Can Cumulative Selection Explain Adaptation?

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Two strong arguments have been given in favor of the claim that no selection process can play a role in explaining adaptations. According to the first argument, selection is a negative force; it may explain why the eliminated individuals are eliminated, but it does not explain why the ones that survived (or their offspring) have the traits they have. The second argument points out that the explanandum and the explanans are phenomena at different levels: selection is a population-level phenomenon, whereas adaptation occurs on the individual level. Thus, selection can explain why individuals in a certain population have a certain trait, but it cannot explain why a certain individual has this trait. After pointing out that both arguments ignore the significance of the limitation of environmental resources, I will construe a positive argument for the claim that cumulative selection processes can, indeed, play a role in explaining adaptations.

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1. Introduction. Why do we have two eyes? Why is it the female mosquito that bites? Why do cats have sharp teeth? The answers to these questions are supposed to be provided by what are usually called adaptation-explanations. Adaptation-explanations aim to explain the supposed or real teleology of the world. As Brandon says:

> Adaptation-explanations [are] answers to what-for questions. Questions concerning putative adaptations, an anteater's tongue, the structure of the human eye, or the waggle-dance of honeybees—are naturally formulated using what-for. (Brandon 1985, 86–87; cf. Brandon 1996, 30–45)

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In other words, in adaptation-explanations, the explanandum is why an organism has the trait it has. But what is the explanans? The obvious suggestion is that the explanans is a selection process. Adaptations should be explained with reference to selection processes that shaped the traits to be explained. Thus we can explain why certain creatures have the traits they have by referring to what these traits were selected for in the course of evolution.

Unfortunately, it has been argued repeatedly that contrary to our hopes to use selection to answer the questions quoted above, selection cannot play a role in explaining adaptation.

The aim of this paper is to contribute to the recent debate about whether such explanations are possible. This debate has been quite severe in the last decade or so. The view that selection can play a role in explaining adaptation has been defended mainly by Karen Neander (1995a, 1995b). (See also Millikan 1990; Nanay 2002.) On the other side of the trench the central figure is Elliott Sober (1984, 1995). (See also Walsh 1998; Dretske 1988; Cummins 1975.) After the arguments of Sober (1995) and Walsh (1998), the position of Neander's side appears rather shaky.[1] The aim of this paper is to provide munitions to this camp.

Before turning to the actual argument, it is important to clarify the framework of the debate. First, it is important to draw a distinction between the scope of this debate and that of adaptationism.[2] The adaptationist's claim is that if an organism has a trait, then there is (or at least tends to be) a selection process that explains why this organism has this trait. In other words, if organism x has trait A, then there is (or at least tends to be) a selection process that explains why x has trait A.

Contrast this with the central claim of the debate about the explanatory power of selection in explaining adaptations: if x has trait A and if x is in a population where trait A has been selected over trait B, then this selection process is explanatorily relevant to why x has trait A. Both claims are concerned with the explanation of adaptation with the help of selection. But they are very different indeed: the second claim does not assume that all or even most traits have adaptation-explanations.

Hence, I will assume in what follows that the question under scrutiny is the following: if in a population a trait has been selected over other traits, can this selection process explain (at least partially) why organisms

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[1] Matthen (1999) criticized Sober's position, arguing that Sober's argument does not work if the selection process is sexual selection, but as Lewens (2001) and Pust (2001) pointed out, Matthen's argument is not conclusive.

[2] On the question of adaptationism, see Gould and Vrba 1982; Gould and Lewontin 1979; Lewontin 1978; Dawkins 1976; Dennett 1995, just to mention the most well-known titles in the very extended literature.

(or a specific organism) in that population have this trait? In other words, I take it for granted that we know the selection process, and we want to tell why certain organisms have the traits they have.

I would like to narrow down the question even further and focus on whether *cumulative* selection can play a role in explaining adaptation.[3] There are noncumulative selection processes that cannot play any role in explaining adaptation: the ones whereby the replicators do not change from generation to generation. The most successful replicator may spread and make all the others extinct, but by doing so it will not change. An example could be the clay crystal that grows faster than the other crystals in the same pool (cf. Bedau 1991, 650–654; Walsh 2000, 142–143). After a certain time the fastest growing crystal will be the only one in the pool, but its structure will not change in the selection process. This is an example for a noncumulative selection process that does not play a role in explaining any adaptation.

Leaving the noncumulative case aside, I will focus on the question of whether cumulative selection can play a role in explaining adaptation. Also, it needs to be emphasized that the question is whether cumulative selection can *play a role in explaining* adaptation, and not whether it can fully explain adaptation.

Two strong arguments have been given in favor of the claim that no selection process can play a role in explaining adaptations. The first one is that selection is a negative force, it eliminates, but it does not create; hence, it cannot play a role in explaining adaptation. According to the second, selection cannot play a role in explaining adaptation, since selection is a population-level phenomenon, whereas adaptation occurs on the individual level. These arguments are often provided together, but I take them to be logically independent. I will take them in turn.

2. Selection as a Negative Force.

Sober claims that selection is a negative force: it does not create; it only destroys (Sober 1984, Chapter 5). The upshot is that random mutations create a variety of individuals (or genetic plans) and selection eliminates some of these, but the explanation of the traits of one of these individuals is provided by random mutation and inheritance (and, of course, some developmental factors), not by the elimination process. Selection can explain why certain individuals were eliminated, but it cannot explain the traits of the ones that were *not* eliminated.

Karen Neander analyzes this argument, which she calls the argument for the Negative View of selection, in great detail (Neander 1995a). She

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[3] Cumulative selection is a selection process whereby the changes of the replicators accumulate: they are transmitted to the next generation. Natural selection, for example, is cumulative.

argues that selection does play a role in explaining why an individual has the traits it has, but only a certain kind of selection: cumulative selection. But she admits that Sober's criticism is valid for noncumulative selection processes.

First, it is important to make some comments on the terminology Neander and Sober use. More precisely, it is crucial to examine whether the opponents and the advocates of this argument mean the same thing when they talk about selection. Sober analyzes mutation as something distinct from selection. The question is how consistent this is with the generally accepted notion of selection.

According to David Hull, selection consists of "repeated cycles of replication and environmental interaction so structured that environmental interaction causes replication to be differential" (Hull et al. 2001, 53; cf. Hull 1981, 40–41). He analyzes selection—conceived traditionally as 'heritable variation in fitness—as cycles of a copying process (replication) and the interaction with the environment.

If we accept this concept of selection, it is hard to see how Sober could maintain that it is not selection, but mutation that plays a role in explaining adaptation, since in Hull's picture, mutation (replication with variation) is one of the two steps of the selection process. If selection consists of repeated cycles of replication and interaction, then replication is obviously part of the selection process. And this replication process must be differential; hence, replication with variation, i.e., mutation, is part of the selection process.[4] According to Hull, selection is replication with variation *followed by* interaction. In light of this, it is a surprising claim that selection cannot play a causal role in explaining adaptations, while mutation can, if mutation is part of the selection process.

This, however, would be too easy a way to oppose Sober's argument. He obviously means something else by selection. It is reasonable to say that what he means is what Hull means by interaction.[5] Interaction is indeed a negative force: all it does is to eliminate some of the interactors.

And here we run into another confusion. Hull's notion of selection is a notion of cumulative selection. If selection is "the repeated cycles of replication and environmental interaction so structured that environmental *interaction causes replication to be differential"* (Hull et al. 2001, 53, my emphasis), then the changes of the replicators must be transmitted to the next generation. If Sober takes Hull's notion of interaction to be

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[4] This is also true under different widespread definitions of selection, such as Darden and Cain's (1989). Note that Darden and Cain's notion of selection is not necessarily a cumulative one, wheras Hull's is. See also Nanay 2001.

[5] The same is true of Vrba's concept of selection: "Selection is the interaction between heritable, emergent character variation and the environment" (Vrba 1984, 319).

selection, then it is difficult to see how he could allow for cumulative selection.[6] Neander, on the other hand, explicitly talks about cumulative selection when she talks about selection; she even admits that noncumulative selection cannot play a role in explaining adaptation, though cumulative selection can. Could it be the case that Neander uses a notion of selection that is similar to Hull's whereas Sober uses a notion of selection that is more similar to Hull's notion of interaction? Is it possible that the whole debate is terminological?

I think not. It seems that Neander accepts the way Sober refers to selection when she argues against his position. In Hull's terminology, both are concerned with the question of whether interaction is causally relevant to the explanation of adaptation. This, of course, leaves open the possibility to argue that *selection* in Hull's original sense does play a causal role in the explanation of adaptation, but this is a possibility I cannot pursue here. Instead, I would like to examine further the Sober-Neander debate that we managed to localize as the question of whether interaction is causally relevant to the explanation of adaptation.

Sober's argument is that, in Hull's terms, it is replication that explains why an individual has a certain trait. Environmental interaction (of the previous generation) does not play any role in such explanation. The gist of his argument is the following. Let us take an organism that has two offspring, one of which has a certain trait A, whereas the other does not. Since trait A is advantageous to these organisms in the given environment, the second offspring dies, whereas the first will have offspring, one of which, call her individual x, also has trait A. The question is of course, what explains that x has trait A. Sober's answer is that it is the mutation as a result of which A appeared in x's mother and inheritance, as a result of which A was transmitted to x. The explanation is simple: A appeared as a result of a random mutation in x's mother and then x inherited it from her mother. What explains the presence of the trait is, hence, mutation and inheritance. Selection is irrelevant, since the life or death of x's uncle does not have any causal influence on whether x has trait A (Sober 1984). (See also Sober 1995, 393; Cummins 1975, 750–751.)

I think this argument is flawed.[7] It would be a correct argument if the

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[6] In fact, the notion of cumulative selection that he endorses (Sober 1995, footnote 10) definitely would not qualify as cumulative selection under the definition of Hull or Neander.

[7] I agree with Sober that if selection has no causal influence on whether x has A, then it cannot play a role in explaining why x has A. What I intend to question is the truth of the antecedent of this conditional.

environmental resources were unlimited. They are not.[8] First, very simplistically: provided that environmental resources are limited, if I eat, my sister does not. If *x*'s mother survived and reached reproductive age, it is because she had enough to eat. If we assume that the environment can maintain only one of these organisms, she could not eat enough, unless her brother died. Hence, *x*'s uncle's death played a causal role in bringing about the fact that *x*'s mother who had trait *A* survived and reached reproductive age. Since *x* could not have inherited trait *A* from her mother unless she reached reproductive age, the fact that *x*'s uncle died is explanatorily relevant to the fact that *x* has trait *A*—which is just the opposite of what Sober claims.

Sober and I agree that inheritance is explanatorily relevant to why a certain organism has a certain trait. The fact that *x* inherited trait *A* from her mother is explanatorily relevant to *x*'s having trait *A*. On the other hand, *x* could not have inherited *A* from her mother unless her mother had reached reproductive age. Further, *x*'s mother could not have had trait *A* and reached reproductive age unless *x*'s uncle (who did not have trait *A*) had died. Therefore, the fact that *x*'s uncle (who did not have trait *A*) died is explanatorily relevant to the fact that *x* has trait *A*.

More slowly and less simplistically: take a population of organisms. The population size is 100. It has always been 100 or less, because the environmental resources can maintain only a population of this size. I take the environment to be stable. There has been no migration. All the 100 organisms have trait *B*, when a mutation occurs and trait *A*, whose fitness is higher than that of trait *B*, eventually goes to fixation. The question is whether the elimination of the organisms with trait *B* in the

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[8] The original Darwinian insight was that if the environmental resources were unlimited, there would be no selection. Some have argued against this assumption, claiming that "natural selection works only among competing entities, but it is not necessary for the individuals of a species to be engaged in ecological competition for some limited resource" (Williams 1966, 32). Or, as Lewontin says: "the element of competition between organisms for a resource in short supply is not integral to [Darwin's] argument. Natural selection occurs even when two bacterial strains are growing logarithmically in an excess of nutrient broth if they have different division times" (1970, 1). I agree with the point made by Lennox and Wilson (1994) that the notion of selection these authors end up with can hardly be called selection. More importantly, if we accept Hull's definition of selection, then the examples Lewontin and Willams give do not count as selection process. However, for the sake of the generality of my argument, I could allow that there are at least some cases where there can be selection while the environmental resources are unlimited. In this case, I need to restrict my argument to those selection processes where the environmental resources are limited. This will not be a major restriction, given that environmental resources are generally limited, and even if they are not, in a couple of generation they will be, as a result of the logarithmic growth.

past generations is explanatorily relevant to why organisms in the present population has trait *A*. If there were no environmental limitations, the answer would be no, in accordance with Sober's argument. But there are environmental limitations: the environment can only maintain a population of 100. Whether these organisms with trait *B* were eliminated alters the chances of the survival of organisms with trait *A*, since, after all, they all compete for the same environmental resources. If an organism (call it *b*) with trait *B* is eliminated, then there will be more environmental resources available for organisms with trait *A*. The probability of the survival of an organism with trait *A* is higher given the death of *b* than the probability of its survival given that *b* does not die (all things being equal).[9] Thus, the elimination of organisms with trait *B* contributes to the survival of organisms with trait *A*. Since organisms in the present generation inherited trait *A* from these organisms with trait *A*, we can conclude that the elimination of organisms with trait *B* does play a causal role in explaining why organisms in the present population have trait *A*.

I take Neander to make a similar point, but in a rather sketchy way:

> Gardeners know that annual pruning doesn't merely eliminate old grow, it also channels and directs new growth. . . . Just so, the tree of life would not have had all of its actual branches, just some more, if there had been no natural selection. (Neander 1995a, 76)

The idea of the importance of environmental limitations may be present in Neander's metaphor of 'pruning the tree of life'. Neander, however, claims that it is the cumulative character of selection that makes it a positive force. Instead, I put the emphasis on the limitations of environmental resources.

The structure of my argument is the following. Suppose that in a population there is selection for trait *A*. Here is what we know about an individual *x*'s trait *A*: (i) The probability of *x* having trait *A* depends counterfactually on whether *x*'s mother survived and had trait *A*. This is a consequence of the fact that *A* is an inherited trait. (ii) The probability of the survival of *x*'s mother (like that of all other organisms in the population with trait *A*) depends counterfactually on the death of those organisms in the population who had trait *B* (of *x*'s uncles). This is true because of the environmental limitations. (iii) The probability of the death

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[9] Of course, this claim is true only if we add ceteris paribus clauses: if we fix the independent causal factors. This would filter out cases where the death of b obviously does not contribute to the survival of *every* organism that has trait *A*. Examples for such cases include (a) scenarios whereby only organisms with trait *B* can defend the population from a certain predator or (b) scenarios whereby there are strong alliances within the population.

of those organisms in the population who had trait *B* (*x*'s uncles) depends counterfactually on the selection process for trait *A*.

Therefore, because of transitivity, the probability of *x* having trait *A* depends counterfactually on the selection process. Therefore, the selection process is explanatorily relevant to why *x* has trait *A*.

A possible worry is raised by the transitivity of counterfactual dependence. David Lewis famously argued that counterfactual dependence is not always transitive (Lewis 1973, 32–35). More precisely, if *P* depends counterfactually on *Q*, and *Q* depends counterfactually on *R*, then *P* may not depend counterfactually on *R* if what we hold fixed in the first counterfactual is different from what we hold fixed in the second. I would not have ducked if the boulder had not come careering down the mountain slope. I would not have survived if I had not ducked. But it is not the case that I would not have survived if the boulder had not come careering down the mountain slope. Thus, there are cases where we are not entitled to make the inference that if *P* depends counterfactually on *Q*, and *Q* depends counterfactually on *R*, then *P* depends counterfactually on *R*. I need to show that in my argument I am indeed entitled to make such an inference.

The reason why the counterfactuals in the boulder example are not transitive is that what we hold fixed in the first counterfactual is not the same as what we hold fixed in the second counterfactual. The second counterfactual can be rephrased in the following way: I would not have survived if I had not ducked, other things (most importantly, the careering boulder) being equal. Part of what we hold fixed in this counterfactual is that the boulder comes careering down towards me. This is obviously not something we hold fixed in the first counterfactual, since this very fact is what my ducking depends on counterfactually.

In my argument, there are no such complications. What I hold fixed in the three counterfactuals is the same. The probability of the death of those organisms in the population who had trait *B* depends counterfactually on the selection process that favors *A* over *B* in every possible world where the laws of biology are in place. The probability of the survival of organisms in the population with trait *A* (including *x*'s mother) depends counterfactually on the death of organisms in the population with trait *B* in every possible world where the laws of biology are in place and where there are environmental limitations in the population. Finally, the probability of *x*'s having trait *A* depends counterfactually on the survival of *x*'s mother who had trait *A* in every possible world where the laws of biology are in place. In other words, all three claims are true in all possible worlds where the laws of biology are in place and where the environmental resources are limited. Thus, we are entitled to conclude that the probability of *x* having trait *A* depends counterfactually on the selection process.

Therefore, the selection process is explanatorily relevant to why *x* has trait *A*.

3. The Scope of Selection. Sober's second argument is more challenging. It claims that selection cannot play a role in explaining adaptation, since the explanandum and the explanans are phenomena at different levels: selection is a population-level phenomenon, whereas adaptation occurs on the individual level (Sober 1984, 1995; Walsh 2000). Even if selection could explain the frequencies of traits in populations, it certainly cannot explain why individual organisms have certain traits (Sober 1984, 150; 1995, 384). In other words, it cannot explain why *I* have two eyes, why *this* cat has sharp teeth, etc. Walsh (1998) elaborates on this argument in more detail; thus, I will analyze the arguments of both Sober and Walsh. Whereas Sober handles this argument (about the scope of selection) and the one about selection being a negative force together, Walsh focuses on the former.

Sober and Walsh claim that selection can provide only population-level explanation: it can only explain why the population consists of individuals who have a certain trait. Adaptation-explanation, however, is supposed to be an individual-level explanation. It needs to explain why a certain specific individual has the traits it does. To go back to Sober's classic analogy (Sober 1984, 149; 1995, 384), if the admission criterion for a class is that the student must be able to read at the third grade level, then what explains that Sam can read at the third grade level is not the admission criterion (that is, the selection process), but, say, the fact that his grandmother spent a lot of time with him reading. The moral is that even though the admission criterion explains why the class (the population) reads at the third grade level, it does not play a role in explaining why a certain individual, Sam, reads at the third grade level.

The differences between these two kinds of explanation can be summed up in the following way (see Walsh 1998, 250). Selection processes can provide the following explanation.

> 1a. If there is selection in the class for being able to read at the third grade level, and if *x* is in this class and *x* can read at the third grade level, then this selection is explanatorily relevant to why it is the case that if *x* is in the class, then *x* can read at the third grade level.

An example of the kind of explanation that would be needed to explain why Sam can read follows:

> 2a. For every *x*, it is the case that if *x* is in the class and if there is selection in the class for being able to read at the third grade level,

> then this selection is explanatorily relevant to why *x* can read at the third grade level.

Similarly, selection processes can provide the following explanation:

> 1. If in a population trait *A* has been selected over trait *B*, and if *x* is in this population and if *x* has trait *A*, then this selection is explanatorily relevant to why it is the case that if *x* is in this population, then *x* has trait *A*.

An example of the kind of explanation that would be needed to explain why a certain individual has trait *A* follows:

> 2. For every *x*, it is the case that if *x* has trait *A* and if *x* is in a population where trait *A* has been selected over trait *B*, then this selection is explanatorily relevant to why *x* has trait *A*.

Claim 1 is generally agreed upon (Walsh 1998). The question is whether Claim 2 is true. Sober and Walsh say *no,* Neander says *yes*. Walsh aims to show that Neander has three arguments for Claim 2, each of which only manages to prove Claim 1. Since Claim 2 obviously does not follow from Claim 1, selection processes cannot explain why a certain individual has a certain trait.

Walsh is right that Neander never manages to prove Claim 2, but this does not mean that Claim 2 is false. Here is an argument for Claim 2, which is very similar to the one I offered in the last section.

Again, let us take good old *x*'s family, in which *x* has trait *A*, because *x*'s mother had *A* and *x* inherited it from her. All of the siblings of *x*'s mother had trait *B*. *x*'s mother was able to transmit it to her offspring, *x*, because she had *A*, survived and reached reproductive age. Without her reaching reproductive age, *x* obviously would not have trait *A*.

This step of the argument was given at the individual level of description. Now comes the population-level element in the explanation. Note that *x*'s mother and any other organisms in the population who had trait *A* (if there are any) could survive and reach reproductive age, because the environmental resources were enough to maintain only a limited number of organisms and because those organisms in the population who had trait *B* (*x*'s uncles) died. If those organisms in the population who had trait *B* (*x*'s uncles) had not died, organisms with trait *A* (*x*'s mother, among others) would not have survived and hence *x* could not have inherited trait *A*. Hence, *x*'s having trait *A* is at least partly explained by the fact that *x*'s uncles, who had trait *B*, did not survive. The fact that those organisms in the population who had trait *B* (*x*'s uncles) did not survive is causally explained by selection processes—by the selective advantage of trait *A* over trait *B*. This Sober and Walsh would grant (this is Claim 1 above). What they deny is not that selection can play a role in explaining the eliminated cases, but that it cannot play a role in explaining the not eliminated cases. What I aimed to show is that selection does play a role in indirectly explaining the not eliminated cases.

This explanation consists of three steps: (i) Selection explains the eliminated cases. This is a population-level step of the explanation. (ii) The elimination of eliminated organisms explains the survival of each of the surviving organisms. This holds because of the limitations of the environmental resources. Also, this is where a population-level phenomenon explains an individual-level phenomenon. (iii) The fact that a certain organism has a certain trait is partially explained by the survival of another certain individual organism (the one this trait is inherited from). This third step of the explanation is entirely an individual-level explanation.

Thus, there is no scope error: this explanation explains why a certain organism has a certain trait.

4. Objections. Finally, two possible objections need to be addressed. I have trait *C*, which is by no means advantageous for me or for anyone else, but which I inherited from my mother, and only my mother had it among her siblings. Each of my uncles died because a brick fell on their head on the street. Couldn't we run the same explanation? If so, doesn't it lead to very counterintuitive consequences? Let us proceed step by step and see what the differences between this case and the selection case are.

I have *C* because my mother had *C*, and I inherited it from her. All of the siblings of my mother had trait *D*. My mother was able to transmit *C* to me, because she survived and reached reproductive age. My mother survived and reached reproductive age, because the environmental resources were enough to maintain only a limited number of organisms and because my uncles died. If my uncles had not died, my mother would not have survived, and hence I could not have inherited trait *C*. Hence, my having trait *C* is at least partly explained by the fact that my uncles did not survive. So far, everything seems analogous between the two cases (given that there are severe limitations on the environmental resources).

The difference, of course, is that the death of my uncles is not explained by selection processes, but by falling bricks. The fact that my uncles did not survive is not explained by the selective advantage of trait *C* over other traits, since there is no such selective advantage.[10] Thus, if the environmental resources are scarce enough, even in this case, my having trait *C* will depend counterfactually on the death my uncles, but it will not depend on any selection process.

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[10] In other words, in the three-step explanation we ran above, Steps (ii) and (iii) apply here, but Step (i) does not.

The second possible objection is the following. We have seen that selection for trait *A* in *x*'s population explains why *x* has trait *A*. Couldn't we run the same argument for any other trait *x* has? Suppose there is selection for trait *A* (thus, against *B*) in the population. Now this selection process explains why organisms with trait *B* died. But the death of other organisms in the population, in turn, explains why *x*'s mother, who has trait *A* as well as a different trait, *C*, survived. Finally, the survival of *x*'s mother explains why *x* has trait *C*. But this is surely wrong: we do not want to say that the selection process for trait *A* (thus, against trait *B*) explains why *x* has trait *C*. Where did we go wrong?

The answer is that we cannot run this analogous argument. The second step of the original argument was that the elimination of organisms without trait *A* raises the probability of the survival of those organisms who have trait *A* (including *x*'s mother). Provided that there is no systematic positive correlation between trait *A* and trait *C*, the elimination of organisms without trait *A* clearly does not raise the probability of the survival of those organisms who have trait *C*: the probability of the survival of organisms with trait *C* is not higher if there is selection for *A* than it would be otherwise. If, in contrast, there is systematic positive correlation between trait *A* and trait *C*, then we should not be surprised that the selection for *A* explains why organisms with trait *C* tend to survive.

Thus, in accord with our intuitions, selection for trait *A* can explain why an individual has trait *A*, but it cannot explain why an individual has trait *C*.

5. Conclusion. A note on the relevance of this debate. Whether selection can play a role in explaining adaptations may seem a technical and uninteresting question. In fact, its relevance goes way beyond the limits of philosophy of biology. A very important question in the philosophy of mind is whether it is possible to give evolutionary explanation to the problem of the intentionality of mental states. (See Millikan 1984, 1993; Papineau 1987, 1993; Neander 1995c, 1996a, 1996b, among others. See also Fodor 1990; Dretske 1988, 2000.)

The purpose of this approach, which is sometimes called teleosemantics, is to explain the intentionality of thought and language—the meaning of our words and the content of our thoughts—in evolutionary terms. The title of Millikan's first book is in itself a manifesto: *Language, Thought, and Other Biological Categories*.

Most of our mental states are about something; they refer to something. In other words, they have content. My papaya-thought refers to, or is about, a papaya. In order to understand what the content of my papaya-thought is, we need to explain this relation between my papaya-thought and what it is about: the papaya. In general, the explanation of the content of mental states is the explanation of the relation between these mental states and what they are about. The advocates of teleosemantics aim to explain this relation in evolutionary terms. The proposal (roughly) is that my thought has the content 'papaya' if the fact that papaya-thoughts indicate papayas has contributed to the survival of my evolutionary ancestors. More generally, a mental state *R* of an organism *O* has content *X* if the fact that *R*'s indicates *X*'s has contributed to the survival of the evolutionary ancestors of *O*.

It is easy to see that this explanation is an adaptation-explanation: it aims to explain why an organism has a mental state *R* with content *X* with the help of the selection process that favored having *R* over not having *R* in the population of the organism's ancestors. In other words, it explains why a certain trait is the way it is with the help of a selection process. Hence, unless it is possible to use selection processes in explaining why my mental states have the content they have, the entire project of evolutionary teleosemantics would go down the drain.

Thus, if it is true—as I argued above—that selection can play a role in explaining adaptation, then the question of whether evolutionary explanation can be given for the content of mental states is still open. If, on the other hand, Sober is right and selection cannot play a role in explaining adaptation, then the evolutionary explanation of mental content is not possible.

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