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Three Types of Selection and Three Centuries

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Abstract

This presentation considers the concept of natural selection as it applies to the behavioral and biological sciences in three centuries. The nineteenth century provided Darwin's application of natural selection to the evolution of species. The twentieth century saw the extension of this principle to behavior within the lifetime of the individual organism in ontogenic selection, as in Skinner's analysis of operant behavior. It follows from ontogenic selection that a third level of selection must operate whenever behavior can be passed on from one individual to another. This occurs to some extent in imitation and observational learning, but its most obvious development is in human language. This level of selection has been called cultural selection, and its implications and applications are ripe for analysis. Accounts in terms of the other varieties of selection have met resistance in their centuries and continue to meet resistance today. A reasonable prediction is that the significance of ontogenic selection will at last be fully recognized and the scope and implications of cultural selection will begin to be tested in the twenty-first century.
Key words: natural selection, ontogenic selection, cultural selection.

Resumen

El presente artículo trata de cómo se ha empleado el concepto de selección natural en las ciencias biológicas y del comportamiento. En el siglo XIX se aplicó el concepto darwiniano de selección natural a la evolución de las especies. El siglo XX vio la extensión de este principio a la conducta del organismo individual a lo largo de su vida en la selección ontogenética, como en el análisis de Skinner de la conducta operante. De la selección ontogenética se sigue que debe operar un tercer nivel de selección, dado que el comportamiento puede transferirse de un individuo a otro. Esto ocurre en cierta medida en la imitación y el aprendizaje observacional, pero su desarrollo más evidente está en el del lenguaje humano. Este nivel de selección se ha llamado selección cultural, y sus implicaciones y aplicaciones están listas para el análisis. Las explicaciones en términos de otras variedades de selección han encontrado resistencia en sus respectivos siglos y continúan encontrándola aún hoy. Una predicción razonable es que la importancia de la selección ontogenética será finalmente reconocida y que el alcance e implicaciones de la selección cultural comenzarán a ponerse a prueba en el siglo XXI.
Palabras clave: selección natural, selección ontogénica, selección cultural.

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The most significant contribution to the biological and behavioral sciences in the nineteenth century was Darwin's account of natural selection as a theory of biological or phylogenic evolution (Darwin, 1859). Selection was well known even before Darwin, as it was used in horticulture and animal husbandry. People knew how to breed plants or livestock selectively for various characteristics, and part of Darwin's insight was that a similar kind of selection occurred in nature, without human intervention. Darwin's work did not lead to arguments about the existence of artificial selection. Instead, what many saw as the problem was natural selection.

Late in the nineteenth century, Darwinian selection passed through what has been called an eclipse (Bowler, 1983; Catania, 1987). Along with other difficulties such as substantial underestimations of the age of the earth, Mendelian genetics seemed inconsistent with natural selection because it could not provide the variations necessary for natural selection to operate. Genetic research in the early twentieth century demonstrated frequencies of mutation sufficient to support the Darwinian account, and led to the revival of natural selection in its synthesis with genetics.

We are most familiar with selection as it operates in evolution (phylogenic selection), but it is a more general process that can occur in other circumstances, and we here consider two additional varieties of selection; ontogenic selection, corresponding to operant selection or the selection of behavior by its consequences within the lifetime of an individual organism; and cultural selection, corresponding to the selection of behavior as it passes from one individual to another (Skinner, 1981). There are both parallels and differences between phylogenic and ontogenic selection (e.g., Catania, 1978, 1987; Catania and Harnad, 1988; Skinner, 1966, 1975, 1988; Smith, 1986) and between phylogenic and cultural selection (e.g., Dawkins, 1976, 1982, 1986; Harris, 1977).

Natural and Artificial Selection

Natural selection is ordinarily identified with Darwin's account of phylogenic selection, but the distinction between natural and artificial selection is relevant for ontogenic as well as for phylogenic selection. Behavior can be selected within a lifetime not only as the result of natural interactions between an individual and an environment, but also as the result of artificial interactions explicitly created by a teacher. The distinction between artificial and natural selection is therefore appropriate to both levels of selection. For this reason, we avoid ambiguity if we speak of phylogenic rather than natural selection when we wish to refer to the selection of populations of organisms (or behavior, or genes) over evolutionary time. (Note that at the cultural level, the distinction between natural and artificial is less relevant because cultural selection is in a sense necessarily artificial; behavior selected at this level can often be regarded as behavior that has in some way been taught. The artificial selection involved in horticulture and animal husbandry, for example, is itself a product of cultural selection.)

Each of the three varieties of selection involves some kind of variation that provides the source materials upon which it operates, and each has some mechanism or mechanisms according to which surviving variants are selected. At each level of selection it is

crucial to be explicit about what gets selected and what does the selecting. For our purposes, it will be most appropriate to emphasize behavior as that which is selected, and it is always the environment, whether phylogenic, ontogenic or cultural, that does the selecting (the environment of each organism, of course, includes other members of its own species). It must be noted that, although humans are developing the capacity to modify the nature of selection, we should not regard selection as a purposive activity performed by organisms at any of the three levels: it is environments rather than organisms that select their responses just as environments select the offspring that survive.

Selection both creates and maintains the features of organisms. For example, the ancestors of whales were once land mammals. After they moved back to the sea, the evolutionary contingencies that made legs advantageous no longer selected for well-formed legs. Instead, selection began to favor limbs that were effective for movement through water. The legs of the ancestors of whales gradually disappeared; in a sense they had become extinct (cf. Skinner, 1988, p. 73). Behavior is involved in this variety of selection at a very fundamental level: the evolution of fins versus legs is in the service of the behavior of swimming as opposed to that of locomotion on land.

Although the different varieties of selection often complement one another, it is possible for selection at one level to oppose selection at another. For example, behavior may be selected through ontogenic processes during the lifetime of an individual even though it reduces the individual's reproductive fitness at the phylogenic level (consider the consequences of substance abuse or of sexual behavior that puts partners at risk of disease). Phylogeny produced the capacity for behavior to be selected by its consequences in ontogeny, but this does not imply that the individual will always benefit from that capacity.

Similarly, patterns of behavior maintained through cultural selection among members of a group (perhaps including such cases as celibacy or suicide or modern war) need not be consistent with those maintained by phylogenic or ontogenic contingencies. Each level of selection may require a different kind of analysis. For example, an analysis of the ontogenic selection of the behavior of an individual may not predict the effects of cultural selection, as when behavior that would be less easily maintained by ontogenic selection displaces behavior that would have been more easily maintained simply because in cultural selection the former is more effectively or more rapidly transmitted from one individual to another. For example, there are many advantages of reinforcement over punishment, but punishment is far easier to teach because the delivery of a punisher often has more immediate consequences than the delivery of a reinforcer. Presumably for that reason, aversive contingencies dominate social practices in many cultures. We may profit from exploring parallels among the different varieties of selection, but we must also be prepared for points at which the analogies break down.

Ontogenic Selection

In the Darwinian account, natural selection operates upon successive populations of organisms, and in many organisms this variety of selection creates patterns of behavior

that do not have to be learned. Such patterns of behavior remain functional so long as environments remain relatively stable. But in unstable environments, those organisms whose behavior can be modified by the situations in which they find themselves will have selective advantages over those whose behavior cannot be so modified. Thus, we can assume that the capacity to learn has been selected over phylogenic time. In such cases, selection can operate on successive populations of responses within the organism's own lifetime. In ontogenic or operant selection, responses are affected by their consequences within the lifetime of the individual. Some responses are selected by their consequences (they survive in the organism's subsequent behavior); others do not (they extinguish, or become extinct).

To the reader who is mainly familiar with accounts of learning that appeal either to associations and stimulus-response bonds or to the reorganization of cognitive structures, the idea of learning as selection may seem counterintuitive. But the stream of behavior itself is the source of the replicable units upon which selection operates, and the data that emerge from the analysis of behavior are consistent with the view that much behavior is best interpreted in terms of the strengthening of behavioral units by the consequences they produce (consequences that strengthen behavior are sometimes called reinforcers, but the vocabulary of reinforcers often implies properties appropriate only to earlier approaches such as stimulus-response learning theories). And even where it may be convenient to talk in terms of associations, the associations in such cases are still most parsimoniously treated as products of selection.

This selectionist view is an outgrowth of seminal research by Skinner (1938) and is the central feature of a branch of experimental psychology called the experimental analysis of behavior (cf. Catania, 1998). To put it more colloquially, organisms do things that pay off and stop doing things that do not. The environment determines what pays off, so the environment is what selects the things that the organism does. This kind of selection operates during the lifetime of the individual organism and is therefore ontogenic selection (sometimes also called operant selection, because the behavior operates on the environment and the environment operates in turn on subsequent behavior). This variety of selection arises as a product of phylogenic selection and therefore may be limited by it, in the sense that what is selected depends on both the behavior made available by phylogeny and the features of the environment that phylogeny has made significant to the organism (e.g., the phylogenic importance of food and sexual behavior may make food-getting behavior and behavior that leads to sexual contact especially susceptible to selection by its consequences).

A procedure called shaping is a variety of artificial selection in which an experimenter produces changes in behavior by arranging consequences for some responses but not others. For example, if food is presented only after the strongest lever presses of a food-deprived rat, stronger presses will occur more often and weaker ones less often, and over time the rat's presses will increase in force. Although such selection is ontogenic rather than phylogenic, its properties parallel the kind of selection relative to a population mean that occurs in biological evolution. The opportunity to eat is the consequence that selects some responses and not others; responses within the class that produces food survive, while those outside the class extinguish. In our example of shaping, the relevant

class consists of strong presses, but any dimensions of behavior can define a class, including the stimuli that are present when behavior occurs (e.g., as when consequences are arranged for responding that occurs when a light is on but not when it is off; assuming a sighted organism, only responding in the presence of the light will be strengthened).

As already noted, shaping provides an ontogenic parallel to artificial phylogenic selection. When an experimenter shapes a pigeon's clockwise turns or a behavior therapist shapes the vocalizations of a nonverbal institutionalized child, the effectiveness of shaping is self-evident. What is often questioned is whether ontogenic selection also operates naturally to produce the varied patterns of behavior seen in everyday life. But appropriate contingencies also exist in natural environments. For example, the parents who always wait a while before attending to a crying child may not notice that they have gradually shaped louder and more annoying cries. The attention strengthens the crying and annoying cries are, by definition, the ones most likely to get attention.

The contingencies that produce such problem behavior seldom occur in isolation, so other behavior or new consequences of existing behavior may eventually displace the it. Some might take the spontaneous disappearance of such behavior as evidence that it had a source other than ontogenic selection, but, just as with phylogenic selection, extinction is more likely to be accounted for by changes in the environment (for example, the contingencies that maintain a child's thumbsucking may change drastically when the child begins to spend much more time with peers than with parents or other caregivers). In any case, if artificial ontogenic contingencies deliberately arranged over relatively short periods of time can change behavior, it is reasonable to assume that those that occur naturally over substantial periods throughout a lifetime will also do so. The contemporary analysis of behavior has generated a wide range of applications in education, behavioral medicine, psychopharmacology, developmental disabilities and many other areas of human concern (perhaps for that reason, the first decade of the new century has formally been designated as the Decade of Behavior by the American Psychological Association and other behavioral organizations). The contributions have expanded so rapidly in recent years as to be immeasurable (because of their efficacy, the practices of applied behavior analysis seem to have gained a large selective advantage relative to those of other approaches; this is itself an example of cultural selection).

Cultural Selection

The third variety of selection, cultural selection, occurs when behavior is passed on from one individual to another. The behavior that individuals acquire within their own lifetimes is eventually lost if they cannot pass it on to others. Through cultural selection, behavior can survive the death of the individual who acquired it; it then survives in what others do. It is an important part of the present account that the units acted upon by cultural selection are the same as those acted upon by ontogenic selection; in both cases, selection operates upon classes of behavior.

Like phylogenic and ontogenic selection, cultural selection depends upon variable populations upon which selection operates. But the conclusion that behavior is a product

of cultural selection demands more than the observation that behavior is shared by members of a group. The shared behavior may simply be the product of common phylogenic or ontogenic variables that have operated independently on the behavior of each individual. For the behavior to count as a product of cultural selection, it had somehow to get from one individual to another, and one issue is the sense in which behavior can do so.

The third variety of selection includes observational learning, imitation, and the survival of cultural practices; it manifests itself most significantly in human verbal behavior. For example, what someone has said or written can survive that person's death if it is passed on to and repeated by others. The verbal behavior that has survived within and been shared among the members of a group is part of the culture of that group, but shared in this way it need not be correlated with genetic relatedness (e.g., it is not necessary to be closely related to Darwin or Skinner to be able to repeat their words). Cultural selection has properties in common with the selection of memes as promulgated by Dawkins (1986; see also Blackmore, 1999), but the nature of the meme is, unfortunately, not well defined. As already noted, in selectionist accounts it is crucial to say what gets selected and what does the selecting, and the advantage of the present account of cultural selection is that in its appeal to behavior as that which is selected, it points to phenomena that are directly observable and measurable, as opposed to evanescent entities (e.g., ideas) whose nature is at best controversial and the interpretation of which is under any circumstances variable (Catania, 1995).

Much of what any of us knows has been taught, either in the informal context of interactions between family members and friends and neighbors or in the formal context of educational institutions. Imitation and observational learning seem commonplace because they so often enter into human behavior. It is not clear how often they occur even among nonhuman warm-blooded vertebrates, although their occurrence is well-established among primates (e.g., Mineka, Davidson, Cook and Keir, 1984; Yamada, 1957; Zentall and Galef, 1988). Human cultures, however, depend on the selection that occurs as behavior is passed on from one individual to another (e.g., Harris, 1977; Dawkins, 1976). Certain ways of raising children, of obtaining and preparing food, of building shelters, and of dealing with group members and with outsiders survive over successive generations through cultural selection.

In cultural selection, behavior is selected and maintained by a social environment. Not only do humans acquire behavior by observing the behavior of others; they do so selectively. In early human history, those who could learn by observation how to make stone tools or fire or garments presumably had survival advantages over those who could not (this account assumes that the selection operated at the level of the survival of individual members and not at the level of the survival of the group). Perhaps behavior acquired through cultural selection is then simply maintained by ontogenic contingencies, but this is not necessarily so. As already mentioned, an unfortunate example is the prevalence of punishment rather than reward as a means of control in many human cultures; punishment is easier to teach than reward and therefore can spread more quickly through a culture, even though ontogenic contingencies would probably favor reward over punishment if both began as equally well established cul-

tural practices.

Language and Selection

Language necessarily involves all three varieties of selection (Catania, 1991). First, phylogenic selection endowed the human species with those physiological attributes that are prerequisite for language. A particular language, however, must be acquired by each individual in development, and this acquisition must include ontogenic selection (as when nonnative speech sounds drop out early in a child's vocal development, so that mainly native sounds survive in the older child's repertory). Furthermore, languages shared and perpetuated by human groups can emerge only through cultural selection, in which verbal behavior is passed on from one individual to another. The primary function of language is that it is a very efficient way in which one individual can change the behavior of another. Giving definitions or other verbal information is a special case: it is a way of changing another individual's verbal behavior.

Controversies over verbal behavior have been at the heart of critiques of the analysis of operant behavior. For example, Chomsky's (1959) review of Skinner's book on verbal behavior (Skinner, 1957) has been taken as definitive, even though Chomsky's account of language bears only on its form (the issue of what makes sentences grammatical) and has virtually nothing to say about the functions of language. But the functions of verbal behavior were the primary concern of Skinner's work (cf. Andresen, 1990). It was as if someone who had developed a mathematical description of the coordinations involved in the different gaits of horses had claimed to be able to say when a horse would walk and when it would trot and when it would gallop. The question of whether a sentence is grammatical tells us no more about the circumstances under which a speaker talks or what the speaker talks about than the structure of the horse's gaits is helpful to the equestrian who knows that the horse is capable of only certain gaits but still must train the horse to walk while off the track and to gallop while in the race. The latter questions are functional ones and not structural ones (this distinction is similar to the one between physiology and anatomy in biology). What linguists have had to say about the implications of language structure for the analysis of the functions of verbal behavior is simply irrelevant (cf. Pinker, 1994, on the language instinct; in Pinker's book, sentences that deal with language function as opposed to language structure are hard to find and can probably be counted on the fingers of one hand).

The contemporary battle between ontogenic selection and linguistic creationism has many parallels with the Darwinian history of the nineteenth century. While linguists have argued that language is an evolved human capability, they have simultaneously claimed the irrelevance of ontogenic contingencies (e.g., Pinker and Bloom, 1990). Meanwhile, experimental analyses of the functions of verbal behavior have shown how the properties of verbal behavior can be understood in terms of nested or higher-order classes of behavior. For example, individual phonemes enter into words, and words enter into sentences; similarly, the following of a particular instruction may have consequences specific to the instructed behavior, but instruction-following in general has other more general (usually social) consequences (e.g., Catania, 1998, chapters 9,

14 and 15). The effects of ontogenic or operant contingencies can easily be obscured if the classes of behavior upon which the contingencies operate are not adequately identified. Furthermore, the analysis of higher-order classes allows for a treatment of combinations of classes that addresses the issue of sources of novel behavior (e.g., the variables that result in the production of novel sentences). As in the phylogenic or Darwinian case, the operation of selection at the ontogenic and cultural levels provides an account of the processes that lead to novelty, and despite the claims of Chomskian linguists it is not incompatible with such processes.

Current work in the analysis of behavior is bringing us closer to the practical application of cultural selection to significant human problems. For example, we are learning about ways in which the nonverbal behavior of an individual can be changed by the shaping of what the individual says (e.g., Shimoff and Catania, 1998). We are so immersed in language that we find it difficult to treat it as a variety of behavior, and yet the functions of verbal behavior are crucial to our understanding of human behavior. The interactions between nonverbal and verbal classes of behavior are ripe for study, and bear on the nature of human political institutions, scientific practices, education, and even knowledge and truth. It is reasonable to predict that the distinctive scientific achievements of the next century will include both the re-emergence of ontogenic selection, which has been eclipsed through much of the twentieth century much as Darwinian selection was in the nineteenth, and the growing recognition of cultural selection. How these may lead to the betterment of human behavior throughout the world is a story for the new century.

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