A Conceptual Analysis of Selectionism: Part I

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A. Introduction

Overview

Many behavior analysts have noted similarities or parallels between Darwinian natural selection in biological evolution and selection by consequences in the ontogenetic evolution of behavior and in cultural evolution. Examples, in alphabetical order, are Alessi (1992), Delprato and Midgley (1992), Donahoe (2003), Glenn (2003), Glenn, Ellis, and Greenspoon (1992), Palmer and Donahoe (1992), and Skinner (1974, chap. 3). Some of them have interpreted the similarities or parallels as arising from a common underlying philosophy they call "selectionism," but I give a different interpretation in this paper. Briefly, my interpretation is that, first, biological, behavioral, and cultural selectionism are theories rather than philosophies; second, these theories are similar in many ways because each of them is consistent with the world view (Pepper,1942) called contextualism; and third, the theories refer to different empirical domains, and therefore the relations among them are analogical, or metaphorical, rather than literal. Another preliminary point is that due to space limitation, I will not analyze cultural selectionism at all and will not give complete analyses of natural selection and behavioral selection by consequences. Also, I will say very little about respondent conditioning, even though John Donahoe's "unified reinforcement theory" implies that many of the same things could be said about both kinds of conditioning (Donahoe, 2003, and references he cited). Finally, and again because of space limitation, I have divided the paper into two parts that are about equally long and that are published separately.

Modeling

The easiest way to show how the biological and behavioral theories are similar and different is to use one of them as a metaphorical model of the other. A model is generally not useful unless its domain has already been worked out better than the domain being modeled. Therefore, I will use the biological theory as the model, not to imply that the behavioral domain is reducible to the biological domain, but because the biological theory is more detailed and has more widespread empirical grounding than the behavioral theory. The theories are actually related only by analogies, not by homologies.

Another point about modeling is that the model and the modeled refer to different empirical domains and therefore not every feature of the model has an analogy in the modeled. Specifically, models usually include (a) features that are matched to features of the domain being modeled, (b) features that need not be matched but perhaps can be, and (c) features that must not be matched. Hesse (1966, p. 8) called these sets of features (a) the "positive analogy," (b) the "neutral analogy," and (c) the "negative analogy." The point is that models can be useful even if completely exhaustive mapping is not possible. Another point is that models are likely to be more useful, the more the positive analogy; more deployable, the more the neutral analogy that can be transformed into positive analogy; and more misleading, the more the negative analogy. A final point is that ignoring the neutral analogy is not the same as what Husserl called *bracketing*, or *disconnecting* (1913/1931, Sections 31-32, pp. 107-111). These terms mean that a domain, a thesis, a feature, or whatever, is accepted as valid but is barred from consideration both in itself and in its ramifications. This was the stance taken by classical stimulus-response learning theorists when they ignored mental behaviors on the argument that they could not deal scientifically with these behaviors until the laws of simple learning had been worked out.

B. Natural Selection in Biological Evolution

Overview of Modern Darwinian Theory

The basic premise in modern Darwinian theory is that individuals live, compete, reproduce, and die (Gould, 2002, p. 620). The competition is for environmental resources that are required for survival, or for obtaining mates, or for increasing the number of offspring that survive, and so forth; but in all cases some individuals may have an advantage in the competition because of inheritable variations in their physical structures or in the functioning of their physical structures. No matter how tiny the advantage, these individuals produce more offspring that survive and therefore contribute more of their genes to the next generation than individuals that do not have the advantageous structures or functions. This is the essence of natural selection; but it can be analyzed into 15 principles that are relevant in this paper. They are listed below as an advance organizer. Principles 1 through 6 are discussed in this part of the paper and Principles 7 through 15 are discussed in Part II. In the discussions, I also indicate analogues in behavioral selection by consequences and, sometimes, the whole field of behavior analysis.

Fifteen Principles of Natural Selection

1. Both necessity and chance affect natural selection, and therefore also affect evolution.
2. The unit in natural selection is the individual organism.
3. Competition occurs because environmental resources are limited.
4. Natural selection is selection of the fittest.
5. In the strict Darwinian sense, "the fittest" means producing the most offspring.
6. Adaptation underlies fitness.
7. Natural selection is an outcome rather than a force or process.
8. The environment causes and controls natural selection.
9. Natural selection requires that variations occur.

10. Natural selection requires that some variations have an advantage in the competition.
11. Natural selection requires that the advantageous variations are inheritable.
12. Variations can occur at any age of an individual, and if some variations are advantageous, they can be selected unless their later effects are disadvantageous.
13. Evolution is gradual and slow.
14. Natural selection can be positive or negative.
15. The losers of the competition eventually die out, but they can leave a legacy.

C. Discussion of First Six Darwinian Principles

1. Natural Selection and Evolution Involve Both Necessity and Chance

a. *The Darwinian principle*. Gould (2002, p. 1333) rejected "quantified predictability" as the benchmark of science because its use classifies natural history, including Darwinism, as an inferior science, and this classification is incorrect because natural history is actually a *different* science rather than an inferior one. It is different because it is based on historical explanation and gives true chance a role, not only with respect to random assortment of parental genes to offspring and random mutations of genes, but also with respect to random assortment of environmental variations to individual organisms. Mayr (2001, pp. 119-120, 141, 281) had the same view, accepting chance causality but also saying that characteristics of remote ancestors can sometimes be predicted from characteristics of present species, and the predictions are sometimes confirmed in the fossil record (p. 25).

Another point is that although Gould said that evolutionary change can potentially be in any direction, Darwin (1896, Vol. 1, pp. 106-107) said that some directions which might have been favorable might be unavailable for natural selection because the individuals that could have begun a particular direction, chance not to survive. Chance has not only this eliminative role but also a positive role, in the production of variations. For example, chance variations in environmental conditions can lead to variations in phenotypes, some of which are advantageous and will be promoted in natural selection and others of which are disadvantageous and will be eliminated.

In the mechanistic and organismic world views that Pepper (1942) described, chance is a name given to antecedent causes that are unknown; but in the contextualistic world view, chance can be a true cause. In this respect, and many others that I do not discuss herein, Darwinism is consistent with contextualism.

***b. Analogue in selection by consequences*.** Analogously, both chance and necessity affect behavioral selection by consequences and therefore also behavioral ontogeny. For example, Skinner (1974, pp. 113-115) gave chance a role in "creativity" and response selection; and the research literature on selection by consequences includes many instances of successful prediction. In these respects, and many others, behavior analysis and selection by consequences are consistent with contextualism (e.g., see chapters in Hayes, Barnes-Holmes, & Roche, 2001; Hayes, Hayes, Reese, & Sarbin, 1993). However, the predictions that Mayr mentioned are actually postdictions, and the analogue in behavior analysis--etiology--is often ignored, especially in behavior therapy. This analogy is neutral rather than negative; therefore, it may indicate a fruitful line of behavioral research.

2. Individual Organism Is Unit of Selection

a. *The Darwinian principle*. In mainstream modern Darwinism, the thing that is directly selected in natural selection is the individual organism. It is not any aggregation of organisms--not a group, a tribe, a species, a genus, or any other kind of aggregation. This point is clarified by noting that aggregations cannot interact with the environment except in a metaphorical sense. A mob as such does not do anything; the individuals in the mob do things. The unit of selection is also not any part of the individual organism--not a gene, DNA, a polypeptide, an organ, a trait, or any other part. This point is clarified by a distinction made between "selection of" and "selection for" (Mayr, 2001, p. 126; 2004). Mayr (2001) gave sickle cell anemia as an example: The underlying gene is recessive and therefore the disorder appears in recessive homozygotes, but in heterozygotes the phenotype that is expressed protects against malaria. Therefore, in malarial regions, the processes underlying natural selection result directly in selection of individuals whose genotype includes the relevant gene, and they result indirectly in selection for the sickle cell gene.

Darwin sometimes talked about competition between races within a species (e.g., 1896, Vol. 1, pp. 92-93), but he specified that the competitors are the individual "organic beings" (p. 94). Dobzhansky (1951, p. 77), Lewontin (2000, p. 76), and Mayr (2001, pp. 126-128) also said that the individual organism is the unit of selection; but others have said that the gene is the unit. Gould (2002, p. 615) rejected conceptions of the gene as the unit, arguing that the causal agent and unit of selection is an "interactor," which must be an individual, and that genes are "replicators" rather than interactors.

Gould argued that the individuals that are interactors are not necessarily individual organisms, but can also be aggregations of individual organisms, such as groups, species, or genuses (p. 624, chap. 8), and Darwin himself sometimes referred to group selection (Gould, pp. 133-136). However, Darwin considered group selection to be an unattractive hypothesis and sought explanations in terms of selection at the level of the individual organism (Gould, pp. 129-132). As Gould put it, Darwin believed that "Nature knows no explicit principle of higher-level order" (p. 132), and although Gould argued for selection at higher levels, ranging from groups to clades, he acknowledged that selection at these levels is only a metaphor (p. 716). (A clade is a group of units, such as a group of species, that evolved from a common ancestor.)

A problem for the principle under consideration is how to explain the fact that cross-species mating usually produces sterile offspring. If selection occurred at the species level, the explanation could be that negative selection against producing fertile offspring prevents the emergence of a new cross-species source of competition. If selection occurs only at the level of the individual organism, the explanation is that cross-species sterility emerged not because it was selected but because it was a by-product of other, directly selected phenotypic differences between species, such as differences in the reproductive structures and functioning (see Sun, Ting, & Wu, 2004).

b. ***Analogues in selection by consequences.*** The analogous unit of selection in selection by consequences is a concrete behavior that instantiates a particular operant. This analogy has several implications. Glenn et al. (1992) showed that the operant is analogous to the species; but as Skinner (1953, pp. 91-95) said, concrete behaviors can be consequated but operants themselves cannot. The concrete behaviors are variable--in topography, for example--and the only property they have in common may be that they affect the environment in the same way. Therefore, the reinforcement history of an operant is dispersed across the reinforcement histories of a number of physically different behaviors, just as the evolutionary history of a species is dispersed across the evolutionary histories of a number of physically different individual organisms.

Glenn et al. and other behavior analysts such as Donahoe and colleagues (Donahoe, 2003; Palmer & Donahoe, 1992) endorsed a distinction by Ernst Mayr between the concept of a class in essentialist thinking and the concept of a taxon in population thinking, which respectively characterize the creationist versus Darwinian theories of evolution. Glenn et al. quoted Mayr's saying that "A taxon is a concrete zoological or botanical object" (Glenn et al., 1992, p. 1334, citing Mayr, 1982, p. 253). Actually, though, a taxon is not a concrete object of any kind. If it were concrete, I could see it somewhere other than as a word on a piece of paper. A taxon such as a species or an operant is a class, and even if it is a functional class--such as a response class in behaviorism--it is an abstraction. The operant is a functional class--a class of behaviors that have the same effect on the environment--and I can see a specific behavior and its effect on the environment, even though I cannot see the operant as such.

Selection by consequences also has an analogy to cross-species sterility as a by-product of other, directly selected differences. The analogue is response generalization, which according to Stokes and Baer (1977) does not occur spontaneously but must be learned. According to the analogy, generalization does not occur spontaneously, not because of a natural anti-generalization law but because learning does not *require* generalization.

3. Competition is Pervasive

a. ***The Darwinian principle.*** Darwin said that because resources are limited, "Of all individuals born, only a few can survive" (1896, Vol. 1, p.76) and therefore the individuals that are born must compete for the resources or die prematurely. Of course, plants, nonhuman animals, and probably most humans do not *choose* to compete rather than die, just as hydrogen does not *choose* to combine with oxygen to produce water. These are facts of nature. Another fact is that individuals that have an advantage in the competition are more likely to survive than other individuals. The advantage can be very slight; as Darwin said, "A grain in the balance may determine which individuals shall live, and which shall die" (Vol. 2, p. 278).

Darwin (Vol. 1, p. 79) said that the competition can be between individuals of different species, individuals of different races within the same species, or individuals of the same race within the same species, and that the competition--he said "struggle"--"will almost invariably be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers. In the case of varieties [that is, races] of the same species, the struggle will generally be almost equally severe" (p. 80). Darwin also said that the competition can be between an individual and its environmental conditions, indicating that in general, competition is a "struggle" for survival and does not necessarily require more than one individual at a given place and time.

b. ***Analogue in selection by consequences.*** The behavioral analogue of Darwinian competition is competition between behaviors, but the "competition" is usually between a behavior and its environment rather than between two behaviors. The kinds of behavioral competition most often studied seem to be approach-avoidance, approach-approach, and avoidance-avoidance conflict.

Approach-avoidance conflict is between behaviors that instantiate different operants, on the assumption that avoidance is not merely nonapproach. Therefore, this kind of conflict is closely analogous to Darwinian competition between individuals of different species. In Darwinism these individuals do not need to be in the same place at the same time; analogously, in selection by consequences the behaviors do not need to occur simultaneously or, in a laboratory setting, in the same session. The consequence for the behavior that is performed--which can be called the winner of the competition--is either positive reinforcement or avoidance of punishment. Therefore, the consequence of winning the conflict is analogous to Darwinian survival.

The conditions that prevail on a given occasion of approach-approach conflict lead to competition between either (a) instantiations of two different but highly similar operants, analogous to individuals of different races within the same species, or (b) two instantiations of the same operant, analogous to individuals of the same race and same species. A given operant includes a class of discriminative stimuli, a behavior class, and a class of consequent stimuli. The competing behaviors differ most importantly in their specific discriminative stimuli, but may also differ in the specific movements that actualize them (see Lee, 1992) and may differ in their specific consequent stimuli. Therefore, the choice between alternatives (a) and (b) probably depends mainly on whether the discriminative stimuli are from the same class. In any case, the winner gets reinforced, and the Darwinian analogues are the same as in approach-avoidance conflict.

The same analysis applies to avoidance-avoidance conflict, and I would guess that if the words "approach" and "avoidance" are interpreted metaphorically, the analysis applies to any kind of response competition.

4. The Fittest Are Selected

a. ***The Darwinian principle.*** Darwin (1896, Vol. 1, p. 77) said that the phrases "natural selection" and "survival of the fittest" are synonymous, but he also said that "survival of the fittest" is the more accurate phrase. Actually, it is problematic in two important ways. First, "the fittest" does not mean the best in any absolute or ultimate sense and it means more than is implied in saying that survival of the fittest means only survival of those individuals that in fact survive. It means survival of individuals that are the fittest in the sense that they are the best *available* for natural selection. Second, the phrase is incomplete because natural selection requires not just survival but survival and reproduction (Holsinger, 2002, p. 1291). In fact, failure to survive makes reproduction impossible, and therefore the principle could be called "reproduction of the fittest." However, this phrase is problematic because it may imply an outside agent that does the reproducing. The phrase "natural selection" has a similar problem: It may imply an outside agent that does the selecting. Also, as Darwin (p. 99) commented, "selection" incorrectly implies a conscious choice.

b. Analogue in selection by consequences. The analogue of Darwinian natural selection--or survival of the fittest, reproduction of the fittest, or selection of the fittest--is selection by consequences. The concrete behavior that gets reinforced is the one that is the fittest in the sense that it occurs first, or requires the least energy, or has whatever other property that leads most closely to satisfaction of the environmental demands. Environmental demands are analogues of what geneticists call "selection pressures," especially because both are abstract concepts and not causal agents. For example, the environmental demands in a Skinner box actually include (among other things) an amount of pressure sufficient to move the lever a certain distance; and the selection pressure exerted by predators on prey is actually an individual organism being chased and/or nonmortally wounded by another individual organism.

5. Strictly, Fitness Means Producing Viable Offspring

a. *The Darwinian principle.* The individuals that have the edge in the Darwinian competition are said to be more "fit" or better "adapted" than the other individuals. I will discuss Darwinian adaptation in Section C.6. Darwinian *fitness* means producing offspring that are viable, and therefore it leads to contributing genes to the next generation. With respect to natural selection it means producing more viable offspring than other individuals in the same population, and therefore contributing more genes to the next generation.

b. *Analogue in selection by consequences.* As indicated in Section C.4.b, in a behavioral competition, the concrete behavior that is reinforced is the one that is fittest in the sense that it has the most of whatever property leads closest to satisfaction of the environmental demands. The property might be, for example, speed or energy efficiency. In the strict sense in Darwinism, fitness refers to only one property, production of viable offspring. At one level, the reason fitness has only this property is that it is the only property that is necessary and sufficient for the occurrence of evolution. At another level, fitness has only this property because it is a consequence of survival, which is a consequence of an individual's physical structure or functioning that most closely adapts to the correct selection pressures. Therefore, when analyzed in general terms fitness in selection by consequences is analogous to Darwinian fitness in the strict sense.

6. Adaptation Underlies Fitness

a. *The Darwinian principle.* Adaptation means having traits--physical structures and/or functioning--that facilitate survival of an individual in the current environment for enough time to allow the individual to reach reproductive maturity and to reproduce, and to allow offspring to become independent of parental protection. The production of viable offspring constitutes fitness; therefore, enhanced fitness is an effect of adaptation-enhancing traits. The effect can be direct or indirect. An example of a direct effect of an adaptive physical structure in a bisexual plant is physical separation between the male and female parts such that the fertilizing pollen is more likely to come from another plant than from the same plant. An example of an indirect effect of adaptive functioning in an animal is chicks that scurry away from the hen and into concealment in response to particular clucks by the hen (Darwin, 1896, Vol. 1, p. 329).

Most geneticists say that the characteristic selected in natural selection is *fitness*, but it cannot be because fitness is not a phenotype, it is a result of phenotypes (see Section C.2.a and Part II Section B.7.a). For the same reason, *adaptation* cannot be the characteristic that is selected. Rather, the selected phenotype is either an aspect of physical structure or an aspect of functioning, specifically an aspect that results in better adaptation and therefore greater fitness. An implication is that although adaptation and fitness are *strengthened* when natural selection occurs, the strengthening is a by-product of selection.

b. *Analogue in selection by consequences.* The behavioral analogue of Darwinian adaptation can be inferred from the analogue of Darwinian fitness discussed in Section C.5.b. Behavioral adaptation means performing a concrete behavior that meets the environmental requirements sufficiently well to be reinforced.

Staddon (2003) noted that analogously to the strengthening versus selection distinction in Darwinism, reinforcement does not directly *strengthen* behavior, it directly *selects* behavior. According to this analogy, an animal trainer does not shape a specific behavior by modifying its properties to accord ever more closely with the desired behavior, but rather reinforces a specific behavior until it occurs reliably, then uses differential reinforcement to select another specific behavior that the trainer considers to be closer to the desired behavior, continuing this process until the desired behavior itself occurs reliably.

D. Summary of Part I

1. Both necessity and chance affect natural selection and evolution, and analogously affect behavioral selection by consequences and behavioral ontogeny.

2. The unit in natural selection is the individual organism. Analogously, the unit in selection by consequences is a specific concrete behavior.

3. In Darwinian theory, competition between individual organisms, or between an individual organism and its environment, occurs because environmental resources are limited. The analogue in selection by consequences is that different concrete behaviors "compete" for reinforcement or avoidance of punishment.

4. Natural selection is selection of the fittest. The behavioral analogues of natural selection and "the fittest" are selection by consequences and the concrete behavior that most closely satisfies the criteria for reinforceability.

5. In the strict Darwinian sense, "the fittest" are the individual organisms that produce the most offspring. The analogue in selection by consequences is that the reinforced behavior is the one that most closely satisfies the criteria for reinforceability.

6. In Darwinism, adaptation underlies fitness. The behavioral analogue of adaptation is that at least one concrete behavior

meets the criteria for reinforceability sufficiently closely to be reinforced.

A final comment is that the other nine Darwinian principles listed in Section B.2, and their behavioral analogues, are discussed in Part II of this paper, to be published in the next issue of this journal. To conserve journal space, references are given only at the end of Part II.

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A Conceptual Analysis of Selectionism: Part II

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A. Introduction

Overview

The present paper is the second, concluding part of a paper begun in the preceding issue of this journal. The complete paper deals with 15 principles related to the modern Darwinian theory of natural selection, and analogies of these principles in behavioral selection by consequences. Six of the 15 principles were analyzed in Part I; the other nine are analyzed in the present paper. The references for both parts are given at the end of the present part.

B. The Fifteen Principles

The principles marked with an asterisk were discussed in Part I Section C; the others are discussed in Section B below. Subsections in both parts are indexed with the Arabic numerals given here.

*1. Both necessity and chance affect natural selection, and therefore also affect evolution.

*2. The unit in natural selection is the individual organism.

*3. Competition occurs because environmental resources are limited.

*4. Natural selection is selection of the fittest.

*5. In the strict Darwinian sense, "the fittest" means producing the most offspring.

*6. Adaptation underlies fitness.

7. Natural selection is an outcome rather than a force or process.

8. The environment causes and controls natural selection.

9. Natural selection requires that variations occur.

10. Natural selection requires that some variations have an advantage in the competition.

11. Natural selection requires that the advantageous variations are inheritable.

12. Variations can occur at any age of an individual, and if some variations are advantageous, they can be selected unless their later effects are disadvantageous.

13. Evolution is gradual and slow.

14. Natural selection can be positive or negative.

15. The losers of the competition eventually die out, but they can leave a legacy.

C. Discussion of Principles Seven through Fifteen

7. Natural Selection Is Not a Process

a. ***The Darwinian principle.*** Falconer (1981, p. 301) said, "The 'character' that natural selection selects for is *fitness*." This statement is misleading unless one keeps in mind the distinction between "selection of" and "selection for." Fitness is a trait; therefore, as indicated in Part I Section C.2.a, selection *for* fitness can occur but selection of fitness cannot. Another problem with the statement is that natural selection cannot select anything, because it is not a process. Granted, most geneticists and other scientists say that natural selection is a process, force, or power that causes evolution. Examples of geneticists are Darwin (1872, pp. 77, 102-103), Crow (1986, pp. 144-147), Gould (2002, pp. 139, 619, 627, 655), and Mayr (1992, p. 135; 2001, chap. 6); other scientists include Hogg (1999a, 1999b), Palmer and Donahoe (1992), and Staddon (2003). Actually, however, natural selection is only an outcome, as noted by Gould (2002, pp. 614-637), Mayr (2001, p. 281), Nagel (1977/1979, p., 301), and Skinner (1974, p. 37). Gould said it is useful for the bookkeeping of evolution but is not a cause of evolution; Nagel said it is "not literally an 'agent' that *does* anything"; and Skinner said, "[Natural] selection is a special kind of causality which is not properly represented as a force or pressure."

Evolution is also an outcome rather than a process, and therefore neither natural selection nor evolution can explain change (Nagel, 1977/1979). The processes that explain change are ones that lead to increased probability of survival and reproduction or, more precisely, processes by which "the carriers of different genotypes in a population contribute differentially to the gene pool of the succeeding generations" (Dobzhansky, 1951, p. 77).

b. ***Analogue in selection by consequences.*** The behavioral analogues of natural selection and evolution are selection by consequences and behavioral ontogeny. The fact that natural selection and evolution are outcomes does not undermine these analogies, because selection by consequences and behavioral ontogeny are also outcomes rather than processes. The actual behavioral processes are operant conditioning procedures, perhaps with additional inborn mechanisms that permit learning higher-order operants.

8. Environment Causes and Controls Natural Selection

a. ***The Darwinian principle.*** Gould (2002) said, "In natural selection, environment proposes and organisms dispose" (p. 163). More fully, the environment causes and controls natural selection, but individuals' phenotypes cause and control the actual accomplishment called natural selection (pp. 161-163).

b. ***Analogue in selection by consequences.*** Selection by consequences is closely analogous: The environment offers a behavior the opportunity to be consequated, but the opportunity is ineffective unless the behavior occurs.

9. Variation is Required

a. ***The Darwinian principle.*** The kind of variation that is relevant to natural selection refers to differences in degree of adaptation or, more precisely, differences in the physical structures or ways of functioning that result in adaptation. Darwin said that the source of variation is changes in "conditions of life" (1872, p. 3; 1896, Vol. 1, p. 100), which means changes in the environmental conditions that the physical structures or ways of functioning are adaptive to. Genetics theory adds mutations and recombination of genes as other sources (Mayr, 2001, pp. 279-280). Variation provides the substrate for natural selection--which also implies that variation is not the agent of change. In Aristotle's terms, variation is the material cause of evolution, and the processes that result in natural selection are the efficient causes. A consequence that Darwin emphasized is that variations must be small and evolution must be slow (see Section B.13). The reason, as Gould said (2002, p. 149), is that if variations are large and evolution is fast, the variations themselves are the efficient causes of evolution, and natural selection has only a mopping-up role of eliminating the less fit.

b. ***Analogue in selection by consequences.*** The behavioral analogue of Darwinian variation is behavioral variation, without which selection by consequences has nothing to select. The causes of behavioral variation include variations in the external and internal environment and, as Neuringer (e.g., 1986, 1992) has shown, effects of prior learning, which is also an environmental effect. Examples of relevant environmental variations include variations of discriminative stimuli, current establishing operations, and current setting events, all of which can be external or internal; exclusively internal variations in neural and physiological functions; and variations in prior learning, which are functionally internal.

10. Some Variations Must be Advantageous

a. ***The Darwinian principle.*** Natural selection requires not only that variations occur, but also that some variations are advantageous in the competition for resources, even if the advantageousness results from disadvantageousness of other variations. That is, some variations must be more adaptive than others, because if all of the existing variations are equally adaptive, pure chance determines which ones win the competition, and evolution cannot occur because the tiny steps cannot have a cumulative effect--they are not taken down the path started by the common ancestor.

b. ***Analogue in selection by consequences.*** The behavioral analogue of the Darwinian competitive advantage can be inferred from the analysis in Part I Section C.6.b: The specific concrete behaviors that better satisfy the environmental requirements are reinforced. The directionality of shaping is an analogue of the directionality that evolution has once a path has started.

11. Advantageous Variations Must be Inheritable

a. ***The Darwinian principle.*** Selection can occur if some variations are more adaptive than others, because the individuals exhibiting these variations will produce more viable offspring.

However, unless the adaptive variations are inheritable, the advantage that the parents have is not passed to the offspring, and evolution does not occur. Even if the advantageous trait is inheritable, evolution will stop in the first filial generation if the advantage is lost. The advantage can be lost in several ways. For example, mutation of a gene required for expression of the advantageous trait may result in expression of a different trait, including death of the offspring, and mutation of a previously irrelevant gene may create an epistatic interaction that changes expression of the genotype underlying the previously advantageous trait. The same effect can result from slippage in replication of DNA, physiological injuries, and chance environmental variations that influence how the relevant genotype is expressed. Changes in the environment can also make the trait no longer advantageous. However, these events do not undermine Darwinian theory; they only slow down evolution.

b. ***Analogue in selection by consequences.*** The behavioral analogue of inheritability is relative permanence of the effects of reinforcement and punishment. The relative permanence can be cut short, or at least hidden, by further shaping, differential conditioning, resurgence of instinctive behaviors, extinction procedures, and so forth; but selection by consequences still *generally* has relatively permanent effects, so the analogue is complete.

12. Selection Can Occur at Any Age

a. ***The Darwinian principle.*** Darwin (1986, Vol. 1, p. 105) said that natural selection can occur at any age of an individual; that the effects at a given age can affect traits at a later age, and that the effect on the later traits cannot be injurious because if it were, the species would eventually become extinct.

b. ***Analogue in selection by consequences.*** Selection by consequences can occur at any age, and the result affect behaviors at later ages if it constitutes a "behavioral cusp" in Rosales-Ruiz and Baer's (1997) sense, or functions as a precurrent behavior in a behavioral chain learned later, or is a step in a shaping procedure, or is part of a response class that is being learned and will later constitute an operant or a higher-order operant, and so forth. If the later effect is injurious, the selected behavior will be nonreinforced or punished, and therefore will become extinct. It has an injurious later effect if, for example, it prevents occurrence of a desirable later behavioral cusp, disrupts the behavioral chain, prevents occurrence of a better variant behavior in the shaping process, or is so prepotent that it blocks formation of a response class or blocks transitivity, symmetry, or other functions of an operant or a higher-order operant.

13. Evolution is Gradual and Slow

a. ***The Darwinian principle.*** Evolution is gradual, which means that it proceeds in tiny steps, some virtually undetectable (Darwin, 1896, Vol. 1, p. 131; Vol. 2, pp. 277-279). It therefore requires many generations--thousands or even tens of thousands--and it is consequently very slow. The gradualness principle is often challenged by creationists as implausible. A concrete illustration is that during the evolution of the long neck of giraffes, some individuals had necks that were a tiny bit longer, say a millimeter longer, than the necks of competing individuals, and the ones with the longer necks were naturally selected because they could reach a millimeter more tree leaves than the competitors. The creationist argument is that the extra millimeter of food would not be enough to increase the probability of survival. An answer is that giraffes take very many bites of food each day, and therefore the extra millimeter they get in many of their bites could add up to an appreciably bigger daily intake. A better example for the creationist argument might be that a millimeter increase in the length of protopeacocks' tails would be undetectable by protopeahens, thus giving the longer tails no adaptive advantage. An answer is that the assumed limit on protopeahens' perceptual abilities is not--and cannot be--supported by any observational evidence, but that Darwinian theory and the fact that peacocks now have long tails provide inferential support for assuming that protopeahens indeed detected a millimeter increase in tail length.

b. ***Analogue in selection by consequences.*** In studies of schedules of reinforcement, the characteristic cumulative curves emerge gradually and slowly, analogous to Darwinian evolution even though the size of the steps and the slowness are scaled differently. Other effects of learning that emerge gradually and slowly include relational frames and other higher-order operants, discriminative responding, and some kinds of shaping.

However, in applied behavior analysis the hallmark is relatively rapid change--instead of years of psychiatric sessions, or even more years of psychoanalytic sessions, behavior therapy can eliminate phobias and many other undesired behaviors in a few sessions. Conditioning with punishment procedures can also be extremely rapid. Taste aversions can be learned in one or two trials, perhaps via Pavlovian aversive conditioning, and in the Watson and Rayner (1920) study with "Little Albert," an operant response was suppressed after only two trials with a punishment contingency. The first experimental session with Albert consisted of two trials on which his reaching toward a rat was followed immediately by a loud sound; and when the rat was presented on a test trial a week later, Albert withheld the reaching response.

Therefore, selection by consequences is sometimes analogous to natural selection in being gradual and slow, and sometimes it is not at all analogous because it is saltatory and fast. Maybe the analogue for the latter cases is biological extinction resulting from natural catastrophes--a principle that I do not discuss in this paper.

14. Positive and Negative Selection Occur

a. ***The Darwinian principle.*** Both positive and negative selection occurs, respectively preserving advantageous variations and eliminating disadvantageous ones (Darwin, 1896, Vol. 1, p. 98; Gould, 2002, p. 139; Holsinger, 2002). However, positive selection can occur only if at least one variation is advantageous, and negative selection can occur only if at least one is disadvantageous. Also, as indicated in the analysis in Part I Section C.2.a, the unit of selection is the individual organism rather than the advantageous or disadvantageous trait; therefore, positive and negative selection cannot simultaneously affect the same individual.

b. ***Analogue in selection by consequences.*** Reinforcement procedures are analogous to positive natural selection, and punishment and extinction procedures are analogous to negative natural selection. Both kinds of procedure are used in differential conditioning, discriminative learning, conditional discrimination, and certain kinds of multiple schedules, but they are not administered simultaneously. This fact supports the analogies to positive and negative natural selection. The analogies would not be close if the behavior of the individual, which is a specific concrete behavior, is *simultaneously* reinforced and punished. Approach-avoidance and other response conflicts would not be examples, because they involve different concrete behaviors (Part I Section C.2.b). However, an example in research with pigeons is performance of a key-peck that results in simultaneous delivery of grain and electric shock.

15. Losers May Leave a Legacy

a. ***The Darwinian principle.*** When the inherited tiny variations accumulate to a sufficient extent, the selected individuals constitute a new species and the old species becomes extinct because the few individuals that are left in it do not compete effectively with individuals in the new species. However, the new species is in the same line of descent as the old one, and therefore the genome of the new species includes some of the genes in the genome of the old one and the other genomes in the line of descent. Some of these carryover genes are expressed as similar traits, and therefore result in family resemblances across the successive species. Other carryover genes are suppressed in most of the within-species variations somewhere in the succession, but are expressed in some of the other within-species variations. The latter traits are called reversions to older forms (Darwin, 1896, Vol. 1, pp. 194-203).

b. ***Analogue in selection by consequences.*** As Donahoe (2003) pointed out, a behavioral analogue of Darwinian reversions is that behaviors which were previously acquired and then extinguished may reappear sequentially during extinction.

D. Summary of Part II

7. Natural selection and evolution are outcomes rather than processes. Exactly analogously, selection by consequences and ontogeny are outcomes rather than processes.

8. The environment causes and controls potential natural selection, but individuals' phenotypes cause and control the actual accomplishments. Analogously, the environment causes and controls potential selection by consequences, but the potential is actualized only if appropriate concrete behaviors occur.

9. Natural selection requires variations in physical structures or ways of functioning, because otherwise it has nothing to select. Selection by consequences requires behavioral variations for the analogous reason.

10. Natural selection requires that variations differ in adaptiveness, because otherwise chance determines which organisms win the competition for resources. The behavioral analogue is that specific behaviors vary in how well they satisfy the criteria for reinforceability.

11. Evolution requires that advantageous variations are inheritable, because otherwise natural selection does not yield evolution. Analogously, effects of selection by consequences must be relatively permanent because otherwise chance rather than reinforcement history determines the course of behavioral ontogeny.

12. Natural selection can occur at any age provided that the trait selected for is not injurious at a later age. Analogously, behavioral change can occur at any age, but behavioral ontogeny requires that early-learned behaviors do not interfere with desired later learning.

13. Evolution is gradual and slow. Some kinds of selection by consequences are also gradual and slow, but others are saltatory and fast, especially with punishment procedures. Effects of

punishment procedures may be analogous to extinctions resulting from natural catastrophes.

14. Advantageous traits are preserved in positive natural selection; disadvantageous traits are suppressed in negative natural selection. The behavioral analogues are reinforcement procedures versus punishment and extinction procedures.

15. Traits suppressed during evolution may reappear later as "reversions." The behavioral analogue is "resurgence" of behaviors during extinction.

E. Conclusion

Behavioral selection by consequences is analogous in many ways to Darwinian natural selection. Some of the analogies are so obvious that they do not further the understanding of behavioral selection by consequences, but some seem less obvious and they may provide some useful new ways to look at behavioral selection by consequences. A point that must be emphasized, however, is that the relation between selection by consequences and natural selection is metaphorical; that is, the correspondences are analogies rather than homologies.

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