*BIOLOGY AS ALLEGORY: A REVIEW OF ELLIOTT
SOBER'S THE NATURE OF SELECTION*¹

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The two central claims of behavior analysis are that there is a way to understand behavior without resorting to underlying processes, and that this approach is more effective than any of the alternatives (Skinner, 1950). To some extent, these claims have been based upon example: One can point to a large body of research that exemplifies an approach to behavior that eschews mention of underlying processes, and this body of research has indeed been noticeably effective, especially in spawning a technology of behavior. Unfortunately, the relevant body of research covers only a narrow range of behavior, whereas Skinner has suggested that the methods employed to study that narrow range will, if followed patiently and consistently, suffice to provide a complete account of the entire domain. In order to support this suggestion, some reason needs to be offered for thinking that the basis for these past successes is adequate to the larger challenges that lie ahead. The need for such support is especially pressing because of the illustrious history that appeal to underlying processes has had in the natural sciences. Indeed some scholars now think any other approach will ultimately be a dead-end (e.g., Cohen, 1984; Sosa, 1984). To reply to this, as well as to other objections, Skinner has come to rely increasingly upon the support provided by the extensive analogy between operant conditioning and natural selection.

Roughly speaking, the analogy is that the process of operant conditioning stands to the ontogeny of behavior as the process of natural selection stands to the phylogeny of species. (Individual responses are like individual or-

ganisms, operants are like species, reinforcement is like reproduction, and so on.) In both ontogeny and phylogeny, the ultimate cause of change is the process of selection by consequence (Skinner, 1981). Since the ultimate controlling variables are in the environment, it is possible to understand the pattern of change without having to understand the processes that underlie it. Given that the theory of natural selection has sustained a progressive program of research for over 100 years, there is reason to believe that a program of research centered on operant conditioning may be viable (see Sober, 1985b, for an interesting variation on this argument).

All this is merely to explain why, when a highly acclaimed analysis of the concept of selection in evolutionary biology appears upon the scene, anyone interested in the theoretical foundations of operant psychology will take an immediate interest in it. They will recognize that such a work can be read not only as having its overt biological meaning but as having a behavioral meaning as well. It is with respect to this "allegorical" possibility that I propose to look at Elliott Sober's recent book, *The Nature of Selection*.

The main purpose of this book is to analyze the so-called "unit of selection" controversy over the question of whether evolution occurs because of selection at the level of genes, at the level of individual organisms, or at the level of groups of organisms. Sober does not try to resolve this controversy. Instead, he tries to say what sorts of empirical data would support what hypothesis, and why. In order to do so, however, he first analyzes the concept of selection itself, and it is this analysis that I want to focus upon. In particular, I want to summarize three broad consequences for evolutionary biology that Sober derives from his analysis. In each case I explore the possibility of extending the consequences to behavior analysis.

¹ Sober, E. (1984). *The nature of selection: Evolutionary theory in philosophical focus*. Cambridge, MA: MIT Press. x + 383 pp., including references and index.

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THE AUTONOMY OF SELECTIONIST THEORY

One of the more fruitful questions raised by Sober is that of what natural selection explains about evolution. In order to motivate his answer to this question, he considers the example of a classroom of students who read at the third-grade level. There are two questions one might ask about these students: (A) With respect to each student, one might ask why he or she reads at the third-grade level, or (B) with respect to the group itself, one might ask why it is composed only of students who read at the third-grade level. Question (A) is about individual development, whereas (B) is about a population-level property. The answer to (B) might be that students in this classroom were *selected* for their ability to read at the third-grade level. If so, then selection for that ability would explain why the group is composed only of students who read at the third-grade level, even though that selection process would *not* explain why any given individual reads at that level (p. 149).

One of Darwin's contributions to biology, according to Sober, was to pry these two sorts of questions apart, and to see that the answer to one might be quite different from the answer to the other. Only with the help of special assumptions could one theory answer both questions. Lamarck's developmental theory, for example, tried to answer both. It posited a certain developmental sequence through which any lineage would normally evolve. On his theory, the same developmental story that explains why a given individual has a certain property would also explain why the population of which that individual is a part exhibits that property—namely, because all the individuals in the population have gone through the same process of development. The theory of natural selection, however, requires us to distinguish between the developmental question and the population-level question. It explains changes in population-level properties not as the mere aggregation of the developmental histories of the individuals comprising the population, but as the result of individual stasis plus selection among individuals. "In a sense, individual organisms are not really what the theory is *about*" (p. 117, *italics in original*). When conjoined with assumptions about heritability, it may account for why a certain percentage of the individuals

in a population have a certain trait, "but phenotypic and genotypic properties of individuals—properties of morphology, physiology, and behavior—fall outside of natural selection's proprietary domain" (p. 152). And since the population-level properties that evolutionary theory attempts to account for are not reducible to organismic concepts, the theory has a kind of ontological autonomy.

Sober notes a further sense in which evolutionary theory is ontologically autonomous: Its central concepts are "supervenient."

A property is said to *supervene* on a set of physical properties if it satisfies two conditions. First, the property must not itself be physical, in that different objects may share the property and yet be physically quite different. Second, two systems that are physically identical must both have or both lack the property in question. (p. 48)

The biological concept of *fitness* is an example of a supervenient property. There is no physical property that all and only those organisms with identical fitness value have in common. There are simply too many physically different routes to fitness for the concept to be characterized physically. Nonetheless, any two organisms that are physically identical will obviously have the same fitness value. Thus, even though fitness is not a physical property of organisms, what gives an organism its fitness is its physical constitution. Other supervenient properties, such as predator/prey or dominant/recessive (in the genetic sense), play important roles in evolutionary theory. Because evolutionary theory follows the strategy of connecting supervenient properties with other supervenient properties, its laws cannot be reduced to interrelations among physical properties (pp. 125–126).

Sober emphasizes that this form of irreducibility does not rest on the methodological premise that progress towards a certain form of knowledge will proceed more rapidly if evolutionary biology is allowed to maintain its autonomy from physics. When a science incorporates supervenient properties in its laws, it becomes capable of formulating regularities that physics could *never* capture. Thus, evolutionary biology does not need to argue for autonomy on grounds that it would allow us to proceed more rapidly than otherwise; instead, it can make the stronger case that its autonomy allows us to explore aspects of nature that physics by itself simply could

not explore. Supervenience thus provides the basis for a profound form of antireductionism.

On that note, let us turn to some of the analogies with operant theory. One of that theory's distinctive features is its antireductionist stance. Sober's analysis of evolutionary theory affords a new perspective on this feature. For one thing, there is a rather direct analogy between the "population thinking" of evolutionary biology and the kinds of response patterns that behavior analysts typically study. Skinner has said that the crucial event in the development of behavior analysis was the discovery of rate of response as the dependent variable. Rate of response, however, is easily conceptualized as a property of a population of responses. Indeed, the molar approach to operant theory raises this possibility to a matter of principle, by explicitly defining the dependent variable as the average rate of response over a relatively extended stretch of time. Although there continues to be a controversy over whether this molar approach is superior to the targeting of moment-to-moment fluctuations in rate, the analogy with natural selection appears to throw its weight on the side of molarity.

If the future of the field lies in this direction, there would be important implications for Skinner's suggestion that behavior analysis can give a "complete" account of its domain. That domain is often taken to be the relationship of behavior to the environment during the lifetime of the individual organism. Sober's analysis of evolutionary biology, however, suggests that the domain is not nearly so broad. Individual responses may lie outside it.

If so, then the frequently made suggestion that cognitive psychology and operant psychology should complement one another, rather than compete with one another (e.g., Bolles, 1984), would take on new meaning. Usually, this sort of comment is interpreted in terms of the independent variable: Cognitive psychology explains behavior on the basis of underlying cognitive mechanisms, whereas behavior analysis explains behavior on the basis of environmental factors. This, however, may be only half the story; the analogy with natural selection suggests that the two approaches may target different *dependent* variables as well.

We can further develop this theme of antireductionism and complementarity if we

examine the way the concept of supervenience applies to behavior analysis. It has long been known that the concept of an operant will typically be irreducible to any physical (i.e., topographical) property of the organism. Roughly speaking, an operant is a response having a certain consequence (see Catania, 1973, for refinements). It is thus a functional concept—in the same sense that "mousetrap" and "camshaft" are functional concepts (Putnam, 1975, pp. 429–440)—which supervenes on the physical world. What has not been noted, however, is the fact that behavior-analytic conceptions of the *independent* variable are *also* typically supervenient. What, for example, do all the physical set ups constituting variable-interval schedules have in common? Certainly no physical property. They simply arrange for certain contingencies to exist between the operations the organism can perform on the world and the opportunities the organism has later in time (e.g., access to the food hopper). And there are so many physically different ways to arrange for such contingencies to exist that it is unlikely for there to be a physical property that all and only the variable-interval set ups have in common. Like evolutionary theory, then, behavior analysis connects supervenient causes with supervenient effects.

We might add that not only is there no *physical* property common to all and only the responses falling under a given operant, but there may be no cognitive property either. This of course depends on how cognitive concepts are defined. But if cognitive psychologists take the route of "methodological solipsism" advocated by Fodor, then their concepts will have no intrinsic connection with the world outside the skin (Fodor, 1980). Hence, even though cognitive concepts will themselves presumably be supervenient, there may be no way to use them to define the response class coinciding with a given operant. Similar comments would apply to the definition of the stimuli produced by a certain class of schedules. Thus, the dependent and independent variables of behavior analysis may turn out in principle to be irreducible to those of cognitive psychology.

CAUSALITY

Skinner has claimed that "as a causal mode, selection by consequences was discovered very

late in the history of science . . . and it is still not fully recognized or understood" (Skinner, 1981, p. 504). Because the domain within which this causal mode was discovered is evolutionary biology, one may hope that the analogy with natural selection will be helpful in clarifying the use of this concept in psychology.

One of the strengths of Sober's book is precisely its discussion of selection as a unique mode of causality. On the subject of ultimate causation, for example, he says that even though natural selection may be the ultimate cause of certain population-level properties, this does not mean that the environment will always be the locus of the most statistically significant independent variable. For certain kinds of "noise" may enter the process linking selection to its effects, and this noise may cause the environment to exercise less control over the outcome than do more proximate causes.

In explaining an event we are interested in where it came from, and this interest may lead us to look farther back along the causal chain; even though more ultimate causes may confer a lower probability than more proximate ones, they offer an indispensable perspective on why the event occurred. (p. 125)

Hence, ultimate causes have a special role to play in our understanding of evolution, even if they do not always specify the most significant controlling variables.

Sober emphasizes that his analysis of causation in evolutionary biology "is intended to characterize *population-level* causal claims like 'smoking is a positive causal factor in the production of coronaries in the population of U.S. adults,' not *individual-level* causal claims like 'Harry's smoking caused him to have a coronary'" (p. 295). There is an important difference between the logic of the two sorts of claims. At the individual level, it is not contradictory to say that a certain condition caused one person to have a coronary, and then to add that nevertheless the same condition *prevented* another person from having one. This is to say, our concept of individual-level causation is such that whatever causes a given type of event in one context may not only *fail* to cause that event in another context, but may actually *prevent* the event from happening. According to Sober, context dependency of this sort is incompatible with

causal claims at the population level (pp. 281–299). If a certain condition causes coronaries in some individuals and prevents them in others, then we cannot say that the condition is a positive causal factor in the production of coronaries.

This analysis has some interesting consequences. Sober notes, for example, that it refutes the position known as "genic selectionism," which holds that natural selection always consists of selection for or against a single gene (p. 297). Because a gene may be advantageous to an organism in the context of certain genes, but be deleterious in the presence of certain others, it does not seem that selection is always for or against individual genes. Apparently, then, there can be selection for certain *phenotypic* traits without there being selection for the genes that happen to *underlie* those traits.

Can an analogous point be made about the ontogeny of behavior? It is at least conceivable. Suppose, for example, that the dependent variables of behavior analysis were properties of populations of responses, and suppose furthermore that cognitive states stand to the ontogeny of populations of responses as genes stand to the phylogeny of populations of organisms. It is a truism of cognitive psychology that inducing a given belief or desire will *increase* the probability of a given response in certain cognitive contexts, but *decrease* the probability of that same response in certain others. (Ironically, this very truism is often used in arguments against philosophical or analytical behaviorism.) By parity of reasoning, then, it would seem to be possible for the environment to select for a certain type of behavior without thereby selecting for a certain type of underlying structure. Hence, in some cases the environment might be not only the *ultimate* factor causing a certain type of response to predominate, but the *only* factor.

Skinner has stressed the ability of selection to initiate change, and thereby to create novelty (Skinner, 1984, pp. 501–510). Indeed, it sometimes seems as if the *only* thing natural selection explains is change. This of course is not true, for it can also explain the absence of change. In fact, one of the reasons why natural selection is not an *optimizing* process is that a population can reach a local peak of fitness and not be able to move off that

peak to a higher one, because selection prevents the population from doing so (pp. 320–321). One consequence of this fact is that the interpretation of operant theory that emphasizes the analogy with natural selection must be distinguished from the interpretation that asserts that operant conditioning has a certain overall maximizing or optimizing effect. No such effect is associated with natural selection (see also Sober, 1984).

Another important point about selection as a causal mode has to do with the way selection is typically presented as needing to assume that variation is random, in the sense of not being biased in favor of adaptiveness. Sober takes exception to this piece of conventional scientific wisdom, and asserts that variation need not be random for selection to play a role in explaining change (pp. 361–364). As with virtually any other question about the causes of evolution, the answer has to do with the relative *prevalence* of a given factor, and not with its total control over, or total lack of control over, an evolutionary outcome. We might say by analogy that operant conditioning may play a significant role in the ontogeny of behavior even if there are underlying mechanisms that tend to create adaptive responses. The important question is how large a role the two processes play in bringing about behavioral change, not whether one or the other has total control.

THE TAUTOLOGY PROBLEM

Sober's description of evolutionary biology reveals a rather substantial isomorphism between it and behavior analysis. This fact suggests that entire segments of Sober's philosophical analysis of evolutionary biology might be transferred from that field to behavior analysis. To get a sense of how such a transfer might work, consider Sober's deft treatment of the "tautology problem." This traditional bugaboo of the philosophy of biology goes as follows: If the theory of natural selection is simply the principle of selection of the fittest, and if the fittest are by definition those that get selected, then isn't the theory true by definition? And if so, then doesn't this show the theory to be vacuous, and therefore, without explanatory power?

Sober takes a three-pronged approach to this challenge. He begins by deflating it. Sup-

pose the theory does contain a tautology. We should not assume that this somehow ruins the entire theory. As one section heading cheerily declares, "A Little A Priori Truth Never Hurt Anyone" (p. 74). Second, he raises doubts about our ability to recognize tautologies. As Quine (1953, pp. 20–42) has shown, the only kind of tautology we can make clear sense of is the formal tautology; but the principle of selection of the fittest is not a formal tautology. Thus, it is not unreasonable to suspend judgment on whether it is a tautology at all. And finally, if we have a deeper understanding of the concept of selection itself, we see that even if selection of the fittest *is* a tautology, the worry about explanatory impotence is groundless. This final point is worth expanding upon.

To develop it, Sober distinguishes between selection *of* something and selection *for* something. He illustrates this distinction by describing a shaking toy that his niece once played with, which consists of a clear plastic cylinder divided into several horizontal layers and filled with various colored balls.

Each horizontal level [of the toy] contains holes of the same size. The holes on each level are larger than those on the level below. The balls also vary in size. If the balls are at the top, shaking the toy distributes them to their respective levels. This is a selection machine. Balls are selected for their smallness. The smaller a ball is, the more successful it is at descending. Balls of the same size happen to have the same color. The smallest balls, and only they, are green. So the selection process selects the green balls, because they are the smallest. (pp. 99–100)

Even though it is correct to say that there is selection *of* either the green balls or the smallest balls, one cannot say that there is selection *for* greenness. The toy does not select for balls on the basis of their greenness, but only on the basis of their smallness. Thus, "selection *for*" is a more restrictive concept than "selection *of*." This is because "selection *of*" pertains to the *effects* of a selection process, whereas 'selection *for*' describes its *causes*' (p. 100).

How is this relevant to the tautology problem? According to Sober, "selection *for*" is the central explanatory concept of the theory of natural selection. In order for that theory to explain some aspect of evolution, there must

be selection *for* certain traits. Thus, even if we concede for the sake of argument that the principle of selection *of* the fittest is a tautology, the explanatory force of the theory of natural selection is not undermined. For the explanatory force of that theory does not derive from the principle of selection *of* the fittest. Rather, it derives from the ability of biologists to specify the various environmental factors that select *for* certain traits. And it is by no means a tautology that selection *for* a given trait will result in increased representation of that trait within the population.

Why not? For one thing, because the trait may not be heritable, in which case selection for it will not be able to increase its distribution in succeeding generations. Equally important, however, is the fact that selection is not the only force that can produce evolution. Sober discusses several others—genetic drift, migration, meiotic drive, differential rates of mutation—any of which can cancel out the effects of selection. He furthermore notes that selection may occur at various levels: group selection, individual selection, and genic selection. Because selection for a property at one level can be canceled out by selection for an incompatible property at another level, this provides yet another reason why selection for a certain trait does not guarantee evolution in that direction.

Furthermore, underlying mechanisms place restrictions on what selection for a trait can accomplish. For example, two traits may be produced by the same gene (“pleiotropy”), so that selection for the one trait may be offset by selection against the other. Or the trait produced by the heterozygote may be superior in fitness to those produced by either of the homozygotes (“heterosis”), in which case natural selection can never bring about a population composed exclusively of heterozygotes, even if there are no other evolutionary forces at work, for the offspring of heterozygotes are a mixture of heterozygotes and homozygotes.

We see, then, that there is a rich variety of possible explanations for evolutionary phenomena, and as a result, it is by no means tautologous that if there is selection *for* a certain trait, then the frequency with which that trait occurs within the population will increase. Hence, the alleged tautology problem does not rob the theory of natural selection of its power to explain evolution.

Let us turn now to operant psychology and note the parallels that exist between it and evolutionary theory. Sober himself has noted that the tautology problem has been used against both the theory of natural selection and the theory of operant conditioning. And he expresses skepticism about the suggestion that “operant conditioning theory is in trouble in a way that evolutionary theory is not” (Sober, 1985a, p. 91). This skepticism is well grounded, for virtually his entire defense of evolutionary theory against the tautology problem can be transferred to operant psychology.

Obviously, the first and second prongs of his argument transfer without difficulty: A tautology does just as little harm in psychology as in biology, and is just as difficult to recognize. But what about the third prong?

First, we may note that the distinction between selection *for* and selection *of* is already implicit in certain operant concepts. For example, a schedule of reinforcement would seem to be a physical arrangement that selects *for* certain types of responses, in the sense that it makes reinforcement contingent upon them. But selection *for* a certain type of response is not identical with selection *of* it. This non-identity is embodied in several aspects of behavior theory. Take, for example, the concept of schedule-induced behavior, as illustrated by the polydipsia observed in animals run on fixed-interval schedules (Falk, 1966). This concept seems intended to mark exactly the distinction between the behavior the schedule selects *for* and the polydipsia it happens also to select. Schedule-induced behavior thus seems analogous to the biological phenomenon of pleiotropy. Just as the genes for certain adaptive features of the human jaw happen also to be the genes for the human chin, so that “selection for jaws will bring chins along as a free rider” (p. 24); so likewise does the mechanism that underlies the behavior selected for by certain types of fixed-interval schedules happen also to underlie polydipsia, so that in the course of selecting for that behavior, one also ends up selecting polydipsia.

Another example of implicit acknowledgment of the selection-*for*/selection-*of* distinction is provided by the concept of “superstitious” behavior. When we arrange for the food hopper to be available to a hungry pigeon every five seconds regardless of what the pigeon does, certain of the pigeon’s responses get selected (reinforced), even though

those responses are not selected *for*. The point of distinguishing between superstitious behavior and behavior brought about through the contingencies of reinforcement seems precisely that we wish to mark the distinction between behavior that a schedule has selected *for*, and superstitious behavior that got selected *without* being selected *for*. Here again, there is a parallel concept in evolutionary theory. Superstition is the behavioral equivalent of "random genetic drift." When alternative traits are equal in fitness, so that selection by consequence is a neutral force, "evolution may to a considerable extent be the result of a random walk" (p. 25), and the results of that walk are said to exemplify random genetic drift. Analogously, when alternative responses are equal in their probability of being reinforced (because reinforcement is not contingent upon behavior), then the behavior that emerges is no longer under the shaping influence of the environment, and the behavior that results is said to be an example of superstition. And just as random genetic drift can occur even when natural selection is operating (pp. 25–26, and 110ff), so likewise can superstition occur even if operant conditioning is at work. Indeed, one of the skills developed in the operant laboratory is learning to make sure that superstitious reinforcement does not prevent selection of the population of responses one designs the schedule to select *for*. (Hence, for example, the need for a changeover delay when running concurrent schedules.)

Yet another example of a parallel between evolutionary theory and behavior analysis is provided by heterosis (heterozygote superiority), which Sober describes as a case of an underlying mechanism "getting in the way of" natural selection, in the sense that what the environment selects *for* does not spread through the population to the extent that selection would normally predict (p. 42). The analogous phenomenon in the ontogeny of behavior would presumably be provided by the various biological constraints on learning, whose interference with the process of operant conditioning is well documented.

Sober notes that there are more forces at work in evolution than just natural selection, but the same thing can be said about the ontogeny of behavior, where more forces are at work than just operant conditioning. We already have noted what, by the logic of our analogical reasoning, we would identify as

one such force—namely, superstition. (I would surmise that most behavior analysts would balk at referring to superstition as a "force," but in Sober's analysis, drift is a force, and superstition is the analogue of drift.) Others deserving mention include respondent conditioning, released behavior, and possibly equivalence relations.

In view of all these parallels, it should be clear that it is by no means tautologous that if the contingencies of reinforcement are such as to select *for* a given type of response, then the frequency of that response will increase. Showing that a response increased in frequency because the prevailing contingencies of reinforcement selected *for* it is indeed to explain that increase, for there are many nontrivial alternatives to this particular hypothesis. And thus, whatever can be said on behalf of evolutionary biology to defend it against the tautology problem can evidently be said on behalf of operant psychology as well.

CONCLUSION

The analogy between operant conditioning and natural selection supports the behaviorist thesis that behavior can be understood without appealing to underlying processes. There is more to be gained from the analogy, however, than mere support for a single thesis. Indeed, it would seem possible to extend the analogy to embrace the entire fields of behavior analysis and evolutionary biology. If this is correct, then the analogy may provide a principled way to interpret and clarify the nature of behavior analysis, and perhaps even a way to suggest new avenues of behavioral research. Given the high quality of recent work in the philosophy of biology, the prospects for such a program are indeed promising, and there are few better places to start than with Sober's book.

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