely to block obvious counterexamples. The version of GSE I offer here clarifies, in a more precise way, the underlying notion of a causal-interactionist population that functions depend on. I also show how anyone who is committed to any version of the selected effects theory (for the reasons that typically lead people to embrace that theory) should be committed to the claim that proper functions depend on these causal-interactionist populations.

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