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PREFACE

The relations between behavior, evolution, and culture have been a subject of vigorous debate since the publication of Darwin's *The Descent of Man* (1871). The latest volume of *Perspectives in Ethology* brings anthropologists, ethologists, psychologists, and evolutionary theorists together to reexamine this important relation. With two exceptions (the essays by Brown and Eldredge), all of the present essays were originally presented at the Fifth Biannual Symposium on the Science of Behavior held in Guadalajara, Mexico, in February 1998.

The volume opens with the problem of the origins of culture, tackled from two different viewpoints by Richerson and Boyd, and Lancaster, Kaplan, Hill, and Hurtado, respectively. Richerson and Boyd analyze the possible relations between climatic change in the Pleistocene and the evolution of social learning, evaluating the boundary conditions under which social learning could increase fitness and contribute to culture. Lancaster, Kaplan, Hill, and Hurtado examine how a shift in the diet of the genus *Homo* toward difficult-to-acquire food could have determined (or coevolved with) unique features of the human life cycle. These two essays illustrate how techniques that range from computer modeling to comparative behavioral analysis, and that make use of a wide range of data, can be used for drawing inferences about past selection pressures.

As culture evolves, it must somehow find its place within (and also affect) a complex hierarchy of behavioral and biological factors. The three essays by Ghiselin, Odling-Smee, Laland, and Feldman; and Eldredge accordingly center on these hierarchies and how they should be conceptualized. Ghiselin draws on his individuality thesis to explore analogies and disanalogies between species, language, and culture. Odling-Smee, Laland, and Feldman show how the inclusion of cultural factors in a hierarchy of
Chapter 6

PITFALLS OF BEHAVIORAL SELECTIONISM

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ABSTRACT

Numerous analogies have been offered to relate evolutionary and behavioral phenomena. B. F. Skinner (1981/1988), in particular, has suggested that similar processes of selection operate at the levels of evolution, behavior, and culture. This essay examines Skinner's proposed analogy between natural selection and operant reinforcement. We argue that the analogy fails to characterize a shared causal structure. Operant reinforcement mimics superficial aspects of natural selection through entirely different mechanisms; hence no detailed understanding of operant behavior can be expected from selectionist notions. Selection analogies with respect to reinforced behavior are generally useless and probably misleading. The failure of Skinner’s selection metaphor reflects on the current relations of some parts of psychology to evolutionary theory.

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
1. OPERANT BEHAVIOR AND SELECTION

In 1938 B. F. Skinner published the first book-length treatment of his research on how consequences affect behavior. His experimental subjects were rats (Rattus norvegicus), the bit of behavior he studied consisted in lever pressing, and food was the consequence used to increase or maintain ongoing behavior (Skinner, 1938). Whereas previous research on similar issues had relied on discrete trials and complex acts organized in space and time, Skinner's studies (1938) made heavy use of an important innovation. In his new operant paradigm, the relevant behavior was in principle free to recur at any point in time, did not require extensive displacement of the subject's body, and consisted in a bit of behavior sufficiently short to be considered instantaneous. Considering lever pressing as an instantaneous event allowed the analysis to focus on the rate of behavior and how it changed over time, whereas previous research carried out with mazes or puzzle boxes often used latencies or completion times as dependent variables.

Figure 1 presents Skinner's basic findings in an idealized way, time flowing from left to right. A food-deprived rat, previously trained to eat from a food dispenser, was placed into the experimental chamber, which included a lever connected to the dispenser. While exploring the chamber, the rat sooner or later came to depress the lever (Figure 1, line a, first vertical dash on the left), this first lever press being followed by food (black dot in Figure 1). As a consequence, the rate of lever pressing immediately increased (line a). In Skinner's language, the operant response of lever pressing had been reinforced by food. The term operant was coined to distinguish this kind of behavior, emitted as it were in the absence of any clearly identifiable stimulus, and reinforceable by its consequences, from the reflexive or respondent behaviors that Pavlov had previously studied (1927) and that did involve an antecedent stimulus.

The increase in response rate obtained with operant reinforcement was typically instantaneous; contrary to common belief, response rate in Skinner's paradigm did not require numerous response-food pairings to reach an asymptotic level (line e). Plotted as a function of time, the local rate of lever pressing would typically jump to its maximal level after a single response-food pairing (line b). On the other hand, once the response had been reinforced, disabling the dispenser so that lever pressing did not result in food anymore often produced a gradual return to a lower level of responding. (How and why response rate decreases during this extinction procedure is actually a complicated issue, still the focus of much debate.)

In a clever experiment, Skinner (1938) strung reinforcement and extinction together to document how a single reinforcement could affect the time course of operant behavior. He reinforced the first lever press and then immediately turned off the food dispenser. Response rate increased as expected after the response-food pairing and decreased gradually thereafter (Figure 1, lines c and d). Combining reinforcement and extinction episodes over time defines the field of operant schedules, which produce regular but complex behavior patterns (Iversen & Lattal, 1991).

1.1. Development of an Analogy

Skinner's 1938 work contained no hint at a possible analogy between operant reinforcement and natural selection, although metaphorical, selectionist treatments of learning, thinking, and other psychological phenomena had existed in the literature since the nineteenth century (see reviews in Campbell, 1960, 1974; Plotkin, 1987). Skinner's later book, Science and
Human Behavior (1953), aimed at a more general psychological audience, contained only a few allusions to a possible analogy between operant reinforcement and natural selection. On page 90 he wrote: “In both operant conditioning and the evolutionary selection of behavioral characteristics, consequences alter future probability.” And later: “In certain respects operant reinforcement resembles the natural selection of evolutionary theory” (1953, p. 430). Skinner also shortly mentioned a similar selection process in cultural change (p. 434).

Skinner’s writings on such analogies became more frequent in the following decades (Plotkin, 1987, provides a detailed chronology), culminating in an article entitled Selection by Consequences first published in Science in 1981. The core of Skinner’s proposal was that a similar mechanism of selection, conceived as a particular “causal mode” (1981/1988, p. 15), operates in a parallel fashion at the levels of evolution, behavior, and culture. Natural selection is a type of “selection by consequences” (p. 11) that made its appearance with the first self-replicating molecules (p. 11). The selection of behavior by its consequences, on the other hand, consists in operant reinforcement (pp. 12–13), a process whereby responses are strengthened by the events following them. Cultures also exemplify selection by consequences, and evolve when the practices originating within a group “contribute to the success of the practicing group in solving its problems” (p. 14). In Skinner’s framework, a question raised at any one of the three levels must have parallels at the other two and calls for an answer in terms of variation and selection (p. 14), perhaps combined with “structural constraints” (p. 15). The only distinguishing features of operant reinforcement mentioned in a section entitled Similarities and differences are the speed at which reinforcement proceeds (p. 14) and the fact that whereas biological traits and cultural practices are actually passed from one generation to the next, reinforced behavior is “transmitted” merely in the sense “of remaining part of the repertoire of the individual” (p. 15).

Judging from titles such as The Selection of Behavior (Catania & Harnad, 1988) and from the content of introductory textbooks written from a behavioral standpoint (e.g., Baum, 1994, p. 67; Catania, 1992, p. 38), Skinner’s selectionist analogy appears to have played a prominent role in behavior analysis. However, a close reading of the literature reveals that in fact Skinner’s proposal has not fostered any research program that could substantiate the analogy at a behavioral level (Plotkin, 1987). The use of the selection analogy in behavior analysis often amounts to nothing more than a restatement of its general theme, sometimes compounded with the further claim that the “selection” of behavior by its consequences is simply a “fact” established beyond dispute (Chiesa, 1992, p. 1291).

A wholly metaphorical language reminiscent of (some aspects of) evolutionary biology is thus imposed on data that have actually been gathered, and interpreted, without any inspiration from the selection metaphor. If no trace of selectionism can be found in Skinner’s early work, more recent developments in operant research (e.g., Davison & McCarthy, 1988) bear no trace of selectionism either (the few exceptions to this trend will be discussed below). How irrelevant Skinner’s selection metaphor can be to real operant research may perhaps be most easily understood by considering McDowell and Kessel’s (1979) linear-system model of reinforcement. This model simply assumes that operant behavior is driven by reinforcement inputs (see McDowell, Bass, & Kessel, 1983, p. 165) and that the resulting input-output relations can be described by a transfer function. All of the predictions of the model derive from this single hypothesis. No mention is ever made of “variation” and “selection.” The selection metaphor seems even more foreign to the work of behavior analysts who study the modulation of operant performance by stimuli and antecedent operations (e.g., Michael, 1993). Consequently, even some proponents of Skinner’s views have recently admitted that “although selectionist is an adjective often applied to the behavior-analytic paradigm, the serious work of explicating what that means has barely begun” (Glenn & Madden, 1995, p. 249, italics theirs).

1.2. Psychology in Disarray

Why has the “serious work” of explicating behavioral selectionism barely begun? Could more work along these lines eventually prove fruitful and suggest some “underlying identity of process” (Plotkin, 1987, p. 142) between operant reinforcement and natural selection? Or, alternatively, could Skinner’s selectionist view of behavior prove so superficial as to remain useless if not downright misleading? The question, we believe, is significant for three reasons that extend far beyond the confines of contemporary behavior analysis.

Firstly, psychology as a whole has often been portrayed, with some justification, as a confusing patchwork of inconsistent and arbitrary explanatory attempts (e.g., Tooby & Cosmides, 1992, p. 23). Relating psychology to evolutionary biology might well impose some order on this patchwork and diminish the arbitrariness of psychological principles by grounding them in independent evidence and theory (see Barkow, Cosmides, & Tooby, 1992). However, the proposed bringing together could in principle take two paths. A first, “vertical” approach would be to focus on causal dependencies among behavioral and evolutionary processes. The resulting framework should presumably describe complex feedback relations within a hierarchy of behavioral, ecological, and evolutionary levels (cf. Lewontin, 1983; Odling-Smee, Laland, & Feldman, this volume). The
second, “horizontal” approach would be to look not for causal relations but for analogies among levels, in the hope that such analogies reveal an underlying commonality of process. Skinner’s (1981/1988) suggestion that similar mechanisms of selection operate in evolution and behavior clearly belongs to the second class of integrative proposals. Assessing the adequacy of Skinner’s selectionist claims about behavior could have suggestive implications for the respective merits of vertical and horizontal approaches.

Secondly, the notion of operant reinforcement as a process of selection has been apparently accepted at face value by the major proponents of a sweeping selectionism extending largely beyond evolutionary biology (see Campbell, 1960, 1974; Czik, 1995, ch. 7; Dennett, 1995, pp. 374–375; Plotkin, 1987). Showing that the notion of operant selection fails theoretically and empirically could reflect centrally on such views. At the very least, the failure of operant selectionism would suggest caution before accepting a notion of selection sufficiently “substrate-neutral” (cf. Dennett, 1995, p. 82) to have significant implications outside of evolutionary biology, especially when this “neutrality of substrate” is illustrated by reference to reinforcement (e.g., Czik, 1995).

Finally, the contrast between Skinner’s selectionist language (1981/1988) and its general lack of empirical accomplishments confirms the recent suspicion that appeals to evolutionary theory in psychology are not always free of rhetorical motives (see Lloyd, 1999). Most strikingly, while various research programs in psychology all claim some support from evolutionary biology (e.g., Tooby & Cosmides, 1992; Donahoe & Palmer, 1994; Piattelli-Palmarini, 1989), the very same process of operant reinforcement can be presented either as selection (Donahoe & Palmer, 1994, p. 37) or as its exact opposite (Piattelli-Palmarini, 1989, p. 29, p. 35), depending on the author’s allegiance. Making sense of such conflicting claims calls for a more detailed analysis of how evolutionary analogies in psychology actually relate to natural selection.

1.3. Correspondence of Components

Any pair of phenomena taken at random will exhibit shared as well as unshared features. In the analogy between reinforcement and natural selection, as in other analogies, central features must be identified and irrelevant ones left aside; looking for a close analog of haplodiploidy in operant behavior would presumably be a waste of time. On the other hand, the central features of the analogy should be indicative of a shared causal structure (Darden & Cain, 1989). Without detailed implications for causal processes, a purely formal analogy is vacuous. Thus the human face has seven holes, and seven is also the number of days in the week; but nothing follows from this exercise in numerology. Finally, using a metaphorical model adequately should entail specifying exactly what corresponds to what in the two domains being compared. In the absence of such specifications, how a mere metaphor could contribute to our understanding remains unclear.

A main problem with the putative analogy between operant reinforcement and natural selection, however, is that once a few components of the analogy (such as variation and selection) have been mentioned, the correspondance of parts is rarely, if ever, ascertained. Yet natural selection necessitates a very precise arrangement of components (Endler, 1986; Williams, 1966).

Skinner’s (1981/1988) phrase of “selection by consequences” is a good case in point. Talking of consequences seems to identify an obvious commonality of operant reinforcement and natural selection. Yet further reflection reveals suspicious features. In operant reinforcement, consequences like food or water are actually delivered in the environment. Construing such events as agents of selection easily follows from the behaviorist emphasis on the environment as a primary factor of behavioral change (see Figure 1), combined with a selectionist approach. Now consider a simple case of natural selection: Antibiotic is sprayed on two genetically different strains of bacteria. As a result, only one strain survives. Where is the “consequence”? Definitely not in the environment. Spraying the antibiotic cannot be a consequence of anything because antibiotic was sprayed on both strains of bacteria. The only “consequence” we can think of in this example resides not in the environment but in the organism and consists of dying. More generally, in mortality selection the agent that has consequences for reproductive success is not itself a consequence but rather a common ecological challenge (cf. Freeman & Herron, 1998, pp. 267–291). Yet mortality selection is indisputably a case of natural selection (Endler, 1986).

This kind of discrepancy suggests that even though operant reinforcement and natural selection may both involve feedback, the underlying relations are probably arranged quite differently. Evaluating a putative correspondence between operant reinforcement and natural selection thus cannot proceed without an analysis of natural selection part by part. This analysis should move beyond generalities by detailing, not only what natural selection is, but also what it excludes. This second point has often been neglected in evolutionary analogies.

2. SELECTION PROCESSES

Any instance of natural selection must take place in a population whose members differ among themselves in some trait(s). To simplify the argument we focus on a single phenotypic trait with two discrete values A
and B, so that all members of the population are either of the A or of the B type. A phenotypic formulation of natural selection (see Endler, 1986, p. 4) is preferable for a fair assessment of Skinner’s analogy, which was developed at a purely behavioral level; properties of the genetic system will nevertheless be discussed when necessary, capitalizing on the useful fiction of a one-to-one mapping from genotypes to phenotypes.

To ascertain changes in the composition of the population, we need some criterion to identify what constitutes the “same” population across time (see Darden & Cain, 1989). We also need a criterion to include in the same population individuals that differ among themselves. The most relevant criterion, chosen to guarantee some causal homogeneity to the dynamics of a possible selection process, consists in a common environment or set of ecological conditions (for more discussion see Brandon, 1990; Damuth, 1985). Thus, lumping in a single “population” two distant groups encountering radically different ecological challenges, and evolving in entirely independent ways, would be useless from an explanatory perspective even though mathematically feasible (Damuth, 1985, p. 1134; Sober & Lewontin, 1982, p. 170).

2.1. Selection Implies Sorting

Evolution by natural selection implies a change in the numerical composition of the population being considered, but not any change will qualify. At the very least, the change in proportion of A and B individuals should be a case of sorting (Vrba & Gould, 1986), that is, of differential death or reproduction among A and B individuals. A population can evolve through other means than sorting. Mutations and migrations, for instance, do not demonstrate sorting because they involve neither death nor reproduction of different individuals.

Sorting can be accomplished in two different ways, by simple mortality (Figure 2, panel a) or through differential reproduction (Figure 2, panel b). In Figure 2a, the population before sorting includes an equal number of A and B members. Whereas the B members remain alive (or maintain their structure), the A members die (or collapse). The composition of the population therefore changes: from a population including both A and B members to a population including B individuals only. This type of sorting requires no reproduction mechanism passing structure from one individual to another, but merely the differential stability of phenotypes through time (cf. de Duve, 1987). Note that this type of sorting cannot by itself increase the absolute number of either A or B individuals. However, if some background mechanism continuously produces A or B individuals at random, B individuals will eventually accumulate in the environment.

Figure 2b exemplifies sorting through differential reproduction. Starting from a mixed population of A and B members, B individuals reproduce at a higher rate than A individuals do. If the A versus B difference shows inheritance, that is, if it tends to be conserved through reproduction, the composition of the population will shift toward a higher proportion of B individuals (as in Figure 2a, but for different reasons).

Sorting through differential reproduction (Figure 2b) brings us quite close to the classic definition of natural selection as a process combining variation with inheritance and differential reproductive rates (e.g., Lewontin, 1970), although one condition is still missing to obtain full-fledged
natural selection (see below). A clear focus on sorting allows a better understanding of Darwinian evolution through natural selection, which comprises the origin of variants as well as their spread in the population (Endler, 1986, p. 7, p. 51). The first step in Darwinian evolution, the origin of variants, is not a case of sorting but a process of mutation. (For simplicity we neglect all other sources of genetic novelty such as recombination). The second step of Darwinian evolution, phenotypic selection (sometimes called simply “selection” e.g., Wade & Kalisz, 1990), is a case of sorting however (Figure 3).

The distinction between these two steps is fundamental to modern evolutionary theory, which assumes Darwinian evolution by natural selection, rather than Lamarck-type mechanisms (Futuyma, 1998; Mayr, 1982). Evolution by natural selection requires two steps precisely because variation (the first step) is effectively decoupled from adaptation, which results from sorting (see Sniegowski & Lenski, 1995). If variation were always adaptive, no further step would be necessary; variation alone would suffice.

Note, however, that the ability to demarcate variation (the first step) from sorting or phenotypic selection (the second step) in turn implies the ability to discern mortality from mutation, and reproduction from failure to mutate. If these distinctions cannot be made, the very idea of evolution by natural selection (Figure 3) collapses.

2.2. Implications for Temporal Change

Distinguishing mutation from sorting implies that the temporal changes of a single system cannot normally feed into a selection process. A selection process requires spatial variation across different individuals, as opposed to temporal variation in a single individual. For the sake of the argument, imagine an individual (thing, system) passing through the successive states A, B, C, D to later stay in state D. One might be tempted to describe the A → B → C → D changes as “variation,” and the later permanence of D as a step of “selection.” But the “variation” here cannot be distinguished from mortality, nor “selection” from failure to mutate. Does the A → B transition, for instance, document the death of A immediately followed by the birth of B, or just a mutation from A to B? Does the persistence of D document its “staying alive” or its failure to vary?

This logical problem raises serious doubts about selectionist analogies that treat purely temporal change as “variation” (e.g., Campbell, 1956; Skinner, 1981/1988). Although such analogies nominally appeal to the couple of variation and (phenotypic) selection, they may not allow any actual distinction between variation and sorting. Now in evolution by natural selection, mutations also occur across time in individual lineages. But this temporal variation will be acted upon by sorting only after being converted into spatial, across-member variation through the branching process of reproduction. That developmental (Sober, 1984, pp. 147–155) or transformational (Futuyma, 1998, pp. 21–22) evolution could in principle take place in a single lineage, whereas evolution by natural selection cannot, is presumably no accident.

A related concern is that repetition over time does not imply reproduction. In Darwinian evolution, individuals that multiply through reproduction accumulate in space as well as in time. Branching actually entails the availability of individuals for further sorting. But how reproduction could occur in the temporal domain of a single individual is unclear. On the other hand, the successive transformations of a single system easily generate recurring events. When a heated neuron increases its rate of firing, for example, its spikes repeat but do not reproduce: Spikes do not play any positive causal role in bringing out later spikes, as should be the case if firing involved reproduction. Temporary events like spikes, that repeat but neither persist nor reproduce, cannot be submitted to sorting.

2.3. Selective Processes Versus Processes of Selection

Even when the processes dubbed “selective” in some evolutionary analogy or another properly involve variation across individuals, these processes rarely qualify as sorting. Selectionist metaphors frequently fail to distinguish processes that are merely selective from processes of selection. A selective process is just any process that affects an individual rather than another. A process of selection, however, must at the very least involve sorting, that is, mortality or reproduction (Vrba & Gould, 1986). An obvious difficulty with the notion of selective process is that almost any physical
process may be construed as selective, contradicting the more technical concept of selection. Imagine three buckets for example, all of them empty. Someone fills one of the buckets up to the top. The filling is selective: It affects one bucket rather than the others. No sorting is involved, however. No bucket died, no bucket lost its structure, no bucket multiplied.

Failing to demarcate selective processes (“selection” in the colloquial sense) from processes of selection (in the technical sense implying sorting) would turn evolutionary theory into nonsense. Within an evolutionary context, migration can certainly be a selective process. Some individuals may migrate whereas others stay in the population (defined by geographical and ecological boundaries). Yet migration is not selection (Falconer & Mackay, 1996, ch. 2). Worse, mutation can also be a selective process. Imagine a population of two members where a mutation arises, but only in one individual. The mutation is by definition selective since it affects one individual rather than the other. But does this mutation exemplify selection? Obviously not (Falconer & Mackay, 1996, ch. 2). Another case of selective mutation might involve two strains of bacteria, only one of them exposed to a mutagen such as caffeine. Because of the mutagen, mutation rates will probably be higher in one strain than in the other. Exposing only one strain to the mutagen is thus a selective process, though not a process of selection. (Of course, mutants may be exposed to phenotypic selection, hence sorting. But mutation itself cannot exemplify selection.)

A focus on sorting suggests some caution before adopting Jerne’s well-known distinction (1967) between instructive and selective processes, a distinction on which some selectionist analogies rely heavily (e.g., Cziko, 1995; Piattelli-Palmarini, 1989). This distinction originates in the context of immunology. Jerne (1967) defines selection as any “mechanism in which the product under consideration is already present” (p. 205) before the arrival of a “signal” and is thereafter “recognized and amplified.” However, any system in which the amplification happens must be “capable of receiving a signal” and is therefore “subject to instruction by this signal” (p. 205). Jerne’s distinction between instruction and selection is thus one of level: What appears as “instruction” at the level of a whole system may actually involve “selection” at the level of its building blocks (pp. 203–205).

One case mentioned by Jerne (1967) involves the translation of messenger RNA in proteins. This process is said to involve selection at the level of individual transfer RNAs (if not of the proteins themselves) on the ground that the messenger RNA must “select” among a pool of available subunits (p. 204). Yet the selective choice of transfer RNAs implies no more sorting than the choice of a bucket to fill it with water. The proposed example of selection does not even seem to fit Jerne’s (1967) requirement that selection should involve the amplification of a preexisting product. In the recognition of transfer RNAs no “product” (transfer RNA) is “amplified.” Again, a process that is merely selective has been confused with a process of selection. On the other hand, Jerne’s explicit definition of selection (p. 205), once restricted to amplification through differential reproduction, may correctly imply sorting. In any case, some selective processes apparently involve neither “instruction” nor sorting.

Finally, dubbing “selection” any interaction whereby a complex system takes one path rather than another, on the ground that the environment must have “selected” one course of action over the others, bears no coherent relation to the concept of selection in evolutionary biology. On this ground, any putative case of mutation induced by the environment (see Lenski & Mittler, 1993; Thaler, 1994) would necessarily count as “selection.” But sorting can operate only on concrete individuals (Hull, 1980) and not on possible courses of actions or other potentialities.

### 2.4. Selection and Drift

Although natural selection entails sorting (differential death or reproduction), not all cases of sorting constitute natural selection (Vrba & Gould, 1986). A last condition must hold. The sorting process must involve heritable differences and be actually influenced by one or another of the heritable differences being sorted. If various heritable differences are being sorted simultaneously, an influence of all of them is not actually required; a heritable difference that does not influence sorting may well be selected through its correlation with another heritable difference that does (cf. the distinction between “selection of” and “selection for” in Sober, 1984). But the causal influence of at least one heritable difference is needed to exemplify natural selection. Sorting processes that take place irrespectively of any heritable difference do not exemplify natural selection. They are normally classified as drift (see Hodge, 1987; cf. Beatty, 1984, 1992).

Imagine a population of birds with red and green individuals, for instance. The red birds are less cryptic and predation affects them disproportionately: As a result, the proportion of green birds in the population increases. Because sorting is influenced causally by a heritable difference (being green versus being red), this example qualifies as natural selection. A causal relation actually holds between the heritable difference in color and differential predation. Now imagine another population of green and red birds. A forest fire destroys an area of the birds’ habitat where, “by chance,” (read: for reasons independent of any heritable difference) red birds happen to be more numerous. As a result, the proportion of green birds in the population increases. In this case differential mortality, or sorting, is independent of any heritable difference. No causal relation actually holds between the difference in color, or indeed any other heritable
difference, and the fact that the red birds are differentially exposed to the fire and die. In this case, therefore, the observed sorting cannot qualify as natural selection.

A common mistake, encouraged by the careless use of the notion of “chance,” is to believe that drift is somehow uncaused or that any difference among the individuals being sorted is irrelevant to it. Further reflection shows that drift is no less a causal process than natural selection (Hodge, 1987) and that some differences among individuals are relevant to it; but these differences are not heritable. In drift the differences that govern the course of sorting involve temporary, non heritable temporal and spatial relations. In the example of the fire, what causes the red birds to die disproportionately is a physical property of these birds: their physical property of being in the zone, call it X, where fire strikes. The (physical) difference between occupying and not occupying X presumably shows no inheritance, however; hence the observed sorting cannot exemplify natural selection.

Other phenomena usually classified as drift, such as the founder effect (Falconer & Mackay, 1996, p. 78; Futuyma, 1998, p. 304; Hartl & Clark, 1997, p. 291), document a similar involvement of non heritable, spatio-temporal differences in the causation of sorting. Brandon (1990, p. 46) thus discusses the example of two genetically different types of seeds, a and b, dispersed by the wind over a patchy field of fertile and toxic soils. “By chance” (read: for reasons entirely independent of their genotype) a disproportionate number of a’s land in fertile soil, so that the proportion of a’s in the field as a whole increases. This change of proportion exemplifies sorting but not natural selection: Differential reproduction affects the proportion of a and b seeds, but is not itself affected by the a versus b difference, nor indeed any other heritable difference.

Of course, if some seeds inherited a mechanism for influencing where to land, and if having this mechanism entailed a higher reproductive success, a causal relation from heritable variation to sorting would be restored, and sorting would document natural selection (on habitat choice). In the absence of such a causal relation, however, any observed sorting tells us more on the heterogeneity of the environment than on the properties of the individuals being sorted (Brandon, 1990, p. 46). Again, consider two genetically different strains of bacteria, only one of them being sprayed (“by chance”) with an antibiotic. The fact that the bacteria in one strain die more than in the other cannot be attributed to natural selection. From the viewpoint of natural selection, the mortality rates in the two strains cannot even be meaningfully compared, the observed sorting resulting directly from the heterogeneity of the environment (antibiotic versus no antibiotic) rather than from any heritable difference among the strains. One strain does worse than the other not because of its genetic composition interacting with the environment, but simply because of a spatial coincidence with the antibiotic. Had the other strain been at the same place and at the same time, it might have suffered equally.

In sum, natural selection is a process where at least one heritable difference among the members of a population causally influences the sorting of these members (see Hodge, 1987). How sorting proceeds can in principle be studied by counting the individuals of different types. Once the properties of inheritance and sorting (differential reproduction or mortality) have been worked out, the composition of the population changes according to the laws of “probability” (Endler, 1986, p. 5) or better, arithmetic (counting). Counting can of course raise difficulties of its own (Janz, 1977); but the very existence of such problems suggests that the individuals actually submitted to sorting have not been properly identified (cf. Buss, 1983). An added complication is that sorting can take place at different levels simultaneously (Lewontin, 1970; Sober, 1984; Vrba & Eldredge, 1984). Sorting leads to evolution unless counteracting factors, such as a bias in the inheritance system, intervene.

Although the present definition has been set in a biological context, it generalizes easily to any population of entities exhibiting heritable variation and submitted to sorting. Thus our sketch does not necessitate any mention of genes, cells, or organisms (cf. Lewontin, 1970). We stress, however, that some criteria distinguishing death (or loss of structure) from mutation, and reproduction from failure to mutate, must be available; otherwise the very idea of evolution by natural selection, relying as it does on the two logically distinct steps of variation and sorting, collapses.

3. EVALUATING SKINNER’S SELECTION ANALOGY

Were Skinner’s selectionist metaphor (1981/1988) basically correct, operant behavior should exhibit features analogous to heritable variation and sorting. In fact Skinner’s metaphor fails on both counts. Consider the putative “variation” and “selection” of operant behavior, for example. In its initial explorations of the operant chamber, the rat’s performance is undisputably variable. After the rat presses the lever for the first time, and after this first lever press is reinforced by food (as in Figure 1), behavioral variation immediately diminishes as the rat now spends most of its time pressing the lever and consuming food from the dispenser.

However, the “variation” of performance involves time, a fact that already raises grave doubts as to the validity of any analogy with natural selection. As the rat explores its environment, each of its moves involves a continuous reorganization of the whole body, a transition from one
configuration to another. In this continuous "stream" of behavior (Golani, 1992; Schoenfeld & Farmer, 1970), how can response mortality be distinguished from mutation? How does selection differ from failure to mutate? In the absence of empirical criteria for discerning the genealogical relations among responses, attributing a response change to sorting (granting that the concept makes sense in the temporal domain) rather than mutation or failure to mutate, seems highly arbitrary.

But let us waive such logical objections. Let us simply postulate with Skinner that any increase in the rate of a reinforced response results from the operant analog of sorting, free of any contribution from response mutation (cf. Staddon, 1977a). If this postulate is accepted, the increase of response rate through reinforcement should be analogous to a process of reproduction. However, the notion that responses reproduce seems to make little empirical sense. Even at a purely formal level the notion fails, as the existence of phenomena like discrimination proves (Timberlake, 1988). In discrimination training, a response (B) is reinforced in the presence of a stimulus E, for example, and never in its absence (see Catania, 1992, ch. 7). If all goes well responding will eventually occur only in the presence of E, and the experimenter will be able to turn responding on and off simply by manipulating the stimulus. However, that responses reappear when E is turned on, even though response rate was literally zero in the preceding time interval (in the absence of E), is inexplicable from the viewpoint of behavioral selectionism. Analogously, if an allele has been lost from the gene pool, selection cannot reintroduce it back: A frequency of zero cannot increase by reproduction. On the other hand, mutation could reintroduce the lost allele. The modulation of response rate by a stimulus E is thus analogous to directed mutation.

Countering that reinforcement "selects" entire relations between environment (E) and behavior (B), rather than mere responses (B), does not make the selectionist analogy any more defensible. Explaining in selectionist terms how a relation E → B (absent as it is when E is absent) can reappear on command in the presence of E is just as difficult as explaining how a mere response (B) could do so; unless the "relations" alluded to turned out to be "potential" relations, in which case the selectionist analogy violates the basic requirement that sorting can affect concrete individuals only.

3.1. Further Objections

Discrimination is not the only operant phenomenon where a response, apparently lost, can suddenly reappear when the environment changes (e.g., Brimer, 1972). The difficulties that such phenomena raise for behavioral selectionism have been implicitly admitted by some of its advocates. Glenn and Field (1994), for example, have been led to distinguish the operant unit, a population spread across time and comprising various "instances of operant behavior" (p. 243), from these instances (the individual responses) themselves. Whereas selection properly applies to the operant unit, questions about its individual instances cannot be answered fully in selectionist terms. The occurrence of individual responses is rather explained by postulating an "instantiating function" of the environment (p. 252). In discrimination for example, selection would explain why responding persists at all at a global level, whereas the reappearance of responses when a stimulus E is turned on would result from E's "instantiating function."

Postulating such an "instantiating function" amounts to concede that responding is modulated locally in ways different from what a selectionist perspective allows. But once an "instantiating function" (analogous to directed mutation) has been added to the selectionist outlook, why postulate "selection" and an operant "unit" at all? Glenn and Field's (1994) try to distinguish "the existence of operant units" from "the occurrence of operant instances" (p. 242, italics theirs), but what evidence is there for the "existence" of an operant unit, aside from the occurrence of the very instances that it is said to comprise? Glenn and Field's (1994) proposal that selection accounts for some "population characteristics" (p. 247) like the frequency of individual responses (p. 245) similarly fails. The frequency of responding averaged across stimuli (say, across E and non-E) can be manipulated at will merely by changing the frequency of the stimuli (E) evoking each response instance (B). Hence a frequency averaged across stimuli cannot serve as a valid index of "selection." The frequency of response within each stimulus condition (E), on the other hand, cannot be the result of a selection process either (see above); according to Glenn and Field it is the result of an "instantiation." Either way, selectionist analogies cannot cope with so basic a behavioral fact as discrimination (see Timberlake, 1988).

If behavioral selectionism fails in terms of variation and sorting, its supposed source of feedback, reinforcement, also proves problematic. The sharp increase in responding evident after a single response-food pairing (Figure 1) does not necessarily occur because of a causal relation actually holding between responding and food. The rat locked in the chamber has no actual contact with the reinforcement apparatus hidden behind the wall. Thus if food is dropped into the chamber wholly independently of responding, but happens "by chance" to follow a lever press with the same temporal and spatial relations as in Figure 1, line c, response rate must increase exactly as it does in Figure 1, line c; to believe otherwise is to credit the rat with extrasensory perception. Of course, the long-term effects of presenting food independently of responding differ largely from those of
consistent reinforcement (for further analysis see Staddon, 1977b). These differences in the long term, however, must again involve purely spatial and temporal relations among responding and food, for these are the only relations exemplified inside the chamber (as opposed to the other side of the wall, where the programming apparatus resides).

The fact that a response can be reinforced entirely "by chance" (Henton & Iversen, 1978) suggests a last fundamental difference between natural selection and reinforcement. For natural selection, by definition and in contrast to drift, cannot be produced entirely "by chance." Granting the evolutionary analogy, the reinforcement of lever pressing through a temporal relation with food parallels Brandon's example (1990) of some seeds growing more quickly because of their purely spatial relation to a fertile patch. In both cases, the observed increase is caused not by any heritable difference (seed type a versus seed type b, pressing versus not pressing) but by some non heritable relation to the environment (a spatial relation in the case of the seeds, a temporal relation in the case of lever pressing).

Reinforcement is thus "superstitious in the most fundamental sense" (Donahoe, Crowley, Millard, & Stickney, 1982, p. 515). It takes place, not because a causal relation actually holds between the reinforced response and the reinforcing agent, or indeed between any response and the reinforcing agent, but because some response occurs in "a specified temporal relation" (Donahoe et al., 1982, p. 515) to this agent (as in Figure 1, line c). Natural selection is never superstitious in this sense, however (Endler, 1986). It takes place because a causal relation actually holds between at least one of the heritable differences being sorted and its rate in sorting. Hence even if operant reinforcement had an analog in evolutionary theory, this analog could not be natural selection but should include various forms of drift.

This last difficulty may not appear as damaging as the others we have reviewed: After all, both natural selection and drift exemplify sorting. But when all of the difficulties are pieced together, the resulting picture seems rather disheartening. Skinner's selectionist analogy fails in virtually all of its aspects. With or without amendments such as Glenn and Field's (1994) "instantiating function," the metaphor of selection cannot even address a phenomenon as basic and ubiquitous as stimulus discrimination. That Skinner's analogy requires ad hoc modifications even in its early stages of development is in itself quite revealing.

3.2. The Analogy at the Neural Level

Some advocates of behavioral selectionism have recently suggested that their program will better succeed if it includes neural as well as behavioral elements. The suggestion is to develop separate analogs of replicators and interactors (Hull, 1980, 1981) instead of pursuing the selectionist program at a purely behavioral level. Accordingly, the operant responses observed in any reinforcement experiment are seen as interactors analogous to whole organisms, and their neural precursors as replicators analogous to genes (Donahoe, Burgos, & Palmer, 1993; Glenn & Madden, 1995).

Skinner's purely behavioral metaphor is also compared to evolutionary biology before the modern synthesis. According to Glenn and Madden (1995), for example, "if neural events are the behavioral units of replication," then standard behavior analysis is in much the same position as "evolutionary theory was before the rediscovery of Mendel" (p. 247). Adding neural replicators (p. 247) to operant interactors (p. 241) is supposed to complete the evolutionary metaphor and perhaps unleash its hidden explanatory power (also see Donahoe, Burgos, & Palmer, 1993, p. 19).

We are skeptical of this historical comparison and its supposed lessons. Darwin's ignorance of genetic mechanisms, although troublesome, did not prevent him from giving clear evidence of inheritance and sorting (e.g., Darwin, 1859, ch. 1) and from devising independent tests of his views (pp. 358-363 for instance). His theory of common descent also made sense of an enormous array of facts that had no explanation on competing accounts. By contrast, the identification of genealogical relations among reinforced responses seems to be purely definitional, a matter of free postulation. Yet, even this postulation of inheritance and selection in the abstract fails on simple grounds (see above).

Let us nevertheless grant operant selectionists their historical claims, and examine their approach to neural replication and behavioral interaction (Glenn & Madden, 1995). The most developed models in this "biobehavioral" approach to operant selection (Donahoe & Palmer, 1994) have the general outlook of the connectionist networks that have recently become popular in psychology (e.g., Rumelhart et al., 1986). A complicated net of input units, intermediary nodes, and response units is supposed to underlie the reinforcement process. Any presented stimulus (E) activates some input unit, the resulting activation tracing its way inside the network until some response (B) gets emitted as output. Operant reinforcement strengthens any active connection, so that the E → B relation most active at reinforcement time gets preferentially strengthened (see Donahoe, Burgos, & Palmer, 1993, Appendix, for more details). This kind of network can indeed simulate many aspects of reinforcement, extinction, and discrimination (Donahoe, Burgos, & Palmer, 1993; Donahoe & Palmer, 1994).

The simulations reported in the literature are certainly provocative; at the very least they demonstrate the heuristic value of modelling operant performance in terms of "selection networks" (the term chosen by Donahoe and colleagues to describe their connectionist models). But do these
accomplishments, impressive as they are, actually establish some parallel between reinforcement and natural selection? That connectionist networks can be made to simulate various aspects of behavior is well known, and the connectionist movement did not wait selection metaphors to proceed (e.g., Anderson, Silverstein, Ritz, & Jones, 1977; McClelland & Rumelhart, 1985; Sutton & Barto, 1981). The only technical rationale provided for a selectionist description of reinforcement networks is that the proposed neural mechanism “selects” the connections that most reliably coincide in time with reinforcement (Donahoe, Burgos, & Palmer, 1993, p. 28). As in other evolutionary analogies, a selective process is confused with a process of selection.

Taking their lead from Campbell’s own “evolutionary epistemology” (1974), Donahoe and Palmer also state that their reinforcement models document processes of “variation,” “selection,” and “retention” parallel to those of evolutionary theory (1994, pp. 18–20). A closer look at how reinforcement networks actually function, however, shows that selectionist descriptions are misguided. First of all, these networks do not present the kind of variation that could feed into a selection process. The changes of activity in any given unit are transitory, purely temporal changes, which immediately rules them out as possible contributors to a selection process (cf. above). On the other hand, the network does present spatial variation, in the form of a set of different nodes and pathways. But this variation is never worked upon by any selection process, for the nodes and pathways neither die nor reproduce, even metaphorically. A reinforcement network of 10 nodes and 25 links before “selection,” for example, will still comprise exactly 10 nodes and 25 links afterwards. Thus the proposed replicators do not replicate and cannot be submitted to sorting.

But the most serious confusion may involve the proposed mechanism of selection. In selection networks, behaviors are supposedly analogous to organisms (interactors) and neural elements to genes (replicators). Implementing this distinction was actually the rationale behind such networks (Donahoe, Burgos, & Palmer, 1993, p. 19). One would therefore expect the selection process of reinforcement networks to involve changes in the interactors and not the replicators. The distinction between interactors and replicators (Hull, 1980) was devised precisely to separate issues of interaction (phenotypic selection) from issues of replication (typically involving genes). In reinforcement networks however, “selection” affects the replicator. The “selection” step consists in changing weights of connections inside the network (Donahoe, Burgos, & Palmer, 1993), which is analogous to modifying the genetic material. This way of proceeding, in what nominally is a model of selection, infringes on the fundamental neo-Darwinian distinction between genetic variation (previous to sorting) and selection itself. Although the “selection” process of reinforcement networks is selective, in the sense of affecting one neural connection rather than another, it cannot be analogous to natural selection at all. Instead it is suggestive of directed mutation.

Finally, in reinforcement networks the proposed interactors may not interact with the environment. Reading the operant selectionist literature (Donahoe & Palmer, 1994, p. 18, p. 32; Glenn & Madden, 1995) suggests that the interactors in operant “selection” are responses or environment-behavior relations. But, aside from the issue of drift already mentioned, the reinforced responses and environment-behavior relations virtually never interact with a reinforcing stimulus such as food. The latter is typically consumed after the emission of the operant response, and sometimes after an extended delay (e.g., Lattal & Gleeson, 1990). The possibility of delayed reinforcement seems to contradict the very notion of reinforced behavior as an interactor in a selection process; for two entities that do not even overlap in time cannot interact. Whereas any genuine interactors should overlap temporally with the selection agent, this condition virtually never holds in operant reinforcement. Hence here again, operant selectionism fails.

4. CONCLUSION

If our analysis is correct, the parallel evoked by Skinner (1981/1988) between operant reinforcement and natural selection is basically at odds with the facts. With or without its recent adjuncts, such as reinforcement networks, Skinner’s selectionist analogy simply cannot account for many basic features of operant behavior, such as the existence of discrimination and delayed reinforcement. The analogy itself exemplifies recurrent confusions between the colloquial and technical uses of terms reminiscent of evolutionary theory. Purely temporal changes are said to document “variation,” and a process that is merely selective is confused with a process of selection. In fact temporal variation can hardly feed into a selection process, and selection requires much more than selectivity. The most serious confusion involves presenting as selection what is actually reminiscent of directed mutation—granting the validity of such analogies for the sake of the argument. Finally, mere repetition is taken as analogous to reproduction, which it is not. Talking of reproduction or replication imposes some basic formal requirements on the dynamics of the processes at hand, basic requirements that reinforced behavior does not meet. All of the empirical evidence suggests that reinforced behavior repeats (e.g., McDowell, Bass, & Kessel, 1983) but does not reproduce, even metaphorically.

Note that the problems we raise involve no dispensable detail (such as the nonexistence of sexual reproduction in operant behavior), but rather
fundamental infringements on the neo-Darwinian principles of variation and selection that supposedly underlie the evolutionary analogy (e.g., Skinner, 1981/1988). A particularly puzzling aspect of operant selectionism is that the facts most clearly opposed to it, such as discrimination, are well known and have already been modelled without selectionist notions (e.g., Davison & Nevin, 1999). On the other hand, most of the variables that actually affect reinforced behavior have no clear equivalent in evolutionary theory, even at the vague metaphorical level (e.g., Davidson, Aparicio, & Rescorla, 1988; Dickinson & Balleine, 1994; Premack & Collier, 1962; Timberlake & Allison, 1974). What is the equivalent, in micro- or macro-evolution, of three hours of water deprivation or of pairing a stimulus with reinforcement? Many of the resulting phenomena are beyond the reach of any selectionist metaphor. (“Selection” networks could probably model such phenomena, but we have already argued that these models present no coherent parallel with natural selection.)

The future of selection metaphors in behavior analysis remains unclear (Richelle, 1987; Smith, 1994; Staddon & Simmelhag, 1971). Operant reinforcement mimics some superficial features of natural selection by modulating response rate as a function of previous spatial and temporal relations. Because the mimicry does not extend to any shared causal structure, no detailed insight into behavioral causation is to be expected from selectionist analogies (cf. Amundson, 1989). On the other hand, limited uses of them are conceivable to the extent that they focus on the statistical properties of natural selection (Endler, 1986, pp. 4–5) and not its causal functioning. Vaughan and Herrnstein (1987), for example, have demonstrated formal parallels between frequency-dependent selection and the aggregated effect of some reinforcement schedules. These formal parallels merely concern issues of equilibrium, and are largely free of implications for the detailed study of operant processes (cf. Staddon, 1991). Progress in understanding the later will probably involve, and indeed already involves, non-exclusive analogies taken from a whole range of disciplines such as chemistry (Staddon, 1977a) and physics (e.g., Marr, 1992; Nevin & Grace, in press; Staddon, 1982).

Beyond any analogy, the difficult work of integrating behavior analysis and evolutionary biology remains to be done. Until recently the points of contact mainly involved foraging theory (e.g., Fantino & Abarca, 1985), but we can expect more varied attempts at integration in the future. These will necessarily explore a complex network of interactions among behavior, ecology, and evolution. Skinner's (1981/1988) preference for analogies over hierarchical integration has not proved very helpful in this respect. The difficulties we have identified in his approach may not generalize to others, equally metaphorical views (e.g., Campbell, 1974; Piattelli-Palmarini, 1989); indeed, it may not even generalize to Skinner's own selectionist view of culture (but see Orr, 1996). Any claim to have established a similarity of process between natural selection and one psychological phenomenon or another should nevertheless be examined with critical care.

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REFERENCES

Pitfalls of Behavioral Selectionism


Chapter 7

BEING CONCRETE ABOUT CULTURE AND CULTURAL EVOLUTION

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1. ABSTRACT

Culture consists of behavior. The units are practices shared by members of a group and acquired as a result of membership in the group. Although it is common to define the units of culture as abstractions, such as cultural or memes, these abstractions in no way help to explain a group's practices. Instead, they only direct research away from the context and consequences that result from transmission of a practice from one group member to another. If culture is to be described as an evolutionary process, one must have a sufficiently general definition of "evolutionary process" to allow genetic evolution and cultural evolution to be examples. This may be accomplished by defining an evolutionary process as composed of variation (within a pool of replicators), transmission (by copying), and selection by differential transmission). The replicators of cultural evolution are practices, which are units of operant behavior (i.e., behavior under control of consequences and context). Practices are transmitted from individual to individual by imitation and instruction. Instruction may be understood with the concept of a rule, which is a verbal discriminative stimulus (i.e., a verbally created context). Instruction consists of rule-giving, which results in rule-following on the part of the instructee. New rules come into a culture frequently as a result of rule-making, the generation of new rules on the basis of non-social

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