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Title (ECAD00052)

Evolutionary biology and the natural selection of behavior

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Abstract

Evolution is a name for how biological populations have changed over the history of our planet. The most successful theory of why those populations changed is Darwin’s natural selection. Accounts of evolution tend to emphasize anatomical and physiological properties, like the brain and its organization. But evolutionary contingencies select organisms based on what they can do, so brains and other structures evolved in the service of behavior. In that sense, behavior always comes first. Selection as a causal mode differs from traditional push-pull causalities. It extends from the familiar level of phylogeny, evolutionary change over generations, to ontogeny, in behavior that evolves within the lifetime of an individual organism, and to evolving cultural practices, as behavior is passed on from some individuals to others. At each level behavior has consequences, and these consequences determine the extent to which the behavior is replicated and evolves.

(144 words)

Keywords

Evolution, selection, selection by consequences, ontogeny, phylogeny, culture, verbal behavior

Main Text

Evolution happens. It is not a theory. It is a name for how biological populations have changed over the history of our planet. Theories about why those populations changed, such as Lamarckism and orthogenesis, have come and gone. One remains with us: the theory of evolution by natural selection, introduced by Charles Darwin and his contemporary, Alfred Russel Wallace, and developed in greatest detail by Darwin (1859).

Accounts of evolution tend to emphasize anatomical and physiological properties, like the brain and its organization. But evolutionary contingencies select organisms based on what they can do, so it is crucial to recall that brains and other structures evolved in the service of behavior. In that sense, behavior always comes first (Catania, 2013; Skinner, 1953).

This entry highlights selection by the environment as a causal mode, in contrast with traditional push-pull causalities, which range from those of the ancient Greeks to those of Newton and beyond. It extends natural selection at the level of phylogeny to ontogeny, in the evolution of behavior within the lifetime of individual organisms, and to the evolution of cultural practices, as behavior is passed on from some individuals to others. Each type of evolution is related to selection by consequences, the fundamental process that produces change in each of these cases (Skinner, 1981). At each level, behavior has consequences, and these consequences determine the extent to which the behavior is replicated. What follows discusses the three selective systems and the parallels that exist between them.

The Origins of Selectionist Thought

Inspired in part by breeding done by humans in horticulture and animal husbandry (artificial selection) and bolstered by careful and extensive observations of the natural world, Darwin came to argue that environmental selection plays the central role in the evolution of form. If phenotypic traits are distributed unevenly across a population of organisms and are at least somewhat heritable, and if also an organism's relative likelihood of reproduction depends on its interactions with a resource-limited environment, it follows that phenotypic variability in the population will be a function of the degree to which traits have been positively related to reproductive success.

In selection, Darwin discovered how undirected natural processes could produce varied and complex outcomes. In each case, differential consequences determine the character of subsequent populations. Darwinian evolution by natural selection remains the central organizing principle of modern biology, without which little in its purview can be properly understood (but see also Laland et al., 2015).

The evolution of particular morphological characters is necessarily linked to their behavioral advantages across generations. In this sense, behavior is primary. The appearance through mutation of a patch of light sensitive tissue, for example, is only likely to propagate through a population of organisms in environments that include light. Should such mutations emerge in entirely dark environments, no reproductive advantage is conferred, so the trait would not likely be sustained in the population. Similarly, once-useful light-sensing organs that no longer provide a reproductive advantage are likely to be selected against and therefore lost (e.g., the cave-dwelling eyeless Mexican tetra).

Any discussion of selection by consequences must begin by considering the conditions under which it occurs. Environments can produce evolutionary change by selecting members of populations (whether genes or organisms or classes of behavior) only if those members vary. Whether variation in particular characteristics matters depends on the environments in which they are expressed. Sensitivity to light can only be an advantage in lighted environments. But exactly what counts as an advantage? A satisfactory account of selection by consequences must address this question.

Units of Selection

A discussion of evolution via selection by consequences depends on identifying the units of selection. What, precisely, is selected, and how should the selection be measured? Biologists and behavioral scientists alike have hotly debated such questions. One review of the problem put it this way: "The problem of the units of selection has engaged the attention of evolutionists ever since Darwin. It concerns whether traits evolve because they benefit individual organisms or because they are good for the group in which they occur [or] because they benefit the genes that code for them" (Sober & Wilson, 1994, p. 534). Candidates for the units of selection have included, among others, the gene, the organism, and the group.

The now-conventional view in biology, advanced most strongly by Dawkins (1982), is that the gene is the only fundamental unit that is selected and thus replicated. He writes, "The existence of a Darwinian adaptation, then, implies the sometime existence of genes for producing the adaptation.... It is always legitimate to postulate genes in any discussion of Darwinian adaptation.... Objections, such as I have heard made, to the 'unnecessary geneticizing' of the language of functional ethology, betray a fundamental failure to face up to the reality of what Darwinian selection is all about" (Dawkins, 1982, p. 27). Dawkins has also steadfastly argued that phylogenetic selection operates on individuals and not on the groups of which they are members. Wilson & Sober (1994), on the other hand, have highlighted disagreements regarding group selection, making the case that social groups are themselves adaptive units that cannot be reduced to the actions of their individual members and arguing that selection at this level may produce group-level adaptations. While acknowledging the still unsettled nature of the argument, we may tentatively posit that units of selection are those things differentially reproduced via selection by their consequences. In this sense, any units (morphological, behavioral, or otherwise) are *selected for* (Sober, 1984, p. 97-102). Features that increase in frequency within populations of organisms or behavioral classes do not *necessarily* reflect units selected by their consequences, because free riders (e.g., through linkages to advantageous genes in pleiotropy) may result in evolving forms in the absence

of consequences for those features. Therefore, it is critical to document not merely the changes within populations but also the extent to which those changes were selected by the environments within which they were expressed.

Selection as a Causal Mode

Populations vary. If this variation results in the differential reproduction of a given character over generations, a population will evolve. To the extent that sensitivity to visible light is advantageous, eyes should evolve and proliferate, as long as requisite initial and heritable variation exists in the baseline population. To analyze any evolutionary process we must identify the relevant population, the characteristics that are differentially selected (i.e., the units of selection), and the contingencies that produce selection. There is no reason to limit evolution in this sense merely to characteristics produced over generations of organisms, as in Darwinian natural selection. It should occur in any scenarios in which units of any kind differentially reproduce with variation. In the context of discussing memes, replicable units in human cultures, Blackmore (1999) explains: "...if there is a replicator that makes imperfect copies of itself only some of which survive, then evolution simply *must* occur. This *inevitability* of evolution is part of what makes Darwin's insight so clever. All you need is the right starting conditions and evolution just has to happen" (p. 11, emphasis in original).

Presumably selection originated as a causal mode in biological systems at the very start of what could be defined as life; the first level of selection began with the first self-replicating molecule. The subject matter of biology came into existence when a molecule first replicated itself, with its reproduction a first biological consequence. Any replicator, even a slow or inefficient one, will come to dominate over similar non-replicating entities. To the degree that replication was imperfect and descendants were differentially successful at replication (e.g., with respect to its rate), phylogenetic selection produced variants increasingly better at self-replication. Evolution by natural selection was then off to the races: In an important sense, reproduction itself was the critical first consequence by which selection made its appearance in biological systems (Skinner, 1981).

Selectionism and Behavior

Just decades after Darwin's (1859) *Origin*, selection was extended to learned behavior by Thorndike (1898) in his Law of Effect: "Of several responses made to the same situation, those which are accompanied or closely followed by satisfaction to the animal will, other things being equal, be more firmly connected with the situation, so that, when it recurs, they will be more likely to recur." This formulation includes all three components needed to complete an analogy with Darwin's natural selection: variation ("several responses made to the same situation"), differential consequences ("satisfaction"), and the differential subsequent reproduction of variants ("more likely to recur") depending on those consequences (cf. Cumming, 1999). B. F. Skinner's work was influenced in part by Thorndike's formulation. Skinner (1953) went on to clarify and expand the role of selection in the production of behavior, examining behavior on its own terms and without appeals to physiology (Catania, 1999), and proposing three levels of selection: phylogenetic, ontogenic or operant, and cultural (Skinner, 1966, 1981). Behavior is a function of contingencies operating over phylogenetic time, of the differential consequences of behavior within an individual lifetime, and of the contingencies set up by social environments.

This view defines behavior not by its topography or its overtness, but by its relation to antecedent and subsequent environments. Neurophysiological accounts of behavior can be valuable, but to the extent that they leave out the relevant environmental interactions, these important properties of behavior cannot be reduced to neurophysiology (cf. Krakauer et al., 2017). Just as a table cannot be seen as a table once it has been reduced to the mere molecules of which it is composed, behavior cannot be seen as behavior once it has been reduced solely to its constituent neuronal firings and muscular twitches; we find the significance of both cases in their environments. Attributing behavior to inner causes while neglecting initiating events in an organism's environment is a bit like attributing the movement of traffic to the drive

trains and differentials, the ignition systems and tires, and the fuel and batteries that make up automobiles while omitting drivers and road conditions.

On the Nature of Contingencies

What gets selected is determined by the contingencies of selection. At each level of the selection of behavior, the contingencies include three terms: antecedents, responses, and their consequences given those antecedents. Behavior is defined in terms of its relation both to discriminative stimuli, stimuli that precede its emission, and to its consequences. All behavior occurs in some context, and phylogenic and ontogenic selection differ in how contexts exert control over the evolution of behavior or, in other words, in how they shape behavior. Phylogenic behavior is insensitive to its immediate consequences, though primitive forms presumably had longer-term consequences in terms of the reproductive success of ancestral organisms (Robinson & Barron, 2017). We observe behavior attributable to phylogeny when selecting contingencies are stable over ancestral history. A human pupil dilates in darkness because of a long history in which this stimulus-bound behavior conferred a reproductive advantage. Ontogenic or operant behavior, on the other hand, is controlled by its consequences from moment to moment within an individual lifetime.

At a third level, that of cultural selection, a significant portion of the behavioral repertoire of an individual depends on behavior acquired from others. For the individual, this is also part of ontogeny, though the differential reproduction and transmission of behavior from individual to individual in a group or culture depends on different contingencies than those that engender operant behavior. Cultural transmission allows for adaptive behavior that has not been shaped by direct contact with relevant contingencies, as when, in verbal governance, a child learns to follow instructions. A child whose behavior depends on verbal contingencies may, for example, avoid aversive outcomes by following the verbal behavior of others; reaching into a hot oven will be punished by its natural consequences, but a child with an appropriate verbal history may not reach at all if a caregiver says, "Stop or you'll get burned!" In such cases, we must look to the contingencies that select relevant verbal behavior as well as the contingencies that select the nonverbal behavior to which it relates. Contingencies at one level of selection may support those at another level, but they may also oppose each other, as when the short-term ontogenic effects of an addictive drug may select drug-taking during pregnancy, with the long-term phylogenic effect of reducing the fetus' viability. In the military, the life-threatening physical contingencies on a battlefield conflict with the social contingencies that maintain the following of orders. Selection in either phylogeny or ontogeny may be affected in turn by supporting or opposing cultural contingencies.

When natural Darwinian processes select morphological or behavioral features, relevant consequences are couched in terms of differential reproductive success. The *fitness* of an organism directly reflects the degree to which the organism reproduces (or, alternatively, the degree to which the organism's genes successfully replicate themselves via the vehicle of the organism). Fitness is not an explanation for reproductive success, but instead a term that encompasses it. Structural adaptations may make organisms more likely to reproduce via different forms of natural selection. Familiarly, particular characteristics (behavioral or otherwise) in a prey animal species may make it less likely to be attacked and eaten by a predator; camouflage is one example of a feature that evolved many times by virtue of this form of selection. On the other hand, a feature that increases the conspicuousness of an organism (and presumably the likelihood of its being preyed upon) may be selected by virtue of its direct relationship to reproductive success, in the form of sexual selection. The bright pigment of male songbirds, the details of the peacock's tail, and behavior one might call *bold* are all examples of such characters. Females of some species may be disposed towards mating with males that express features that appear incompatible with the male's fitness. This goes to show that natural selection is not concerned with *survival* per se, no matter its traditional and still-common misconception as "survival of the fittest" (Spencer, 1864, p. 444). Only insofar as survival is correlated with reproduction will this be true. In many species (e.g., salmon, some spiders, praying mantises), individuals mate only once and then promptly die. Invariably, these species

produce plentiful offspring from a single reproductive opportunity. Strictly speaking, contingencies of reproduction are the stuff of phylogeny and are *not* contingencies of survival.

When behavior is strengthened by some consequence in ontogeny, as when a rat's lever press produces food and then occurs more often, the response is said to be reinforced and the consequence is called a reinforcer. The seeming circularity of the definition of the reinforcer was once an issue: The phenomenon was itself used to define what qualified as a reinforcer. The apparent tautology provided no *a priori* means of identifying reinforcers and was troublesome for those advocating a selectionist account of behavior in ontogeny. Premack (1959) resolved the matter with the principle that the opportunity to engage in highly probable behavior can reinforce behavior that is otherwise less probable. Take, for example, a rat below its free-feeding weight. All else equal, if given food the rat is likely to eat; if it also has access to a lever the odds are that it will eat rather than press the lever. Now if an opportunity to eat depends on pressing the lever, the probability of lever pressing will increase. One way to identify reinforcers, therefore, is to weigh the relative likelihoods of the response to be reinforced (here, lever pressing) and the responses that become available as its consequence (here, eating). Given its relatively low probability, lever pressing is unlikely to reinforce eating, but as many parents know, the opportunity to eat highly preferred foods can be used to reinforce the eating of those less preferred. To the extent that probabilities are reversible, so too are reinforcers and the responses they reinforce. For example, depending on whether a rat has been deprived of food or exercise, the delivery of food may reinforce running in a wheel or the opportunity to run may reinforce eating (Premack, 1962).

On the Shaping of Phylogenic Behavior

Skinner (1975) clarified how phylogenic shaping contributed to the migratory behavior of the green turtle (*Chelonia mydas*), which travels more than a thousand miles from its feeding sites to breed at a tiny island in the middle of the Atlantic Ocean. In ontogeny, behavior can change quickly; a trainer skilled in working with pigeons can use reinforcers to shape an arbitrary response like turning in a circle in just a few minutes. But making sense of phylogenic origins depends on taking stock of a lengthy geologic history. Ancestral turtles had a far smaller gap to traverse 150 million years ago. The gap increased gradually as the sea floor spread, so subsequent generations of turtles had to travel only slightly further than their ancestors. A similar account applies to the navigation of the eel (*Anguilla anguilla*), which travels approximately 12,000 miles as a part of its life cycle. "As with the green turtle, it is hard to believe that this extraordinary behavior could have arisen from natural selection under present environmental conditions. But if the distances were at first short, and if they increased *no more than a few inches each generation*, as the theory of continental drift implies, then some members of each generation could have satisfied the new contingencies and bred to transmit the behavior" (Skinner, 1975, p. 118, emphasis in original).

Behavior that would be prohibitively unlikely to emerge spontaneously as a complete unit may thus come about as the product of a lengthy, iterative process of natural selection. Skinner suggested this form of shaping over geologic time as a plausible means by which such "instinctive" behavior may be built by consequences, though he declined to speculate on any mechanism of heredity. More than a decade later, Tierney (1986) similarly suggested that hardwired instincts may have foundations in the behavioral plasticity of ancestors, but, like Skinner, did not specify a plausible mechanism of inheritance by which such a transformation could occur. The investigation of epigenetic processes (i.e., heritable changes in gene function that do not depend on changes to the DNA sequence) has led to the suggestion that the same cellular and molecular mechanisms may explain *both* instinct and learning, with epigenesis as their link: "Evolutionary changes in epigenetic mechanisms may sculpt a learned behavior into an instinct by decreasing its dependence on external stimuli in favor of an internally regulated program of neural development" (Robinson and Barron, 2017, p. 27). This sculpting calls for selection by both reproductive and reinforcing consequences over evolutionary time, with a gradual shift in the control of behavior from recent and prevailing contingencies to ancestral ones. Counterintuitively, this implies that initially plastic behavior comes first, and becomes innate only later over generations of selection.

On Shaping in Ontogeny

Complex sequences of behavior are improbable and do not ordinarily emerge as a whole without simpler antecedents. Skinner discovered a way in which ontogenic contingencies could bridge the gap between simple and complex instances (Peterson, 2004). In shaping by successive approximations, reinforcement initially depends upon an action only remotely resembling the target response. From that point, behavioral mutations more and more closely resembling the target response are reinforced until the target response occurs.

The contingencies that govern the development of complex behavior in organisms are analogous to those that govern the development of complexity in species. Darwin was famously inspired by the success of selective breeding programs in the production of novel forms of organisms (e.g., modern dog breeds). His primary insight was that natural contingencies could similarly create change. The “artificial” directed shaping of behavior (e.g., as in the training of service dogs) is analogous to selective breeding as it occurs in animal husbandry or in horticulture (Catania, 1995). As with phylogenetic evolution, behavior may be shaped by either natural or artificial contingencies. This argument in terms of functional relations is similar to Darwin's arguments in support of evolution. But like Darwin's arguments and despite relevant experimental support (e.g., Epstein, 1981), it is still often rejected, especially for verbal behavior and for behavior commonly called insightful or creative.

The development of echoic behavior, in which a person repeats another's verbal behavior, depends on the shaping of articulations by their consequences (Skinner, 1957, p. 58). Long before infants express differentiated vocal behavior, they discriminate between sounds in their native language from those in unfamiliar ones (Mehler et al., 1988). This suggests a means by which children's vocalizations may be shaped, as their own production of familiar sounds may be differentially reinforced (Friedlander, 1968); without relevant consequences (as with the hearing-impaired), this behavior does not develop. Just like with other forms of behavior, complexity in vocal behavior increases in development. The babbling of infants initially reflects simple stress patterns of speech. This is followed by vowel sounds and then consonants, beginning with the ones easiest to produce (Vihman, 1996). Only after these repertoires have developed do children begin to produce echoic speech.

On the Evolution of Cultural Practices

Cultural selection is the third level of selection by consequences, but it is not concerned with the survival of cultures. The unit of selection is again critical (cf. Stahlman & Leising, 2018), and Skinner's approach evolved from one concerned with cultural practices to one concerned with the differential survival of classes of behavior as they are passed from some members of a group to others. Cultural practices may contribute to the maintenance and growth of a group, but practices may propagate through a group that are deleterious with respect to group survival. For example, a culture can be progressively undermined by widespread drug abuse. Furthermore, at this third level of selection practices can spread across cultures as well as within them. For example, ethnic food preparation does not respect cultural boundaries, be they geographic or political.

One way for behavior to be passed from one individual to another is imitation. Though imitation occurs in other species, it is especially common in human behavior, and presumably was itself selected over the course of human cultural evolution. Individuals who imitate others are likely to make direct contact with the same consequences or contingencies of reinforcement that originally engendered the behavior that is imitated (e.g., Laland & Rendell, 2013). Once imitation has been reinforced in specific instances, selective contingencies can shape imitation as a generalized class, with duplication of novel instances of a model's behavior (Baer, Peterson, & Sherman, 1967). Once this has happened, organisms (e.g., humans) are in a position to acquire adaptive behavioral repertoires that are very large in comparison to those of organisms that do not imitate.

Imitation is a variety of replication in which behavior is passed on from some individuals to others. Dawkins (1976) coined the term *meme* as a unit of cultural selection propagated across a population of social organisms. Successful memes make more copies of themselves, just as genes do. Dawkins (1982) and others have argued that each form of replicator (e.g., the gene, the meme) has an

independent existence in which it seems to work for its own selfish self-interest. But the meme might best be regarded as a unit of behavior, most obviously manifested in verbal behavior. Some common memes would then be prevalent verbal units, selected as such in the course of human social interactions. For example, the phonemes of different human languages are units of vocal behavior passed on from speakers to listeners both within and across generations.

If the emergence of language was part of the evolution of our hominid ancestry, it must have depended on this third level of selection. "The human species took a crucial step forward when its vocal musculature came under operant control in the production of speech sounds. Indeed, it is possible that all the distinctive achievements of the species can be traced to that one genetic change" (Skinner, 1986, p. 117). This account of language posits a plausible origin for language while embracing the position that verbal behavior is not fundamentally distinct from other, nonverbal, behavior: it too arises as a function of selection by consequences. It is unique not because of structural characteristics (e.g., grammar), but because its consequences are brought about through social contingencies within a verbal community.

On Boundaries

"It is inevitable that a continuous process like evolution should raise the question of boundaries. Systems for the classification of species are attempts to solve one problem of that kind. At what point can we say that man first appeared on earth? ...there was presumably no point at which an essence of man came into existence" (Skinner, 1986, p. 121). From early on, Darwin too was concerned about boundaries, and expressed his dissatisfaction with species as essential categories: "From these remarks it will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, and for mere convenience sake" (Darwin, 1859, p. 52).

Variation and selection not only accommodate adaptation at each of three levels (phylogenetic, ontogenic, and cultural), but also are relevant to the formation of boundaries at each level. In cell biology, such boundaries may develop as cells differentiate from primitive forms (i.e., stem cells) and take on specialized functions; when regions of different types of cells are adjacent to one another, boundaries form between them. "First, a tissue is subdivided into compartments.... Subsequently, short-range signaling between compartments establishes compartment border cells, and then long-range signals emanating from the compartment border cells regulate the further growth and patterning of the tissue" (Irvine & Rauskolb, 2001, p. 191). The outcome is bounded regions of tissue subserving distinct functions in the behavior of the organism (Kiecker & Lumsden, 2005).

At the ontogenic level, differential contingencies can establish boundaries between operant classes, as when a pigeon's pecks during a green stimulus produce food but those during red do not. We must deal not only with what separates one class from another, in the speciation of behavior classes, but also with what holds the responses within a single class together (Keller & Schoenfeld, 1950). We must examine how classes can intersect and nest within other classes in higher-order relations. Behavior classes are created by common contingencies. That has implications not only for arbitrary classes but also for classes that seem structurally constrained by sensory capacities and/or properties of the environment. Both types of classes necessarily involve common contingencies, and the evidence forces the conclusion that, as in the analogous Darwinian account, behavior structure is a derivative of selection (Catania, 1996).

For example, as an operant class a hungry rat's lever presses are not distinguished by whether it presses with one paw or two, or with great or reduced force, or with nose or rump. The topography of any instance is unique but of secondary relevance. The consequences of pressing the lever are what matters in defining the class. If pressing produces food, the rat will be more likely to press again. The shared contingencies bind all effective presses into an *operant class*. Consider now a behaviorally challenged child who gains attention by self-injury or by shouting obscenities, along with several other variants of attention-getting behavior. The behavior therapist who fails to recognize that each is a member of a single class of attention-getting and instead assumes a boundary exists between these classes may try, probably

without success, to treat just one or just the other. Identifying the boundaries between classes and the contingencies that may create them or break them down is a critical component of behavior analysis.

Selectionism is in Opposition to Traditional Causal Modes

Selection as a causal mode does not depend on agencies or mechanisms, unlike many traditional formulations of causality as pertaining to organisms. One may call selection “bottom-up,” in that complex phenomena are built progressively from simpler successful antecedents, each of which had been shaped by selection by consequences. In this sense, the internal economy of the organism is a product rather than an originating cause. An organism’s structure does not explain its behavior. Instead, current behavior is caused by (is a function of) historical contingencies more properly regarded as the “causes” of current behavior. Substituting *function* for *cause* distinguishes a selectionist account of behavior from traditional causal accounts. This framing also implies that behavior is often, perhaps usually, multiply caused, rather than depending on a particular singular antecedent. “Selection is a special kind of causality, much less conspicuous than the push-pull causality of nineteenth-century physics, and Darwin’s discovery may have appeared so late in the history of human thought for that reason. The selective action of the consequences of behavior was also overlooked for a long time” (Skinner, 1972/1999, p. 399).

In biology, both structure and function both came to be seen as derivatives of selection, each reciprocally constrained by the other. Locomotion, for example, is jointly determined by common functions (e.g., capturing prey, escaping predators) and by structural limitations arising from differences in vertebrate and invertebrate body plans (e.g., muscle configuration, number of limbs), themselves the products of long phylogenetic histories.

One implication of selection as the source of complex adaptations is that acts of special creation become less plausible as worthwhile explanations. Darwin (1859, 1871) was well aware that his work would have ramifications for our understanding of ourselves, and scholars since Darwin have recognized that great leaps in scientific progress have often brought with them the diminution and displacement of our place in the universe. In showing how interlocking and complex systems could emerge naturally from more primitive forms, Darwin’s theory unseated us from our privileged place in the natural world. “The Copernican revolution was resisted at least in part because it eventually forced us to see our world not as the center of the universe but as a small planet in orbit around a minor star. The Darwinian revolution raised similarly troubling questions about our biological origins” (Catania, 1992, p. 152). Where we have natural explanations for physical phenomena, there is no room for the miraculous. A through-going selectionism accounts for all of biology and behavior in terms of in-principle observable features of the natural world.

These considerations make the case for unifying the sciences of behavior and biology. The common and indeed fundamental element of each is that environments determine the production of forms. Behavior takes place and has consequences against this backdrop. While there have been many suggestions about how environments relate to phylogeny, Darwin’s theory of evolution by natural selection remains mostly unscathed as the most elegant explanatory framework for biology. Once a small number of criteria have been met, evolution of form must occur over phylogenetic time. The power of selectionism is further illustrated by the production of novel forms during an individual lifetime, and in the evolution of cultures. Complexity in both biology and behavior emerges as the necessary product of a class of contingencies. In biology, these contingencies ultimately relate to the consequential reproductive success of organisms. In behavior, the relevant contingencies are those of reinforcement, in which forms of behavior are differentially reproduced by virtue of their consequences in the life of an individual. The evolution of behavior within lifetimes is itself necessarily an evolved characteristic that came about because it contributed to the reproductive success of ancestral organisms. Therefore, behavior and modern biology are properly subsets of a greater science.

SEE ALSO:

ECAD00001, ECAD00002, ECAD00027, ECAD00029, ECAD00061, ECAD00064, ECAD00070, ECAD00078, ECAD00079, ECAD00093, ECAD00094

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