

The Misuse of Sober's Selection for/Selection of Distinction

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ABSTRACT: Elliott Sober's selection for/selection of distinction has been widely used to clarify the idea that some properties of organisms are side-effects of selection processes. It has also been used, however, to choose between different descriptions of an evolutionary product when assigning biological functions to that product. We suggest that there is a characteristic error in these uses of the distinction. Complementary descriptions of function are misrepresented as mutually excluding one another. This error arises from a failure to appreciate that selection processes can be described at several different theoretical levels.

Keywords: Targets of selection, biological function, etiological theory

1. ETIOLOGICAL THEORIES OF BIOLOGICAL FUNCTION

A pure etiological theory of function, of the sort advanced by Karen Neander (1983, 1991a, 1991b), claims that the proper functions of a type are those effects which played a role in its selective history. These effects help to explain the presence of the type at the time at which the function is ascribed. It is a function of the human heart to pump blood, because this effect helps explain the prevalence of muscles of that type in humans.

The pure etiological theory replaces proto-etiological theories, such as Larry Wright's (1973, 1976), which make a similar claim about selective history but require, in addition, that the item be capable of performing its function at the time at which the function is ascribed. Wright's theory is unable to cope with the fact that organs retain their functions when they are damaged. A sick heart may lack the capacity to pump but it is still its function to do so. The pure etiological theory has no such difficulty. Damage to the item may deprive it of the relevant causal powers but leaves its history, and hence proper function, intact. This mismatch between actual and 'intended' causal powers gives rise to malfunction. It is even possible, as Neander stresses, for malfunction to be the statistically normal state of an organ, as when a pandemic virus diminishes the photo-synthetic capacity of the leaves of the 'variegated' varieties of certain plants.

Opponents of the etiological theory, such as Elizabeth Prior (1985), recognised that this simplification of the etiological theory allowed Neander to cope with the cases they had urged against Wright, but suggested that it left the theory unable to cope with vestigiality. Prior offered the following dilemma:

Neander's account allows us to make sense of the notion of malfunction and to ascribe functions to organs at times when they cannot perform those functions... However, what we here gain on the roundabout we lose on the swings for Neander's analysis is unable to accommodate the phenomenon of vestigial organs. On Neander's analysis the function of the appendix in man is (still) the breakdown of cellulose. (1985, p. 319)

A simple amendment to the etiological theory, alluded to by Ruth Millikan (1984, p. 32), distinguishes recent (or 'proximal') selective episodes, giving rise to current functions, from ancient selective episodes, giving rise to vestigial

functions. This proposal has been worked out in detail by Griffiths (1992, 1993). The notion of a proximal selective episode for a trait is formally defined in terms of the mutation rates at loci for that trait.

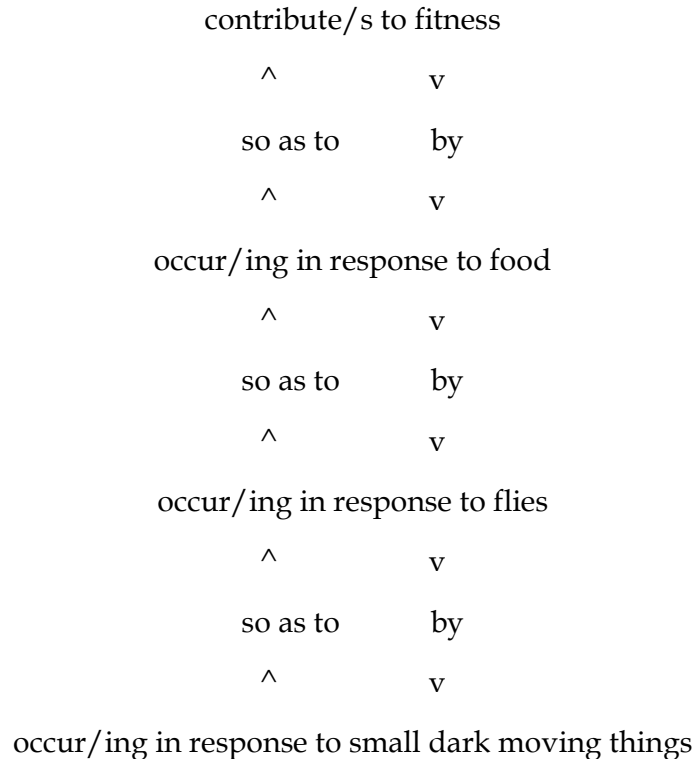
2. THE APPARENT INDETERMINACY OF ETIOLOGICAL FUNCTIONS

In a now famous study, Lettvin et al (1959) described part of the visual system of the frog *Rana pipiens*. The frog has a particular perceptual state (call it 'S') which occurs when it is confronted with certain stimuli and which causes it to strike out with its tongue and ingest what it so captures. In its natural habitat, this behaviour predominantly causes the frog to ingest flies. Under other conditions, however, any small dark moving object may be ingested: 'choice of food is determined only by size and movement.' (1959, p. 231)

There is an obvious adaptive story to be told about the selection of this mechanism in ancestral frogs. It ought therefore to be possible to determine the function of the mechanism. But the attempt to do so leads to a proliferation of apparently conflicting function ascriptions. Kim Sterelny (1990) has argued that the function of the mechanism is to detect and capture flies (or whatever taxa of insects form the frog's ancestral prey). Lawrence A. Shapiro (1992) has argued that the function of the mechanism is to detect food. Finally, Karen Neander (in press) has argued that the function of the mechanism is to detect small dark moving things. All three positions gain support from the etiological theory of proper function. Ancestral frogs did well because they could detect small dark moving things. They also did well because they could detect flies, and because they could detect food.

3. LEVELS OF THEORY IN BIOLOGY

Karen Neander (in press) has proposed that the various descriptions of a biological proper function can be arranged in an ordered series. The state S



Similar series can be constructed for most other biological traits. We believe that the series corresponds to a series of theoretical levels in evolutionary biology, each with a proprietary way of classifying the frog's trait. There are (at least) four such levels, and describing the frog at each level allows access to a different body of generalisations about evolution.

At the most abstract level of biological explanation, the evolution of representational state S may be explained by generalisations of the kind found in population genetics and evolutionary games theory. In such an

explanation, the evolution of S is explained by an equation in which the frequencies and fitnesses of S and competing alternatives to S are represented. From this, the frequency of S in the population after any given number of generations can be computed². Models like John Maynard-Smith's 'hawk-dove' game (1982) and 'mouse-haystack' model (1964) are often misinterpreted, because they are developed using the illustrative examples from which they take their names. In fact, such models require no biological assumptions except genetics (or some simple heritability assumption) and fitness values. We might follow Sober (1984c) and call this level of biological explanation the 'consequence level', because these explanations rely on laws about the consequences of fitness differences rather than the sources of fitness differences. In this paper, however, we use the self-explanatory phrase 'population dynamic level'.

In another class of biological theories, the frog's trait may be considered as a device for striking out at food, and figure in ecological generalisations. These generalisations are the sort appealed to in traditional adaptive explanations. They are examples of what Sober (1984c) terms 'source laws', as they describe the causes of the differential fitness of traits. An example popularised amongst philosophers by Peter Godfrey-Smith (1991) is signal detection theory. This theory predicts that the frog's representation will maximise its fitness if it is triggered by a level and type of sensory stimulation that correctly balances the proportions of correct, false-positive and false-negative responses, given their relative values to the frog. Ecological level explanations of this kind are less abstract than models at the population dynamic level. But they are still very far from the history of any particular species. They purport to apply to any organism facing a particular adaptive problem.

General ecological descriptions are realised in particular cases by particular lineages of organisms or traits. David Hull (1987) talks of 'genealogical actors in ecological roles'. One lineage's solution to the signal detection problem is the trait in the frog (*Rana pipiens*) which detects the presence of flies. We imagine that many people will ask what use evolutionary theory could have for such a specialised classification. In reply, we note that several recent authors have argued against the tendency to downplay 'natural history' - the study of the actual evolution of a particular, historically delimited class of systems - in favour of 'evolutionary theory' - the abstract results of such disciplines as ecology and evolutionary games theory (Sober 1984b, O'Hara 1988). The claim that the classification 'fly-catching mechanism' (where 'flies' denotes a particular historical group) is a useful one amounts to the claim that there is sufficient pattern in the particular historical events of terrestrial evolution to allow the formulation of useful generalisations. One suggestion for such a pattern comes from Sterelny (1990), who suggests that frogs are 'diachronically tracking' flies. In other words, were members of the relevant lineage(s) to become predominantly transparent, or ground-dwelling, frogs would evolve in such a way as to continue to detect them. Again, this may strike people as implausible, but similar co-evolutionary 'arms races' have been widely postulated by biologists (Dawkins & Krebs 1979, Trivers 1985).

Finally, the theory in which the frog's trait is considered as an example of a system for striking out at small dark moving things is neuroanatomy. This is one of a cluster of disciplines which describe the actual physical capacities of traits. They are teleological in that they distinguish those physical capacities of an item which correspond to biological functions from those which are unintended side-effects. At this level, we might explain the precise way in which the frog is put together by showing how this arrangement results in the detection and ingestion of objects with a certain appearance. Several

anatomically distinct traits might correspond to a single trait at the 'natural historical' level described in the last paragraph. This point is noticed by Neander (in press). She points out that if the function of the current mechanism is, as Sterelny claims, to detect flies, the function will not change even if future selection modifies the mechanism so that it can distinguish flies from other small dark moving things! Neander notes that this seems inappropriate. She suggests that the function of the mechanism has been refined along with its structure. We believe that we can explain what is happening in this case. The simple and sophisticated fly-detectors fall into the same natural historical category, although they are in different neuroanatomical categories. In other words, the natural historical function has remained constant, while the neuroanatomical function has changed.

The rationale for such multiple levels of theory has been discussed by authors such as William G. Lycan (1987, 1990), Robert Cummins (1975, 1983) and Frank Jackson and Phillip Pettit (1988). The classification of a single domain of objects in a series of increasingly abstract vocabularies allows access to generalisations which are hidden at lower levels by the multiple realisability of the kinds that enter into those generalisations. The generalisations of population dynamics can be stated easily enough in a vocabulary where traits are classified by their fitness values. To state the same generalisations in the ecological vocabulary that classifies the frog's trait as a mechanism for detecting food would involve an indefinitely long disjunction of traits with different ecological roles but identical fitness functions! In a similar fashion, signal detection theory can be stated simply enough if traits are classified simply as mechanisms for coordinating incoming sensory stimulation with object-oriented behaviour. It becomes unmanageable if the possible types of sensory stimulation, of object-oriented behaviour and of object must be enumerated!

We suggest that the series of functions which gives rise to the indeterminacy problem is created by the existence of this series of levels of theory in the study of organisms and their evolution. We have shown how this operates in the case of the frog. We now use this understanding of the sources of indeterminacy to assess a proposed solution to the problem.

4. INDETERMINATE FUNCTIONS AND THE TARGET OF SELECTION ARGUMENT

Both Sterelny and Shapiro employ what we call a 'target of selection' argument to eliminate the apparent indeterminacy of etiological functions. Shapiro uses it to support his contention that the frog's mechanism is a food detector. Sterelny uses it to support his contention that it must be a fly detector.

The target of selection argument appeals to Elliott Sober's famous distinction between 'selection for' and 'selection of' properties (1984a, 1984c). Natural selection results in the differential reproduction of whole ranges of properties. The selection of some of these properties is, intuitively, an 'unintended' side-effect of the selection of some of the others. For example, the thick coat of a polar bear is selected for its thermal properties, but a warm coat must also be a heavy coat, so heaviness is selected just as reliably as warmth. Sober suggests a way of distinguishing the properties which there is 'selection for' (the 'targets of selection') from those which there is only coincidental 'selection of'. They can be distinguished by the fact that only the targets of selection play a causal role in the selection process. This comes down to the truth of certain counterfactuals. If the polar bear's coat had been

warm but not heavy, it would still have been selected. But if the coat had been heavy but not warm, it would not have been selected. So warmth, rather than weight, is the target of selection.

We think this distinction finds its proper home when applied to different properties at the same level of explanation. In this context, it can tell us which properties enter into useful generalisations about selection at that level. In the debate over biological functions, however, it is being applied to privilege a property at one level of explanation over one at another. We think this is a misapplication of the distinction, as can be seen from the following version of the polar bear case. In the actual world, the polar bear's coat is both warm and fitness enhancing. But if the bear's coat had been warm but not fitness enhancing, it would not have been selected. Whereas, if it had been fitness enhancing but not warm, it would still have been selected. So there has been selection for a fitness enhancing coat, but only selection of a warm one. This conclusion, of course, is patently absurd.

It is clear what has gone wrong here. A higher-level explanation is being regarded as an *alternative* to a lower-level one, instead of a supplement to it. The fact that a fitness-enhancing coat would still be selected if it were not warm relies on the fact that some other, lower level property could take the place of warmth. But this does nothing to show that warmth is not causally efficacious in the actual case. To put the matter in the terms used by Jackson and Pettit (1988), the fact that the same general 'programme explanation' can be realised by a different 'process explanation' in other cases does not impugn the causal reality of the process explanation that underlies it in one particular case!

We now show how this fallacy occurs in the debate over the function of the mechanism in the frog's visual system.

The first example occurs in Sterelny (1990). Sterelny argues that the function of the frog's visual system is to detect *flies*, rather than things with the disjunctive property of being either a fly or a bee-bee (a 'fleebee'), as proposed by Fodor (1990). We think that Sterelny is right to reject Fodor's use of grue-like predicates, which play no role in any genuine selective explanation. But we are much less happy with the argument he uses to reject them. Sterelny argues that:

Had flies changed so that their retinal projections were not beebeelike, natural selection would tend to construct mechanisms that tracked the changing shape of flies... There is a diachronic tracking between flies and fly representors. (1990, p. 127)

Sterelny has translated Sober's counterfactuals into statements about what would happen in possible future scenarios, but the basic point is the same. If the objects hunted by frogs were small, dark and moving but not flies, there would be no selection for catching them. But if they were flies but not small, dark and moving, there would be selection for catching them. Sterelny concludes his argument in classic Soberian style:

... there has been selection *for* a fly-detector, but selection *of* both a fly and a fleebee detector. (1990, p. 127; our emphasis)

But the target of selection argument proves to be a two-edged sword for Sterelny. It is possible to iterate the argument against Sterelny in favour of the view that the frog has a mechanism for detecting *food*. If the objects

hunted by the frog were flies but were not nutritious, there would be no selection for detecting and catching them. But if they were nutritious but not flies, the pressure to detect and catch them would be unchanged.

The objection can also be made in a way more strictly analogous to Sterelny's original argument. If flies ceased to be nutritious, selection for fly-catching would cease. There is 'diachronic tracking' between flies and representational mechanisms only because flies are nutritious objects. What is really being tracked is the property of being food.

The second example occurs in Shapiro (1992). Shapiro argues that perceptual state S in frogs and other amphibians should be regarded as a representation of food because the neural sub-system of which it is part is a system selected for detecting food. He attacks the idea that the function of the mechanism is to detect small dark moving things:

Given that black dots are not any sort of currency that wants optimising, that there is no selection pressure for black dots... it stands to reason that the function of the salamander's fly detector is not to represent black dots.
(1992, p. 477)

Shapiro would presumably apply the same argument to Sterelny's contention that the mechanism's function is to represent flies. Shapiro's use of the name 'fly detector' does not commit him to ascribing the device this function, as he states explicitly at the outset of his discussion. Instead, he is unequivocal in his claim that the sole genuine function of the mechanism is to detect food.

Both Sterelny and Shapiro are appealing to the fact that there are higher-level explanations of the evolution of the trait in question, and that if these higher-

level explanations were not correct, the trait would not evolve. If small dark moving things were not flies, there would be no selective advantage in detecting small dark moving things. Likewise, if flies were not food, then there would be no selective advantage in detecting flies. So in both cases, it seems, there is no selection for the lower-level property. We suggest that, by parity of reasoning, we can infer that there is no selection for detecting food either. For if detecting food was not fitness enhancing, then there would be no selection for it. So it seems that detecting food cannot be the real target of selection.

We pause to anticipate a minor objection. What possible world could there be in which detecting food is not fitness enhancing? We admit that such a world is hard to imagine, but we firmly deny that it is logically impossible, and thus that the counterfactual we require is unavailable. As a 'possibility proof' we point to the insect group *Ephemeroptera* in which adult males ingest no food. It seems highly probable that this is an adaptation.

The conclusion that the sole function of state S is to increase the frog's fitness is absurd. Once again, using the selection for/of distinction across explanatory levels misrepresents complementary evolutionary narratives as competing ones. So the target of selection argument is of no use in choosing between the competing descriptions of the function of S.

5. A VARIANT ON THE TARGET OF SELECTION ARGUMENT

A slightly different use of the target of selection idea occurs in a paper by Nicholas Agar (1993). Agar advances a teleosemantic theory of representational content, holding that the semantic properties of mental

representations are determined by their functions. He employs the target of selection argument to determine the semantic content of S, but he does not use it to throw out all lower level properties from the content of S. Instead, Agar accepts as part of the content of S any property of the environment which is relevant to the selective explanation of state S. He accepts that part of S's content is 'small dark moving thing', because in a world in which food is not small, dark and moving, the frog's representation would be significantly different from S. But he still claims that the target of selection argument has some bite. It will eliminate 'fly' from the content of S:

... we should work out which properties we cannot change without modifying the exact structure of S. Properties like the fly's genetic make-up and evolutionary relatedness to bees could be altered; others like the fly's colour and protein content could not. These latter properties will be those which must be represented in the frog's teleocontent. (1993, p. 10)

So, according to Agar, the content of S is something like 'small dark moving food'. It does not include 'fly', because 'changing properties like the fly's genetic code leaving all else constant will make no difference to the frog under any realistic circumstances.' (1993, p. 10) Agar does not consider whether the content might include 'fitness enhancing'.

We suggest that, even in Agar's variant form, the target of selection argument has no bite at all. The content of S should, by Agar's own principles, include 'fitness enhancing', and if 'fly' gets excluded it is because of some mistaken views about biological explanation, not because of the target of selection argument.

Agar ought to say that the content of S includes 'fitness enhancing', because this is a property which 'we cannot change without modifying the exact structure of S.' If S was not fitness enhancing it would not evolve. We anticipate the objection that being fitness enhancing does not explain the *structure* of S, but merely why S exists at all. But the same is true of S's being tokened in response to food. We anticipate the further objection that being fitness enhancing is not a separate property from being food, but we have already countered this objection. The fact that ingesting food is fitness enhancing is an evolutionary contingency, albeit an extremely reliable one.

It is perhaps less obvious that the content of S should include 'fly'. Agar suggests that it is irrelevant whether the things S has evolved to detect are members of any particular taxon. But although many philosophers will share this intuition, it is simply mistaken. S has evolved in a lineage of amphibians as an adaptation to increase ingestion of members of a lineage(s) of insects. S will have changed over time, both for the obvious reason that the frog's fly-catching mechanisms have evolved by the successive modification of some existing structure, and for the slightly less obvious reason that it has coevolved with the prey species. Changes in the appearance and behaviour of flies will have been reflected in changes in S. Current views of evolution suggest that historical contingencies, such as the availability and timing of mutations in the two species, and the frequencies of alternative types at the commencement of a selection process, will critically affect which solution is adopted (Hull 1987, O'Hara 1988). To suppose that the particular historical narrative adds nothing to a broad ecological model is to suppose that a detailed causal explanation adds nothing to a suggestive idealisation!

We suggest that all the levels outlined in Section Three contain genuine evolutionary explanations of S. To suggest that one can be replaced by

another is to commit the fallacy outlined in Section Four. So the target of selection argument has no bite at all. The proper outcome of adopting Agar's principles will be to make the content of S 'small, dark and moving, nutritious, fitness enhancing fly'.

6. CONCLUSION

There is a widespread failure to appreciate the fact that there are several levels of theory in evolutionary biology, a confusion which is reflected in the misuses of the selection for/selection of distinction we have discussed. The apparent indeterminacy of etiological functions is a genuine indeterminacy, but a harmless one. Selection processes can be described at more or less abstract theoretical levels, all of which generate genuine, complementary descriptions of etiological function.

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NOTES

¹Authors names are in alphabetical order. We are equally responsible for any insights or errors that this paper contains.

²In many cases, details of the genetically stable combinations of traits in the population and of mutation rates may also be needed.