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# Let's Get to Work: A Response to Our Commentators

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It's an honour to have so many major contributors to the literature respond to our article and we thank them for their thoughtful responses. There are clear shared themes across these commentaries, so we have organized our response around six major themes rather than individual commentators.

Our target article proposes a canonical statement of the selected effects theory (hereafter 'SET'). We aim to state SET in conventional biological terminology so we can apply the theory to actual evolutionary explanations from the biological literature.

We then argue that there are common and important cases in which the SE function(s) of a trait do not explain either the existence of the trait or its prevalence in a population. The claim that SE functions explain the traits that bear them is often stated as one of the main strengths of SET:

That the koala's pouch has the function of protecting its young does seem to explain why koalas have pouches. That the bee's dance is for directing other bees to pollen does seem to explain why bees dance [Neander 1991: 457]

We argue, however, that SE function explanations usually fail when the evolution of a trait involves frequency-dependent selection or the trait evolves in a heterogeneous environment. The intuition appealed to by Neander and others can only be relied upon when traits evolve in homogeneous environments and with constant fitness functions.

We demonstrate this with three examples of how biologists actually explain the existence and prevalence of traits. We show that SET extracts from each evolutionary explanation the information that would be explanatorily relevant if the trait evolved in a homogeneous environment with no frequency-dependent selection. Even when frequency dependence, the structure of the environment, or the dynamics induced by these phenomena are central to the actual biological explanation of the trait, SET discards that information.

It is in this straightforward sense that the explanations offered by SET in these common and important cases of natural selection are poor explanations. Rather than summarizing the actual explanation of why the trait evolved, they misrepresent

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that explanation: they pick out from the actual explanation only the information that would be explanatorily relevant if the trait had evolved in another way.

We identify six main themes in the replies of our commentators.

# 1. SE Functions are Partial Explanations

All our commentators suggest that we make a basic error by demanding that SE function explanations should be *complete* evolutionary explanations. Dewey identifies this as the core claim in our paper: 'Christie, Brusse, *et al.* argue that selected effects are *insufficient* to explain the prevalence of traits when selection is heterogeneous' ([Dewey 2022: 412], our emphasis). But as the commentators all correctly point out, no evolutionary explanation ever mentions *all* relevant factors. Fortunately, we do not demand that SET provides complete explanations, only that it makes an appropriate selection of explanatory information.

Garson writes that

Sometimes Christie, Brusse, *et al.* make a distinction between the (supposedly stronger) claim that SE 'explains' traits and the (supposedly weaker) claim that it has some 'explanatory relevance' to traits, but I don't follow the distinction. Almost all explanations are partial explanations, so to 'explain' something, and to point to some 'explanatorily relevant' facts, strike me as one and the same. [Garson 2022: 379–80]

We can clarify the distinction using Garson's own example. He writes that

The fact that stripes deter flies explains why some zebras have stripes in the same way in which a driver's intoxication level explains the motor crash. It's not the whole explanation. It's part of it. [Garson 2022: 379]

Now suppose that the intoxicated driver was driving one of the cars in the tragic fiftyone car pile-up that occurred in heavy fog on the UK's M4 motorway in 1991. One driver's intoxication may be explanatorily relevant but it would be thoroughly misleading to attribute their accident to intoxication and not mention the fog or the pile-up.

We do not demand that SE functions serve as complete evolutionary explanations. Our objection is that, in the cases we highlight, SE function explanations discard critical explanatory information.

### 2. SET Does Not Try to Explain the Existence and/or Prevalence of Traits

Garson [2022] and Kingsbury [2022] argue that we have misidentified the target of explanation. SET does not try to explain the *existence* or *prevalence* of traits. It tries to explain what traits are *for*. Shea [2022] makes a similar point in the specific context of teleosemantics, and our response to Shea (Theme 4) expands on what we say in this section.

Kingsbury writes that

The selected effects theorist starts with a currently existing trait that we have reason to believe has a proper function, and gives an account of what grounds that proper function. Given that aim, it is appropriate to focus on the periods during which the trait has in fact contributed to fitness. [Kingsbury 2022: 369]

#### In the same vein, Garson writes that

You have to know what a theory's supposed to do before deciding whether it's doing a good job of *it*. But how do you decide what it's supposed to do? You see it as a move within a longer conversation—in this case, one that's been taking place for over two millennia. [Garson 2022: 383, italics in original]

#### Garson says that SET

restores final causation to biology [by showing] how selectionist explanations can be a subtype of teleological explanation, insofar as they allow one to cite the effect of a trait in an explanation for the current existence of that trait. [Garson 2022: 383]

Notwithstanding his reference to explaining 'current existence', Garson takes the explanatory target to be the fact that traits exist *with functions*. Because he is seeking to explain why a trait exists with a function, rather than merely why it exists, that licenses a partial explanation which focuses only on ways in which the trait has increased fitness relative to some alternatives.

The problem with this defence of SET is revealed by Kingsbury's remark that, '[t]he selected effects theorist starts with a currently existing trait that we have reason to believe has a proper function' [2022: 369]. How can an SET theorist, who defines function in terms of past evolution, have reason to believe that a trait has a function *before* investigating how it evolved? The only possible reason is 'Paley's watch': the trait looks intuitively as if it was designed for something. It is because SET can turn Paleyan intuitions about design into respectable evolutionary explanations that Garson calls it 'a crowning achievement of twentieth-century philosophy of science' [2022: 378]. So far so good. We don't disagree with the truism that SET makes room for teleological explanations in a Darwinian world. But making room for such explanations is a long way from showing that they are correct. Darwin accepted some of the teleological explanations he inherited from the Paleyan tradition, but he rightly rejected others.

Garson is convinced that contemporary biology strongly supports the idea that organisms consist of parts that evolved to serve specific functions. He repeatedly expresses bafflement that we should question this: 'on the surface, it seems incredible that someone would deny that SE function statements are explanatory' [2022: 379]; 'short of citing that [fitness-enhancing] effect, we're trading in satire, not science. It would be like trying to explain a car's engine without mentioning what it's for' [2022: 382]. But we just don't think this is true. Contemporary biology takes very seriously the idea that natural selection is strikingly unlike a design process in which parts are constructed to serve specific functions.

The doyen of evolutionary medicine, Randolph Nesse, has used the slogan 'tacit creationism' to label the view that organisms consist of discrete traits each of which has some specific function(s).<sup>1</sup> Instead, he argues, organisms are highly integrated, 'organically complex' systems built by genes most of which affect many aspects of the organism. Organisms evolve under the influence of natural selection acting on these genes and questions about why organisms have specific traits are often best answered by exploring the evolutionary dynamics of those genes rather than by asking for the function(s) of each trait.

It would be absurd to describe Nesse as 'anti-Darwinian', or 'anti-adaptationist'. He is not trying to diminish the power of natural selection, but merely to point out how

<sup>&</sup>lt;sup>1</sup> https://www.randolphnesse.com/articles/tacit-creationism

different natural selection is from the vulgar idea that Mother Nature designs living machines.

In the same vein, philosopher of medicine Maël Lemoine has discussed how attributions of specific functions to specific components 'dissolve out' as the causes of dysfunction are traced downwards into the molecular and physiological networks that underpin a surface trait [Lemoine 2015: 37].

Samir Okasha has identified another way in which natural selection is very different from an agent choosing the best solution:

we expect a real agent to have stable preferences. However, in game-theoretic scenarios the fitnesses of the different phenotypes (or strategies) is frequency dependent, so the selective environment is always changing; thus the fictitious agent's preferences change too. It is as if mother nature continually chooses the phenotypic alternative she most prefers, only to find that her tastes have changed a moment later, so she needs to choose again; and this process can continue indefinitely. [Okasha 2018: 19]

Considerable scientific work is needed to define adaptation in a way that vindicates the idea that, in the common and important forms of natural selection we discuss in our article, traits have an adaptive function. We are pleased that two leading philosophical contributors to that work, Okasha and Shea, have written commentaries, to which we now turn.

#### 3. SET Needs a Modern Understanding of Adaptation

Okasha and Shea take the phenomenon of frequency dependence and environmental heterogeneity more seriously than Garson. These are not merely 'biological curiosities [...] [which] have been floating around in the functions literature for decades' [Garson 2022: 382]. The importance of such phenomena to evolutionary dynamics is now routinely conceded by population biologists and the consequences for evolving populations are often anything but mundane [Stevens 2011]. Shea says that, '[w]ork is needed to clarify how selected effect functions arise in cases of frequency-dependence, mixed equilibria and bet-hedging' [Shea 2022: 400] and Okasha that, 'the SE theory is tailored to simple evolutionary scenarios, and that its applicability to more complex scenarios has been insufficiently examined' [Okasha 2022: 387]. We will focus here on Okasha's attempt to reformulate SET for these more complex scenarios. We address Shea in the following section.

We have no issue with Okasha's evolutionary game-theoretic analysis of our examples. But we do not think that Okasha's results are as reassuring for SET as he suggests.

Okasha thinks all three problem cases we raise for SET can be construed as cases of frequency-dependent selection (hereafter 'FDS'). This is explicit in our case of negative FDS in Gouldian finches, whereas FDS is implicit in bet-hedging strategies for seed allocation in a stochastic environment, and in Red Queen style coevolution between parasitic biting flies and their zebra hosts. In each case, according to Okasha, there is a readily available conception of adaptation as optimality, one which requires that 'each individual should exhibit a trait (or play a strategy) that maximizes its fitness *conditional on the trait distribution in the rest of the population*' [Okasha 2022: 388]. More formally, a trait variant or strategy is an adaptation if and only if it is an evolutionarily stable strategy (ESS) or a strict Nash equilibrium. A trait or strategy is an

adaptation if it represents a 'best response' to its selective environment [Brandon 1990]. Okasha contrasts these 'well-behaved' adaptation-as-best-response cases with more difficult cases, such as his side-blotched lizards whose three distinct male morphs exhibit rock-paper-scissors dynamics with continually cycling trait values and thereby no corresponding ESS. In these 'naughty' cases he thinks there is no principled sense in which one could claim that any of the three phenotypic traits is a best response and consequently an adaptation.

We are puzzled by Okasha's suggestion that rock-paper-scissors dynamics present an insurmountable problem for SET while the Red Queen dynamics in our parasitic biting fly example do not. Studies of host-parasite coevolution reveal how the relative fitnesses of different parasitic types change as a time-delayed function of their frequencies because hosts tend to develop resistance to the most common type [Frank 1994]. Delayed negative frequency dependence of this sort can lead to population cycles of exactly the same kind as the rock-paper-scissors dynamics. So both cases present the same challenge for SET, namely continual cycling of the selected value of the trait. We think Okasha is simply mistaken that Red Queen dynamics can be accommodated by SET whereas rock-paper-scissors dynamics cannot. The adaptation-as-best-response approach gives no succour to SET in either case.

We accept that Okasha's conception of adaptation-as-best-response can be applied to our other two cases of negative frequency-dependent selection in Gouldian finches and bet-hedging strategies for seed allocation in a stochastic environment. But we think the impact on SET of adopting this view of adaptation is greater than Okasha supposes. For a start, defining adaptation in this manner is controversial both theoretically [Diekmann 2004] and philosophically [Orzack and Sober 1994]. This tension goes unacknowledged when Okasha [2022] says that '[m]any evolutionary theorists argue, and I think they are right, that the concept of adaptation can apply in cases of FDS so long as it is suitably understood,' or that 'adaptation in the sense of bestresponse is a straightforward generalization of the standard notion of adaptation that applies when selection is frequency-independent' [ibid.: 388]. This sounds very reassuring, but in other presentations Okasha acknowledges that the issue is less clear cut:

What about individual optimization? Here an ambiguity should be noted. Some authors understand the statement that evolution optimizes individuals' traits narrowly, to mean optimization of a one-placed function mapping individual trait value onto fitness (e.g., Diekmann 2004). In this sense, optimization only occurs when selection is frequency-independent (and even then not always). However, others take optimization to include 'best response', that is, having a trait that maximizes individual fitness conditional on the trait distribution in the rest of the population. [Okasha 2018: 108–9]

For Okasha, '[t]his issue is largely semantic; however, [he] favour[s] including best response as part of optimality, in order to preserve the conceptual link between adaptation and optimality' [2018: 109].

Adopting this conception of adaptation comes at a cost that advocates of SET will find high. It blurs the distinction between SET and accounts of function that focus on current fitness. In standard formulations of SET the *past* fitness-enhancing effect(s) of a trait constitute its *current* function(s). So, standard formulations of SET would ask what actual payoffs each strategy achieved in the recent past. Whether a strategy is a best response to its current environment is irrelevant. This focus on past rather than current selection is supposed to be one of the great strengths of SET, allowing it to distinguish between what a trait actually does and what it is 'meant to do'.

Okasha's adaptation-as-best-response account replaces the *historical* explanations of standard SET with *equilibrium* explanations. Okasha regards a strategy as an adaptation, and hence as having a function, if the population has evolved to a state where that strategy is a strict Nash equilibrium. Whether that strategy was an equilibrium in the past is irrelevant. This is why adaptation-as-best-response copes so smoothly with our examples in which selection has consistently acted *against* a strategy until the population reaches equilibrium: it only cares about equilibrium once attained.

If a population has been at equilibrium for some time, then standard SET and the adaptation-as-best-response account will coincide—what is best now is also what was best in the past. But it is an important feature of standard SET that it *only* considers the past. If the proportion of competing strategies in a population changes, then individuals who play an old, outdated strategy which is no longer the best response are functioning correctly, while individuals who play the strategy that is now the best response are malfunctioning.

On Okasha's 'adaptation-as-best-response' account, in contrast, the old strategy, which was the best response in the past, is no longer an adaptation. The strategy that is now the best response is an adaptation even if it was selected against in the recent past. This is the inevitable result of defining adaptation in terms of the equilibrium state rather than the actual payoffs obtained with different strategies in the past.

The adaptation-as-best-response account seems to have as much in common with the view that the function of a trait is its contribution to the ability of the organisms to survive and reproduce in their current environments. [Bigelow and Pargetter 1987; Griffiths 2009, 2016] as it does with standard SET. We expand on this in the next section.

We do not take this as a criticism of Okasha's proposal, but rather as an example of how progress in thinking about function can be achieved by paying more attention to how population biology actually explains traits, as we urged in our paper. If Okasha is right, then what is often taken to be one of the most fundamental distinctions between philosophical analyses of function—between backward-looking analyses and current fitness analyses—looks less significant.

#### 4. SE Functions Do the Right Explanatory Work for Teleosemantics

In his commentary, Shea [2022] outlines his program of analysing the normativity of representational content in terms of the evolutionary 'success conditions' of representations. Shea's program is inspired by Millikan's original 'teleosemantic' approach to naturalizing semantics, but connects this with a rich body of theoretical work on the evolution of signalling between and within organisms.

Like Garson and Kingsbury, Shea thinks that we have misidentified the target of explanation. But his point is specifically about the target of explanation in teleosemantics:

If we were concerned with explaining why a trait evolved and stabilized at a certain frequency, then it would indeed seem arbitrary to focus on its positive contribution to fitness and ignore the circumstances in which it reduced fitness [Shea 2022: 404]

It is legitimate for Shea to focus on positive contributions to fitness because his theory only 'relies on selected effect functions in order to home in on outcomes that count as successes' [Shea 2022: 404].

We have two responses to Shea. First, we are sympathetic to the idea that if the aim is to distinguish successful from unsuccessful interactions with the environment, then it makes sense to focus on occasions when a trait is fitter than its competitors. As Shea notes, one of us has made a similar move in order to distinguish development from ageing [Griffiths and Matthewson 2018]. But, although Shea says, 'I largely agree with the points about biological functions made by Samir Okasha' [Shea 2022: 401], this focus on 'success conditions' actually brings him into conflict with Okasha about rock–paper–scissors cases. Because Okasha links the idea of function to that of adaptation, he does not ascribe function in cases where there is no 'best response' to the environment and hence no adaptation. But Shea thinks that rock–paper–scissors traits have success conditions. The success condition for 'rock' is presumably that it meets 'scissors' not 'paper' and hence, in Shea's view, it is a 'stabilized function' of 'rock' to defeat 'scissors'.

In fact, Shea's formulation of SET in terms of 'success condition' is fundamentally different from Okasha's in terms of 'best response' (strict Nash equilibrium). The idea of best response is *atemporal*—whether a strategy is a Nash equilibrium can only be evaluated with reference to the very population of which an individual playing that strategy is a member. Hence, for Okasha, a trait is an adaptation in a population because it represents an equilibrium in that population and this equilibrium is the result of natural selection. But Shea defines 'success conditions' *temporally*, with reference to past successes: 'Evolutionary success conditions are conditions that figure in an explanation of how an effect contributed systematically to survival and reproduction' [Shea 2022: 402]. So, for Shea, a trait can retain its SE function without currently being adaptive. But for Okasha it cannot, since that would imply that the trait is not a best response to the actual population in which it exists and hence not an adaptation. Shea uses ancestral populations as a reference class to evaluate the effect of a trait token on fitness, while Okasha necessarily uses the actual population in which the trait token occurs.

Zachary Gabor's proposal converges on Shea's idea of success conditions. Gabor proposes that when fitness is frequency-dependent we should focus on each of the competing morphs one at a time and ask what makes each morph successful. Gabor's idea seems to be that we can make frequency dependence go away if we replace the question 'what made a successful finch?' with 'what made a successful red-headed finch' and 'what made a successful black-headed finch'? These seem to be questions about 'success conditions' rather than about the existence or prevalence of traits.

Second, we applaud the recognition by Shea, Godfrey-Smith, and Cao [2018] that the ways in which a trait interacts with the environment to promote fitness may be varied, with some of these interactions being more significant than others in the evolution of the trait. Shea and his collaborators apply this graded approach to teleosemantics by treating representational content as a vector with different components corresponding to the various success conditions of different 'direction' and strength that have helped stabilize the signal. In the general literature on SE function, John Matthewson [2020] has suggested that a trait has each of its SE functions *to some degree*, where that degree represents a measure of how significant this specific positive contribution to fitness has been in the evolution of the trait. If we follow Okasha's lead and tie the notion of function to the idea of adaptation as that concept figures in contemporary population biology, then something like Matthewson's suggestion seems inevitable.

#### 5. Exegesis of Millikan's Work

Ruth Millikan objects that we have misunderstood key terms such as 'Proper' and 'Normal', and that the selected effects theory of function we criticize has little if any resemblance to the theory she presented in her massively influential *Language, Thought, and Other Biological Categories* [1984] and has refined and developed in many later publications.

This is partly because our 'SET' represents an entire tradition of theorizing in recent philosophy. Like Shea, Millikan's focus is the philosophy of language, as she emphasizes in her commentary. But Millikan's work has been inspirational for the broader project of naturalizing biological teleology. That project—SET—is normally introduced by citing Millikan and Karen Neander as its twin founders, as Kingsbury, who is an important contributor to the secondary literature on Millikan, does in her commentary:

According to the selected effects account of biological function, it is the fact that blood-cleansing is the thing that my ancestors' livers did that contributed to their survival and reproduction ... That, at least, is the version of the selected effects theory (SET) endorsed by Karen Neander ... and Ruth Millikan [Kingsbury 2022: 367]

It is this Millikan-inspired and widely advocated theory of biological function that is the target of our paper.

We agree that our use of the term 'Proper function' is quite different from Millikan's. We decided to use that term stipulatively to refer to the class of functions of which SET is meant to be the correct analysis. We did this so that we could raise the possibility that SET is not, in fact, the right analysis of this class of functions. Perhaps this stipulation was a mistake on our part, but some such convention is needed if the adequacy of SET is to be questioned. We certainly did not intend to imply that our stipulated use of this term is true to Millikan's usage.

We are less clear that we have misrepresented Millikan's important concept of the 'Big-N' Normal. Perhaps we have missed some of the subtleties of the relationships between Normal conditions and Normal explanations, but we stand by our central point, which is that the idea of the 'Big-N' Normal picks out just those episodes of selection in which a trait was historically successful. The 'Big-N' Normal is thus different from the ideas of normal environment, historical environment or environment of evolutionary adaptedness (EEA) which are—for good reason—used in actual biological explanations of the existence and prevalence of traits.

The most important point of difference, however, is that Millikan asks what function a *trait token* has in virtue of its membership of a 'reproductively established family', which is a lineage of trait tokens. We tried to translate this into claims about the evolution of homologous traits in a population. But Kingsbury's insightful commentary argues that this is not true to Millikan or, she suggests, to most SE theorists. Kingsbury notes that Griffiths' [1993] version of SET already differed from its contemporaries in being explicitly expressed in terms of populations of traits. But, for Kingsbury, it is a key feature of SET that it explains the functions of trait tokens, as stressed by Neander [1995a, 1995b]. The theory 'will look at the particular lineage that Walter belongs to, and what blue heads have done, if anything, for the individuals in that lineage.' [Kingsbury 2022: 370]. Kingsbury points out that our criticisms of SET rest on features of the population-level statistical explanations that are characteristic of evolutionary biology. If SET relies on a different kind of evolutionary explanation, one which tracks the specific events in a specific family tree leading to some individual like Walter and explains how certain individual episodes of success led to Walter having his traits, then our criticisms may simply miss the mark.

We think this is an important point. However, it seems to us to highlight exactly the weakness of philosophical work on function to which we are trying to draw attention. If SET rests on these blow-by-blow causal explanations in family trees, then whether such explanations succeed is a complete unknown. Nothing like this can be derived from the science of evolutionary biology. It is hard to overstate the extent to which evolutionary biology is a science of populations. Only suitably structured populations can experience natural selection [Godfrey-Smith 2009]. The key concepts of natural selection simply are not defined for a family tree. Family trees do not have effective population sizes. A family tree cannot have replicator dynamics. Nothing is an evolutionarily stable strategy in a family tree, and so forth. The idea of a blow-by-blow causal history of the traits of each member of a lineage has no more resemblance to evolutionary biology than Laplace's demon tracking every particle has to physical theory.

#### 6. There is No Alternative to SET

Garson in particular seems to think that SET is the only game in town. No other theory of function can vindicate teleology in a Darwinian world. We do not agree.

One class of alternatives are 'organizational' theories of function [Christensen 1996; Mossio, Saborido, and Moreno 2009]. Garson admits that these theories can vindicate teleological thinking, but rejects them as an '*awful* theory on other grounds' [Garson 2022: 382]. Those grounds are primarily that organizational theories do not define the word 'function' in a way that accords with current usage [Garson 2017]. In contrast, we think that organizational theories represent a rich tradition in theoretical biology that has done a great deal to illuminate the distinctive nature of living systems. If the goal is to understand why living systems appear teleological, rather than to define the term 'function' in a way that preserves current intuitions about function, then organizational theories are powerful alternatives to SET.

Some of us also think that accounts of function and teleology in terms of how parts and processes contribute to fitness are strong competitors to SET [Griffiths 2009, 2016].

Most importantly, we think that SET itself requires further development, of the kind suggested by Okasha and Shea. Even if SET were the only game in town, that would be no reason to ignore its deficiencies.

#### 7. Niche-construction

Clint Hurshman's [2022] commentary stands alone from the rest because it urges us to look at niche-construction. Functions, he argues, may be produced by niche-

construction as well as natural selection. We applaud any proposal to introduce more of the complexity of modern biology into the functions literature. But Hurshman's proposal seems fundamentally unworkable. He suggests that organisms may adopt a strategy that does not currently increase fitness because it initiates a niche-constructing process that will make that strategy fitness-enhancing for future generations. But organisms can't do something in the hope that it will construct a niche for future generations! As Kim Sterelny has said, 'do not ask for credit as extinction often offends' (pers. comm). A niche-constructing trait might, of course, spread by drift and later acquire a function in the new niche, or the niche-constructing behaviour might be a side effect of some adaptation and only acquire a function in the new niche, but this raises no new issues for thinking about function.

# 8. Conclusion

Garson is correct that Darwin made a giant step forward in explaining the appearance of design in living organisms. But it is not, as he seems to suppose, only a small further step to the conclusion that each mental illness (for example) results from one or more traits failing to fulfil the function for which they were designed by natural selection. In areas where the relevant aspects of the environment are constant and frequencydependence plays little role, the SET approach to biological function works smoothly. In other areas, and the evolution of human cognitive adaptations is surely one of them, serious work is needed to show that SET can be applied. In our view, this is likely to require the development of more sophisticated versions of SET that move away from the idea that natural selection is akin to design and towards the idea that natural selection produces complex and sometimes counter-intuitive dynamics in evolving populations. We applaud the suggestions by Shea and Okasha of how to develop SET in a way that tracks how adaptation is understood in contemporary biology. Biologically informed approaches to function like this are what is called for by our target article.

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