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The Coelacanth Still Lives: Bringing Selection Back to the Fore in a Science of Behavior

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There is little scientific debate regarding the validity of Darwin's theory of evolution by natural selection, which effectively describes how relevant ancestral histories produce both an organism's genetic characteristics and innate behavioral repertoires. The combination of variation and selection in the production of novel forms can be extended beyond Darwinian theory to encompass facts of ontogeny. The present article sheds light on an underappreciated and critical insight, namely, that the consequences of behavior have a selective effect analogous to that observed in biological evolution. Three levels of environmental selection (phylogenic, ontogenic, and cultural) constitute a full account of the causes for action. This perspective identifies the relevant functional contingencies of which behavior is a product, it accurately and parsimoniously predicts a wide variety of disparate behavioral findings, it resolves old debates on nativism and empiricism, it unites psychological science under a central organizing principle, and it specifies psychology's position in relation to biology. Wholesale adoption of this perspective should be considered a positive advance for the field of psychology.

Keywords: behavior, evolution, nature and nurture, selection, unification of psychology

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The coelacanth (genus *Latimeria*) is a lobe-finned fish that has been referred to as a *living fossil*, a term for organisms that have physically changed little in many millions of years. Long believed to have gone extinct alongside the dinosaurs at the end of the Cretaceous period, a living specimen was caught by commercial fishermen in 1938 off the coast of South Africa. A common term for organisms like these, discovered alive after being presumed extinct, invokes resurrection: They are called *Lazarus species*.[1] Pulling a living coelacanth out of the water on that day was the piscatorial equivalent of a crop-duster encountering a Pteranodon in the skies over Kansas. In recent decades, technological advancement has allowed for human beings to observe living coelacanths in their natural habitat. As feeding, reproducing, living, breathing organisms, they are and have been relevant in an understanding of modern Earth's biosphere. Scientists have been able to study the biology and behavior of the living coelacanth as a subject and not merely a historical footnote (e.g., Fricke et al., 2000).

Educators teach students that science marches forward. Students are taught that old ideas, once found to no longer be relevant, can be shelved away as historical curiosities. Thus spins a narrative of inexorable progress, of each day bringing scientists to a more complete understanding, and for human beings to be increasingly less wrong about the nature of the universe. This reassuring story holds that as an essential part of the process, scientists adopt new and more accurate views of the world as needed to accommodate the data. Outside the classroom, however, many justifiably doubt that this is what actually happens. Famously, Planck was said to have quipped that science advances one funeral at a time (for recent validation of this, see Azoulay, Fons-Rosen, & Zivin, 2015). Ideas, scientific or otherwise, gain traction not merely as a function of the degree to which they accurately reflect reality but also as a function of various human cultural factors that are inimical to the investigation of the natural world. Therefore, one must conclude that *coelacanthish ideas* are not merely possible but probable.

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[1] Lazarus is a biblical character whom Jesus is said to have raised from the dead.

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Essential scientific formulations may remain below the surface, still relevant, still useful, and still valid, despite a widespread belief in their long-ago extinction.

Many psychological researchers have prematurely declared an important scientific idea to be extinct. The idea is this: that relevant contacts with an external environment are the decisive causal events of interest with respect to all organismal behavior. This idea has important implications for two central issues in psychology. The first is the entropy of explanation in modern psychological inquiry. There are no widely accepted general principles by which scientists may be brought to understand "the mind" and all behavior. Different subdisciplines thus develop and investigate their own paradigms, models, and theories, many of which are necessarily in mutual conflict (e.g., Beckers, De Houwer, & Dwyer, 2016). One might erroneously conclude that these fields of inquiry were each examining fundamentally different organisms. Psychological scientists have suggested that different frameworks are required to study and explain particular facets of human behavior (McNally, 1992; Sternberg & Grigorenko, 2001). However, the philosophical position that a single, parsimonious account of organismal behavior is both possible and worthwhile cannot be easily dismissed. Second, an environmental analysis both clarifies and provides a final verdict in the long debate between nativism (i.e., "nature") and empiricism (i.e., "nurture"). A proper analysis unifies nature and nurture under a single causal process of environmental selection. The only important distinction is that the former refers to environmental selection in an organism's ancestral line, whereas the latter references selection in environments within which the individual has lived. Multiple levels of environmental selection (e.g., Sober & Wilson, 1998), comprising phylogenic, ontogenic, and cultural functional contingencies, are the ultimate explanation for behavior.

In presenting a positive argument for selectionism as the central process in the subject matter of psychology, this article addresses these long-standing concerns. It therefore favors an approach that involves bringing greater numbers of physical phenomena under fewer explanatory umbrellas. As Uttal (2007) stated,

> Science must be orderly and, by implication, converging. That is, science must proceed from the aggregation of a large number of observations to a small number of general and synoptic principles summarizing the meanings of those observations . . . some success must be achieved in finding universal rules that help us to understand and explain. (p. 33)

For various reasons, scientific psychology has not yet seen a convergence in terms or in an overall theoretical approach (see, e.g., Blumberg & Wasserman, 1995; Schlinger, 2004; Staats, 1999; Wynne, 2007) found in other sciences. The following details an approach to psychological science that fulfills this demand and, in so doing, places psychology firmly beside biology by virtue of a shared (between-disciplines) and unifying (within-discipline) process.

Selection in Biology

Charles Darwin's (1859) enduring contribution was his theory of evolution by natural selection. Inspired in part by results of "artificial" breeding programs and bolstered by countless careful observations of the natural world, Darwin famously came to argue that environmental selection plays the critical role in the evolution of form. If phenotypic traits are (a) distributed unevenly across a population and are (b) at least somewhat heritable, and if (c) *an organism's relative likelihood of reproduction is dependent on its interactions with a resource-limited environment*, it holds that (d) phenotypic variability in any population of organisms is a function of the degree to which traits have been positively related to reproductive success. Though this is now standard narrative, in the decades after the publication of Darwin's *Origin of Species* there were many challenges raised regarding the validity and the importance of natural selection as the central process in speciation. This Darwinian eclipse (Bowler, 1983) saw other evolutionary mechanisms gain support before the formulation of the modern evolutionary synthesis of natural selection and Mendelian genetics (Huxley, 1942; Mayr & Provine, 1998), a paradigm that has continued to dominate biological science.

Darwin scrawled, "Nothing for any purpose," on the back of his Red Notebook, which he carried during the auspicious voyage of the *Beagle* (Darwin, 1837/1987, p. 81). Though many are tempted to discuss the purpose of, for example, beaks and eyes, it is critical to recognize that no biological feature is *for* anything. Characteristics exist because of

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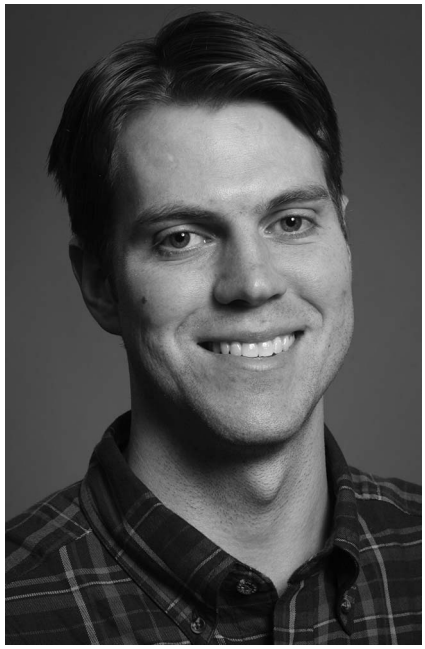

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particular histories wherein ancestral qualities were generated, shaped, and extinguished by differential reproduction over generations. What was once considered indicative of purpose is revealed, in a naturalistic universe, to be a product of utter mindlessness. Darwin's *Origin* may have been a final, definitive, and negative answer to the scientific question of purpose in the natural universe, but this requires an extension of evolutionary thought beyond biology. Indeed, Darwinian-style selection has been usefully applied to varied topics, as far-flung as immunology (Hull, Langman, & Glenn, 2001), prejudice (Neuberg & Schaller, 2016), economics (e.g., De Vany & Walls, 1996), and literary analysis (Moretti, 2013). To begin to understand how a selectionist account of behavior marginalizes the notion of purpose in psychology, we first review the selective contingencies that characterize the ancestral history of organisms.

Relevant Contingencies in Phylogeny

The products of Darwinian evolution are products of a class of functional relationships in which environmental variables determine the value of a particular variable of interest (e.g., genomic structure). These relationships are the *contingencies of reproductive success*, or more simply, the *contingencies of reproduction.* The "value" (i.e., fitness) of a phenotype is contingent on the environment in which it is expressed. Reproduction is itself a product of the relation between phenotype and the environment, where the environment plays a selective role in that it determines which characteristics are favored to reproduce. For example, a mutation that results in a patch of light-sensitive tissue on an organism has no value apart from the reproductive advantage that it may provide in an environment where visible light is a feature.

It is instructive to consider speciation in the context of environmental determination. Branching of the evolutionary tree represents points at which subpopulations of ancestral species became reproductively isolated. A diverse range of environments will, with time, differentially select for a great diversity of morphological and behavioral characteristics in organisms. To the large extent that genotype correlates with these characteristics, it too will reflect environmental selection. An examination of an organism's genotype is thus unavoidably the examination of the effects of ancient environments on the organism's ancestors. Though the unambiguous identification of historical environmental events and their impact is difficult (e.g., DePalma, Burnham, Martin, Rothschild, & Larson, 2013; Ruxton & Houston, 2003), the challenge of arriving at unequivocal answers to questions of origins should not preclude the scientist's conviction that these answers must lie in the ancient environments that gave rise to species.

Phylogeny and Behavior

An animal's behavioral repertoire is substantially a product of the contingencies of reproductive success in the lives of its ancestors. "Innate" behavior falls into this category in all its guises: reflexive behavior (e.g., Sherrington, 1906), unconditional responses (Pavlov, 1927/2003), modal action patterns (e.g., Barlow, 1977), imprinting (e.g., Bateson, 1966; Lorenz, 1937), and instinctual (e.g., Beach, 1955; Tinbergen, 1951) behaviors are included as variants on a theme.

The newborn duckling imprints on and follows the first large moving object it sees, typically its mother, by virtue of its ancestral history. Newly hatched sea turtles struggle across the sand toward the surf by virtue of their collective ancestry. The seemingly clever behavior of a web-building spider is a sort of "ancestral memory" (Robinson & Barron, 2017, p. 27) rather than anything any particular spider learned to do. Spiders build webs because of a history in which web-building was favored and shaped in ancestral environments by virtue of differential success in predation (Blackledge et al., 2009; Staddon, 1983). Though the strength of such innate responses may be modified with experience (e.g., Carew, Pinsker, & Kandel, 1972), whether they are performed is not primarily the result of a personal history. It is worth noting that there are individual differences even in the production of phylogenic behavior; given appropriate environmental conditions, this variation could serve as a substrate for evolutionary change.

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An organism's so-called nature is a necessary product of iterative environmental selection over generations in an ancestral line. Contingencies of reproductive success are the primary functional relations that account for the diversity of species. This way of framing the issue of nature raises an important question. If nature is the product of contingencies of reproduction, is there an identifiable class of functional relations that constitutes nurture?

Selection in Ontogeny

Darwin is as important a figure in the behavioral sciences as in the biological, principally because he discovered a means by which varied and complex effects could be explicated in terms of a simple, undirected, and natural process. The process that Darwin highlighted was, of course, environmental selection, and there is no reason at all that it should be confined as a powerful mechanism in only the origin of species. Instead, it should be critical in any situation where units of any kind differentially reproduce with variation. As Blackmore (2000) explained,

> 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)

It is often said that behavior is strengthened through reinforcement (e.g., Skinner, 1974, p. 44), but this formulation renders opaque the important parallel to biology. Much like phylogenic selection determines the reproduction of morphological traits in future generations, ontogenic selection determines the reproduction of behavioral variants over the course of an individual's lifetime. Under conditions similar to those past, *reinforced behavior is reproduced with variation* (Donahoe, 2003; Skinner, 1935). Reinforcement produces unique descendants of the reinforced behavior (Epstein, 2015). For example, if golf swings of force *X* are reinforced to a greater degree than are other variants, there will be a selective effect manifest as an increased reproduction of responses about the topography specified by *X* as well as a reduction in variation across all possible responses in the class. By virtue of their consequences, certain behaviors become more commonplace in the repertoire of the organism, whereas others remain improbable or become extinct.[2] Recent work has indicated that behavioral variability is so controlled by reinforcement histories, with greater variability linked to a relevant history of low reinforcement (Stahlman, Roberts, & Blaisdell, 2010). Researchers have contended that behavioral variation and innovation are vital for adapting to novel and changing environmental circumstances (e.g., Chappell et al., 2015; Neuringer, 2004; Stahlman, Leising, Garlick, & Blaisdell, 2013), in much the same way that biological variation functions in species.

As contingencies of reproduction determine the rate of occurrence of morphological and innate behavioral traits of species, so too do the ontogenic contingencies produce the learned behavioral repertoire of the individual. The relevant consequences for acquired behavior are identified as reinforcers (e.g., Skinner, 1974). *Contingencies of reinforcement* thus represent the second relation of which organismal behavior is a function. In the laboratory, these contingencies can be instantiated in various *schedules of reinforcement* (Ferster & Skinner, 1957), prescriptions for the delivery of reinforcers upon the performance of some behavior. These schedules produce highly consistent effects across a wide variety of evolutionary taxa (Skinner, 1957a).

The "fitness" of a behavior is thus dependent on the environment in which it is expressed, with the propagation of particular behavioral forms being contingent on their relation to consequences in the environment. The process and role of the environment is thus equivalent to that in contingencies of reproduction, but the nature and timescale of selection differs. Whereas Darwinian natural selection operates on variation within populations of organisms, ontogenic selection operates on variation within populations of behaviors in an individual. In Darwinian natural selection, organisms are shaped by contingencies both natural and "artificial" (as in selective breeding); similarly, both natural and "artificial" contingencies shape ontogenic behavior (see, e.g., Catania, 2001; Glaser, 1990; Peterson, 2004; Skinner, 1953). Just as one can examine the morphology of an organism and make inferences regarding the nature of the controlling selective features of its ancestral environments, one's observations of an organism's behavior allow for inferences regarding its developmental environment.

Behavior comprises physical units that differentially and imperfectly replicate by virtue of their relation to an external environment. There are many advantages to this perspective. For one, it distinguishes the effect of reinforcement from traditional stimulus−response theories of learning (e.g., Hull, 1930). It emphasizes an approach to psychology in which explanations of behavior align more closely with biology than with physics. Finally, it describes behavior in terms that fulfill the necessary requirements for evolution's occurrence (Blackmore, 2000). Natural selection obviates purpose. Simple and undirected, it readily produces biological organization and complexity suggesting purposeful design. Selection by reinforcement does the same with ontogenic behavior; a naturalistic, bottom-up explanation displaces teleology in accounting for the com-

[2] Incidentally, it should not be thought accidental that the term *extinction* refers to the deaths of all members of a species as well as the abolition of a form of behavior (e.g., lever-pressing). A failure to replicate dooms both species and behavior.

plexity of behavior suggestive of purpose or volition (Neuringer, 2014).

Selection in Culture

Adopting a Darwinian approach to the evolution of culture has been advanced by many authors and has met with success (see, e.g., Alexander, 1979; Boyd & Richerson, 1988; Campbell, 1975; Mesoudi, Whiten, & Laland, 2006). *Cultural evolution* is often described as the manner in which ideas and practices spread between individuals in a population. This form of transmission characterizes social species. There are clear potential advantages, both to an organism and to its group, that one's behavior be a function of the behavior of others. An antelope that sprints away when it sees an approaching lion is likelier to survive; an antelope that does not see the approaching lion but runs because it sees a conspecific doing so is also likelier to survive (Skinner, 1984). In another case, imitation tends to bring one into contact with the same contingencies that control the imitated behavior (Laland & Rendell, 2013). Once imitation exists, selective contingencies would then be able to shape other behavior, like modeling. For example, adult humans speak in an exaggerated fashion when addressing preverbal children.

Just as definitions of phylogenic and ontogenic selection may be rephrased to emphasize the essential reproductive, functional contingencies of each, so too can cultural selection be reconsidered. Cultural evolution is the differential reproduction of cultural practices as it impacts the fecundity of the group.[3] Cultural variants that reproduce more effectively become the more prevalent. Absent this sort of replication, cultures suffer the same fate as that faced by, for example, nonreinforced behavior: extinction. Admittedly, the analysis here becomes even more challenging than at either the genetic or behavioral levels. Identifying particular cultural practices may not always be easy, and it may be challenging to identify groups (Campbell, 1958). We do not envy the difficulty of the evolutionary anthropologist's task. Nevertheless, one must be at ease with these sorts of fuzzy boundaries as they relate to practice—after all, though it may be facile to identify individual genes or particular instances of behavior, fuzzy boundaries necessarily surround that meant by words like *species* and *response class.* A thoroughgoing selectionist perspective acknowledges variation as a rule and denies the existence of categorical, essentialist boundaries on natural phenomena, including behavior (Palmer & Donahoe, 1992).

Verbal behavior made cultural transmission greatly more efficacious and thus should be considered a topic of central importance in understanding this level of selection. A behavioral account of verbal behavior is principally interested in the function of language (i.e., the effect[s] of a speaker's words). To avoid being burned, a child need not possess phylogenic "knowledge" that a hot oven is dangerous, though something akin to it might have emerged if ovens were a stable and ubiquitous part of the environments in which humans evolved. Likewise, a child need not have gotten burned to "have a memory" of the experience and thus avoid hot ovens, as would be demanded by ontogenic contingencies. And a child need not observe someone else being burned upon touching a hot oven. Instead, an individual can simply *tell* the child to avoid the oven. It is important to note that, of the distinct foregoing scenarios, *any* could result in a child's retreat. Culturally transmitted behavior enables the child to avoid physical harm.

Dawkins (1976) popularized the notion of the *meme*, a unit of cultural selection that may be propagated in the substrate of a population of social organisms. The suggestion is that memes emerge, multiply, mutate, and go extinct just like genes and behaviors do and are subject to selection in the same way. As such, successful memes act to produce more copies of themselves, acting in much the same way that successful genes do in the context of biological evolution. The concept of the meme is controversial. Critics have highlighted its lack of structure as one issue not applicable to the gene. For example, Richerson and Boyd (2005) defended their use of the term *cultural variant* rather than meme thusly: "Some authors use the term *meme* . . . but this connotes a discrete, faithfully transmitted genelike entity, and we have good reasons to believe that a lot of culturally transmitted information is neither discrete nor faithfully transmitted" (p. 63). The present article's argument does not depend on an adherence to the language of structural replicators. To the extent that they are natural phenomena, each replicator (i.e., gene, behavior, meme) is a product of its own class of causal contingency.

Conflict Between Levels of Selection

Whereas foundational scientists from competing radical behaviorist and sociobiological camps have agreed that culture is on the proverbial leash of the genetic endowment (cf. Naour, 2009; Skinner, 1981, 1988; E. O. Wilson, 1978), others have argued that replicators may behave independently from one another (Blackmore, 2000; Dennett & McKay, 2006; Richerson & Boyd, 2005). There is little reason to suspect that behavioral expressions of each of the classes of causal contingencies must be compatible with one another under prevailing circumstances. Campbell (1975) astutely noted, "The wisdom produced by any evolutionary system is always wisdom about past worlds, a fittedness to

[3] The long-standing debate in biology regarding group selection is relevant. It is beyond the scope of this article to fully address the controversy, but we note here that the idea of group selection has met with strong rhetorical and empirical support in recent decades (e.g., Bell, Richerson, & McElreath, 2009; Smaldino, 2014). For an excellent positive argument for group selection, see D. S. Wilson and Sober (1994).

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past selective systems. If those worlds have changed, the adaptations may no longer be useful" (p. 1106). A wide range of important experimental results and observed facts are explicable in terms of the three branches of the controlling environment (e.g., the origins of tepees, violin structure, and jockey behavior; Wasserman, 2012; Wasserman & Cullen, 2016). This suggests an assessment for behavior analogous to evolutionary mismatch theory (Nesse & Williams, 1994), which holds that differences between ancestral and contemporary environments explain a great deal of variance in modern health outcomes. For example, adult lactose intolerance is explicable in terms of the recency of agricultural practices and thus of the availability of milk past infancy as a source of nutrition.

A researcher may present organisms with circumstances wherein actions produced by contingencies of reproduction and of reinforcement, for example, are in mutual conflict. Because such discordances instantiate control of multiple, mutually exclusive actions, they are predicted to produce "conflicted," "uncertain," or "maladaptive" behavior. There is a vast literature indicating that this occurs. For pragmatic reasons, the following section emphasizes only a subset of findings particularly relevant to phylogenic and ontogenic levels of selection, though the reader may consider myriad examples wherein effects of cultural selection may be critical.

Misbehavior

Animals given presentations of a visual stimulus followed by a food item often begin to treat the predictive stimulus similarly to the food. This observation goes back to Pavlov (1927/2003), who observed that his dogs would salivate when given food or when predictors of food were available. This phenomenon includes conditioned approach behavior (Domjan, Lyons, North, & Bruell, 1986), autoshaping of key-pecking (Brown & Jenkins, 1968), and other responses. These behaviors, elicited by the predictive relationship between external stimuli, can be in conflict with those produced by contingencies of reinforcement. In other words, animals may exhibit phylogenic behavior that interferes with performance of ontogenic behavioral tasks.

In a classic example, a raccoon's behavior of picking up a pair of coins and dropping them into a metal box was reinforced (Breland & Breland, 1961). After first reinforcing the behavior of picking up coins, the researchers introduced the box. The raccoon spent minutes at a time rubbing the coins together and dipping, but not dropping, them into the metal container. This behavior was maintained despite being explicitly nonreinforced. Many similar examples of this "instinctive drift" (p. 684) have been observed across a wide variety of evolutionary taxa. Organisms have characteristic behaviors with respect to food and to its predictors. Establishing specific stimuli as reliable predictors for the delivery of food produces species-typical behavior that may be incompatible with performance of certain ontogenic behavior.

In the laboratory, a researcher can explicitly create scenarios in which the performance of a Pavlovian conditioned response *prevents* the delivery of a reinforcer. In one experiment, newborn cockerel chicks were required to run *away* from a bowl in order to acquire the food contained therein (Hershberger, 1986); even after many trials, the animals failed to retreat from the bowl on the majority of trials. In contrast, a group of chicks that could approach the bowl to feed succeeded upon nearly every opportunity. In another example, pigeons that receive trials wherein a lighted key reliably precedes food delivery typically begin to peck the key; they continue to do so even if doing so prevents food delivery (Williams & Williams, 1969; for an example in mammals, see Holland, 1979). These animals' failures to behave optimally are reflective of a conflict between the behaviors produced by each of two environmental contingencies. These experiments construct worlds unlike any the organism's ancestors had ever encountered. In general, animals have not been required to move *away* from food to consume it. An analogous hypothetical situation in humans would be requiring children to stay out of a kitchen in which their meal is being prepared. One can easily imagine the behavior that may arise, particularly as a child grows hungry and predictors of food (e.g., aroma) become more eliciting (Skinner, 1953, Ch. 9) of the punished behavior.

Impulsivity

A child sits at a table, upon which a single marshmallow is placed, and is instructed that it will be possible to have additional marshmallows only by refraining from eating the presented one until the experimenter returns. The experimenter then leaves the room for a short time. Children vary a great deal in their ability to resist temptation in this task. Though contingencies of reproduction may favor eating such an appealing morsel now (Critchfield & Kollins, 2001), the stated contingences of reinforcement may favor holding out for more (Ainslie, 1974; Monterosso & Ainslie, 1999). Because the two responses engendered by the contingencies are mutually exclusive, one should expect to see a great deal of "internal conflict" in the subjects.[4] And indeed, this is precisely what happens: Children twitch, fidget, tap their feet, cover their eyes, look up at the ceiling, and appear to be uncomfortable. Many fail to successfully wait for the prescribed time limit before eating. Nonhuman animals overwhelmingly fail as well, though there is at least

[4] Under this analysis, the conflict is not "internal" in the way usually meant. Any conflict is between contingencies external to the child. These may have internal effects, but nonetheless, understanding the behavior necessitates an analysis of the external conflict.

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one case in which a gray parrot successfully "passed" a form of the test (Koepke, Gray, & Pepperberg, 2015). It is both instructive and amusing to note that this parrot's behavior during a waiting period strongly resembled the behavior of children participating in this task (Mischel et al., 2011; Mischel, Shoda, & Rodriguez, 1989).

Stimulus Belongingness

In a classic case, Garcia and Koelling (1966) allowed rats to drink flavored water from a tube that, when licked, produced an audiovisual stimulus within the experimental chamber. Rats then received either the delivery of an electric footshock or the onset of nausea by irradiation. Subsequently, animals that had been shocked drank preferentially from tubes that yielded flavored water and not from ones that produced the audiovisual cue. Animals that had been made ill, however, exhibited the opposite preference. This result makes perfect sense in light of the competing contingencies of which organismal behavior is a function. Animals rapidly learn relationships that are similar to those from their respective phylogenic histories (Dunlap & Stephens, 2014). It seems clear that illness (i.e., by poisoning) has accompanied the consumption of novel foods in ancestral history. Similarly, it is reasonable to suspect that its ancestors encountered audio and visual stimuli that had been reliable antecedents of critical external events (e.g., predation). It is therefore unsurprising that the rats should avoid drinking from a tube that generates a predictive audiovisual stimulus previously followed by shock, an external threat.

Other documented forms of selective conditioning extend into social learning. In one example, naïve rhesus monkeys watched videos of adult monkeys reacting fearfully to either a snake or a flower. Subsequently, only monkeys that had seen the snake video displayed a fearful reaction to presentations of a toy snake; animals that had seen the flower video did not show fear in tests with a toy flower (Cook & Mineka, 1989, 1990). Again, this difference can be explicated in terms of the relevant events in the ancestral, environmental history of the rhesus monkey. It is advantageous to quickly learn to fear snakes but not flowers. If adaptive behavior can be learned in the absence of direct contact with a snake, all the better. This clearly applies to humans, with phobias of snakes and spiders more commonly reported than those of foliage.

Species-Specific Defense Reactions

Whereas highly complex and variable sorts of behavior are generated via positive reinforcement, behavior performed under aversive threat is restricted in scope. Species-specific defense reaction (SSDR) theory argues that organisms under threat exhibit a very limited behavioral repertoire—animals may flee, fight, or freeze (Bolles, 1970). However, one may establish experimental contingencies whereby other actions reduce threat to the organism. Such actions may be incompatible with the performance of any of the SSDRs available. Consider the following scenario. Rats in operant chambers receive presentations of tones, each followed by moderate electric shocks that are preventable by depressing a lever during tone presentations. These animals could conceivably prevent all shock deliveries—but they typically fail to acquire the lever-press response (Bolles, 1970; D'Amato & Schiff, 1964). Though the ontogenic contingencies alone suggest that lever-pressing during the tone should become commonplace, the tone as a signal for danger evokes a phylogenic response, freezing (e.g., Bouton & Bolles, 1980), which is incompatible with lever-pressing. Comparison animals do, however, quickly begin to avoid shocks when the target response is flight from the chamber (Maatsch, 1959). Fleeing from danger, unlike lever-pressing, is compatible with a prey animal's ancestral history. In humans, the emission of behavior due to contingencies of reinforcement may face interference from elicited SSDRs (e.g., Cannon, 1915). An argument may result in violence despite the punishing contingencies in place that oppose such behavior. The loss of status, resources, or a partner may result in aggressive behavior, though this aggression may be punished (e.g., by imprisonment). This may be related to why crimes of passion are judged less harshly than are premeditated violent acts—they are more obviously controlled by eliciting stimuli rather than by their consequences.

Parallels Across Levels of Selection

Because phylogeny, ontogeny, and culture are linked by the shared process of selection by consequences, one might expect that scientists should observe shared phenomena at each level. The present article has suggested that extinction may represent a common phenomenon in selectionist systems, but there are others of note. In particular, Skinner (1975) identified the contribution of shaping 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 (88 square kilometers) island in the middle of the Atlantic Ocean. To suppose that this behavior could have been formed by natural selection seems, we freely confess, absurd in the highest degree.[5] When one takes stock of a lengthy geologic history, however, the evolutionary origins become clear. As of 150 million years ago, ancestral turtles had a far smaller gap to traverse. This gap slowly and gradually increased as the sea floor spread, requiring subsequent generations of turtles to travel slightly

[5] We gratefully borrow from Darwin's (1859) words here regarding the evolution of the eye.

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farther than did their ancestors. This resulted in the modern turtle that travels enormous distances as a part of its breeding behavior. A similar explanation applies to the navigation of the European eel (*Anguilla anguilla)*, which travels approximately 12,000 miles as a part of its life cycle. Skinner wrote,

> 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. (p. 118)

Behavior that would be prohibitively unlikely to spontaneously emerge as a complete unit may thus come about as the product of a lengthy, iterative process of natural selection. Skinner suggested a plausible means by which such "instinctive" behavior may be built by consequences, though he characteristically declined to speculate on any specific mechanism of heredity involved. More than a decade later, Tierney (1986) similarly suggested that hardwired instincts may have foundations in the behavioral plasticity of ancestors, but like Skinner, he did not state a plausible mechanism of inheritance by which such a transformation could occur. Recently, though, increased focus on epigenetic processes has provided tantalizing possibilities regarding this matter. Robinson and Barron (2017) posited that the same cellular and molecular mechanisms explain *both* instinct and learning and highlight epigenesis as their potential link. They wrote, "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" (p. 27). Presumably, this sculpting would necessitate 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. Behavior that is initially plastic may thus become innate over generations (see also Levis & Pfennig, 2016).

The parallel here to the ontogeny of behavior should be clear. Improbable sequences of behavior generally do not emerge as a whole without simpler behavioral antecedents. A method by which complex behavior is produced is via *shaping by successive approximations* (e.g., Peterson, 2004; Pryor, 1999; Wasserman & Cullen, 2016), where reinforcement is delivered initially upon a probable action that resembles in a small way the target response; from that point, behavioral mutations that progressively resemble the target response are reinforced until the execution of the final response. The directed shaping of behavior (e.g., training protocols) is analogous to selective breeding programs that have produced, for example, modern dogs. The bottom-up production of a final, complex product is evidently the same.

Why Has Selection Been Thought Extinct?

The *coelacanthish*[6] ideas presented here have been disregarded by or are unknown to many prominent modern psychologists. It is worth noting that Skinner's articles specifically on the topics of selectionism and behavior (e.g., Skinner, 1966, 1981) were published well after the commencement of the "cognitive revolution." It is possible that researchers, having moved on from behavioristic grounds to explore vast landscapes of mind, were not inclined to take seriously Skinner's comments on selection. The possibility that a selectionist account "went down with the ship" suggests the need to reevaluate the merit of such an account on its own terms but also warrants recognition that Skinner's behaviorism has been and continues to be mischaracterized by leaders in psychological science (see Todd & Morris, 1992; Watrin & Darwich, 2012). Such common errors include asserting Skinner's behaviorism as being of a stimulus−response variant (e.g., Baron-Cohen, 2014; Dickinson, 1980; Wassermann, 1984), when it is not (Catania, 2001); asserting that Skinner was hostile to biology or to neuroscience (e.g., Pinker, 1999), when he was not (Morris, Lazo, & Smith, 2004; Zilio, 2016); or attacking his account (Skinner, 1957b) of verbal behavior from a profoundly mistaken position (e.g., Chomsky, 1959; see MacCorquodale, 1970, for a thorough refutation of Chomsky's famous critique). It is beyond this article's scope to fully explore these mistakes, but it is reasonable to acknowledge their existence and to recognize the possibility that hostility to Skinner's ideas in general may have impeded acceptance of a selectionist account of behavior in particular.

The view that organismal behavior is a necessary function of only environmental factors explicitly denies traditional, nonscientific formulations of human behavior. Ironically, in doing so, it may be more likely to be shunned by scientists (Wynne, 2007). This rejection seems reminiscent of the familiar theistic repudiation of Darwinian evolution (see, e.g., Dennett, 2009). Evidently, acceptance of selection as a causal process finds difficulties in multiple arenas (Donahoe, 1984). Even some of the more visible proponents of selectionism have failed to recognize its applicability in explaining human behavior. The codiscoverer of natural selection famously declined to apply the process to humans (Wallace, 1864). Darwin (1887/1898) himself wrote, "We can no longer argue, for instance, the beautiful hinge of the bivalve shell must have been made by an intelligent being, like the hinge of a door by man" (p. 279). In *The Blind*

[6] A reviewer pointed out that Skinner (1983, p. 308) himself introduced a similar metaphor to our own invoking the coelacanth. This fact had been unknown to the authors, who heartily agree with the reviewer's assessment that this appears to be an interesting example of convergent evolution.

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Watchmaker, Dawkins (1986, p. 5) wrote, "A true watchmaker has foresight: he designs his cogs and springs and plans their interconnections, with a future purpose in his mind's eye. Natural selection, the blind, unconscious, automatic process which Darwin discovered . . . has no purpose in mind." Our arguments here are that the "intelligence" of a hinge-maker, the "foresight" of a human watchmaker, the "plans," the "purpose in his mind's eye," are constructs improperly discussed as causes for the artisan's behavior. We concur with Wasserman and Blumberg (2010, p. 183), who wrote,

> Uncritical acceptance of purpose and foresight in human design may well be unwise . . . [designer] thinking rests on the familiarity and deceptive simplicity of mentalistic explanations of behavior, as when Dawkins uncritically appeals to the foresight and purpose of the watchmaker rather than entertaining possibly deeper questions about the origins of the watch.

The constructs so commonly invoked are, at best, imprecise structural surrogates for the historical and prevailing selective functional contingencies that generated the actions producing the watch (Wixted & Gaitan, 2002). Just like watchmaking itself, the artisan's felt experience of purpose must be explicable in terms of the relevant environmental contingencies.

In Summary, or, "Everything Is the Way It Is Because It Got That Way"

The quote in this section heading is attributed to D'Arcy Thompson, a 20th-century British biologist and Aristotelian scholar. It is an extraordinarily important idea referencing the path dependence of natural phenomena and thus succinctly asserting the basic role of history. Behavior is a complex but natural phenomenon that may be understood by adopting selectionism as a thoroughgoing explanation for *how things got this way*.

The framework presented in the present article represents the tidy unification of the sciences of life and behavior. Each of these is interested in the organism but separately investigates the fundamental historical relationships of which the organism's behavior is a function. Evolutionary change manifests when the environment selects for the differential reproduction of phenotypes (including behavior), whereas ontogenic behavioral change is characterized as the environment's selecting an organism's previously uncommitted behavior within its individual lifetime. The independent variables of which behavior is a function are environmental by necessity. The first cause is found in the contingencies of reproduction that yield the individual as a unique member of a species. The second cause of behavior is found in the contingencies of reinforcement that change an individual's behavior during its lifetime. Like phylogenic contingencies, the specifics surrounding experienced contingencies may be of a great many kinds, from primary consequences (e.g., food, water) to conditioned reinforcers (e.g., money) and the socially relevant outcomes (e.g., praise, prestige, blame, or ostracism) reflected in culture. A third cause of behavior is found in the cultural contingencies that differentially select for practices in groups of social organisms. That the behavior produced by any set of contingencies interacts with behavior produced by another set at another level is ultimately central to this view of organismal behavior.[7]

Scientific psychology can be unified through a formulation emphasizing environmental selection analogous to that of evolutionary theory. Adopting this scope necessarily brings all important findings in psychology under a common explanatory framework, inexorably joins together the enterprises of biology and psychology, and gives neuroscientists their proper research assignments (Donahoe, Burgos, & Palmer, 1993; Krakauer, Ghazanfar, Gomez-Marin, MacIver, & Poeppel, 2017). A natural science must ultimately be able to account for all psychological phenomena and may eliminate as causes of behavior constructs that are, in principle, unobservable (Catania, 2013; Uttal, 2007). Mental and neurophysiological correlates of overt behavior, if they are real phenomena, are themselves products of the same controlling historical and environmental features.

There is only a single, primary category of initiating cause for behavior, and that is the environment. Behavior is defined by its functional relationship to antecedent and postcedent environmental conditions. Therefore, the primary goal of psychological science should be in the examination of ancient, recent, and prevailing environmental contingencies and their effects. The collective rediscovery of and appreciation for the three levels of environmental selection should be invaluable to psychology. A return to an emphasis on these functional relations clearly identifies the boundaries of psychological science and crystallizes its

[7] Other approaches, it may be noted, have on occasion drawn near to this argument. Behavior systems theory (e.g., Timberlake, 1993; see also Burghardt & Bowers, 2017, and Krause & Domjan, 2017, for worthwhile synopses) posits the existence of organized systems, equipped with subsystems and modules, that are engaged for what one may call coarsely grained categories of behavior (e.g., feeding, predatory defense, reproduction). Activation of one system and its corresponding behavior interferes with the activation of others (and their corresponding behavioral repertoires). An animal under predatory threat is far less likely to engage in consummatory behavior than is an animal that is not. Another important field, evolutionary developmental biology (see West-Eberhard, 2003, for a comprehensive introduction), is similarly structural. A primary topic in evolutionary developmental biology is the role of specific mechanisms in influencing and constraining evolution (e.g., Brakefield, 2003). Though similar in certain respects, a principal difference in the present article's argument is its focus on assessment of the functional contingencies between behavior and environment, rather than positing internal mechanistic and hypothetical structural explanations for behavioral phenomena. Any such structures and systems, if natural phenomena, are the products of the three classes of contingencies relating behavior and environment.

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aims in the same manner as did Darwin's work did in biology. Such a development should be most welcome.

References

Ainslie, G. W. (1974). Impulse control in pigeons. *Journal of the Experimental Analysis of Behavior, 21,* 485–489. http://dx.doi.org/10.1901/jeab.1974.21-485

Alexander, R. D. (1979). *Darwinism and human affairs*. Seattle, Washington: University of Washington Press.

Azoulay, P., Fons-Rosen, C., & Zivin, J. S. G. (2015). *Does science advance one funeral at a time?* http://dx.doi.org/10.3386/w21788

Barlow, G. W. (1977). Modal action patterns. In T. A. Sebeok (Ed.), *How animals communicate* (pp. 98–134). Bloomington, IN: Indiana University Press.

Baron-Cohen, S. (2014). *Radical behaviorism*. Retrieved from https://www.edge.org/response-detail/25473

Bateson, P. (1966). The characteristics and context of imprinting. *Biological Reviews, 41,* 177–217.

Beach, F. A. (1955). The descent of instinct. *Psychological Review, 62,* 401–410. http://dx.doi.org/10.1037/h0049138

Beckers, T., De Houwer, J., & Dwyer, D. M. (2016). Reasoning versus association in animal cognition: Current controversies and possible ways forward. *Journal of Comparative Psychology, 130,* 187–191. http://dx.doi.org/10.1037/com0000024

Bell, A. V., Richerson, P. J., & McElreath, R. (2009). Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceedings of the National Academy of Sciences of the United States of America, 106,* 17671–17674. http://dx.doi.org/10.1073/pnas.0903232106

Blackledge, T. A., Scharff, N., Coddington, J. A., Szüts, T., Wenzel, J. W., Hayashi, C. Y., & Agnarsson, I. (2009). Reconstructing web evolution and spider diversification in the molecular era. *PNAS: Proceedings of the National Academy of Sciences of the United States of America, 106,* 5229–5234. http://dx.doi.org/10.1073/pnas.0901377106

Blackmore, S. (2000). *The meme machine*. New York, NY: Oxford University Press.

Blumberg, M. S., & Wasserman, E. A. (1995). Animal mind and the argument from design. *American Psychologist, 50,* 133–144. http://dx.doi.org/10.1037/0003-066X.50.3.133

Bolles, R. C. (1970). Species-specific defense reactions and avoidance learning. *Psychological Review, 77,* 32–48. http://dx.doi.org/10.1037/h0028589

Bouton, M. E., & Bolles, R. C. (1980). Conditioned fear assessed by freezing and by the suppression of three different baselines. *Animal Learning & Behavior, 8,* 429–434. http://dx.doi.org/10.3758/BF03199629

Bowler, P. J. (1983). *The eclipse of Darwinism: Anti-Darwinian evolution theories in the decades around 1900*. Baltimore, MD: Johns Hopkins University Press.

Boyd, R., & Richerson, P. J. (1988). *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.

Brakefield, P. M. (2003). The power of evo-devo to explore evolutionary constraints: Experiments with butterfly eyespots. *Zoology, 106,* 283–290. http://dx.doi.org/10.1078/0944-2006-00124

Breland, K., & Breland, M. (1961). The misbehavior of organisms. *American Psychologist, 16,* 681–684. http://dx.doi.org/10.1037/h0040090

Brown, P. L., & Jenkins, H. M. (1968). Auto-shaping of the pigeon's key-peck. *Journal of the Experimental Analysis of Behavior, 11,* 1–8. http://dx.doi.org/10.1901/jeab.1968.11-1

Burghardt, G. M., & Bowers, R. I. (2017). From instinct to behavior systems: An integrated approach to ethological psychology. In J. Call (Ed.), *APA handbook of comparative psychology* (Vol. 1, pp. 333–364). http://dx.doi.org/10.1037/0000011-017

Campbell, D. T. (1958). Common fate, similarity, and other indices of the status of aggregates of persons as social entities. *Systems Research and Behavioral Science, 3,* 14–25. http://dx.doi.org/10.1002/bs.3830030103

Campbell, D. T. (1975). On the conflicts between biological and social evolution and between psychology and moral tradition. *American Psychologist, 30,* 1103–1126. http://dx.doi.org/10.1037/0003-066X.30.12.1103

Cannon, W. B. (1915). *Bodily changes in pain, hunger, fear and rage*. New York, NY: Appleton.

Carew, T. J., Pinsker, H. M., & Kandel, E. R. (1972). Long-term habituation of a defensive withdrawal reflex in aplysia. *Science, 175,* 451–454. http://dx.doi.org/10.1126/science.175.4020.451

Catania, A. C. (2001). Three types of selection and three centuries. *International Journal of Psychology & Psychological Therapy, 1,* 1–9.

Catania, A. C. (2013). A natural science of behavior. *Review of General Psychology, 17,* 133–139. http://dx.doi.org/10.1037/a0033026

Chappell, J., Cutting, N., Tecwyn, E. C., Apperly, I. A., Beck, S. R., & Thorpe, S. K. S. (2015). Minding the gap: A comparative approach to studying the development of innovation. In A. B. Kaufman & J. C. Kaufman (Eds.), *Animal creativity and innovation* (pp. 287–316). http://dx.doi.org/10.1016/B978-0-12-800648-1.00010-3

Chomsky, N. (1959). A review of B. F. Skinner's *Verbal behavior*. *Language, 35,* 26–58. http://dx.doi.org/10.2307/411334

Cook, M., & Mineka, S. (1989). Observational conditioning of fear to fear-relevant versus fear-irrelevant stimuli in rhesus monkeys. *Journal of Abnormal Psychology, 98,* 448–459. http://dx.doi.org/10.1037/0021-843X.98.4.448

Cook, M., & Mineka, S. (1990). Selective associations in the observational conditioning of fear in rhesus monkeys. *Journal of Experimental Psychology: Animal Behavior Processes, 16,* 372–389. http://dx.doi.org/10.1037/0097-7403.16.4.372

Critchfield, T. S., & Kollins, S. H. (2001). Temporal discounting: Basic research and the analysis of socially important behavior. *Journal of Applied Behavior Analysis, 34,* 101–122. http://dx.doi.org/10.1901/jaba.2001.34-101

D'Amato, M. R., & Schiff, D. (1964). Long-term discriminated avoidance performance in the rat. *Journal of Comparative and Physiological Psychology, 57,* 123–126. http://dx.doi.org/10.1037/h0046678

Darwin, C. (1837/1987). Red notebook. In P. H. Barrett, P. J. Gautrey, S. Herbert, D. Kohn, & S. Smith (Eds.), *Charles Darwin's Notebooks 1836–1844* (pp. 21–81). Ithaca, NY: Cornell University Press.

Darwin, C. (1859). *On the origin of species*. London, United Kingdom: Murray.

Darwin, C. (1898). Religion. In F. Darwin (Ed.), *The life and letters of Charles Darwin* (pp. 274–286). New York, NY: D. Appleton & Co. (Original work published 1887)

Dawkins, R. (1976). *The selfish gene*. New York, NY: Oxford University Press.

Dawkins, R. (1986). *The blind watchmaker: Why the evidence of evolution reveals a universe without design*. New York, NY: Norton.

Dennett, D. (2009). Darwin's "strange inversion of reasoning." *Proceedings of the National Academy of Sciences of the United States of America, 106*(Suppl. 1), 10061–10065. http://dx.doi.org/10.1073/pnas.0904433106

Dennett, D. C., & McKay, R. (2006). A continuum of mindfulness. *Behavioral and Brain Sciences, 29,* 353–354. http://dx.doi.org/10.1017/S0140525X06299084

DePalma, R. A., II, Burnham, D. A., Martin, L. D., Rothschild, B. M., & Larson, P. L. (2013). Physical evidence of predatory behavior in Tyrannosaurus rex. *Proceedings of the National Academy of Sciences of the United States of America, 110,* 12560–12564. http://dx.doi.org/10.1073/pnas.1216534110

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De Vany, A., & Walls, W. D. (1996). Bose-Einstein dynamics and adaptive contracting in the motion picture industry. *Economic Journal, 106,* 1493–1514. http://dx.doi.org/10.2307/2235197

Dickinson, A. (1980). *Contemporary animal learning theory* (Vol. 1). Cambridge, United Kingdom: Cambridge University Press.

Domjan, M., Lyons, R., North, N. C., & Bruell, J. (1986). Sexual Pavlovian conditioned approach behavior in male Japanese quail (*Coturnix coturnix japonica*). *Journal of Comparative Psychology, 100,* 413–421. http://dx.doi.org/10.1037/0735-7036.100.4.413

Donahoe, J. W. (1984). Skinner: The Darwin of ontogeny? *Behavioral and Brain Sciences, 7,* 487–488. http://dx.doi.org/10.1017/S0140525X00026807

Donahoe, J. W. (2003). Selectionism. In K. A. Lattal & P. N. Chase (Eds.), *Behavior theory and philosophy* (pp 103–128). http://dx.doi.org/10.1007/978-1-4757-4590-0_6

Donahoe, J. W., Burgos, J. E., & Palmer, D. C. (1993). A selectionist approach to reinforcement. *Journal of the Experimental Analysis of Behavior, 60,* 17–40. http://dx.doi.org/10.1901/jeab.1993.60-17

Dunlap, A. S., & Stephens, D. W. (2014). Experimental evolution of prepared learning. *Proceedings of the National Academy of Sciences of the United States of America, 111,* 11750–11755. http://dx.doi.org/10.1073/pnas.1404176111

Epstein, R. E. (2015). Of course animals are creative: Insights from generativity theory. In A. B. Kaufman & J. C. Kaufman (Eds.), *Animal creativity and innovation* (pp. 375–393). http://dx.doi.org/10.1016/B978-0-12-800648-1.00013-9

Ferster, C., & Skinner, B. (1957). *Schedules of reinforcement*. http://dx.doi.org/10.1037/10627-000

Fricke, H., Hissmann, K., Schauer, J., Erdmann, M., Moosa, M. K., & Plante, R. (2000, January 6). Biogeography of the Indonesian coelacanths. *Nature, 403,* 38. http://dx.doi.org/10.1038/47400

Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science, 4,* 123–124. http://dx.doi.org/10.3758/BF03342209

Glaser, R. (1990). The reemergence of learning theory within instructional research. *American Psychologist, 45,* 29–39. http://dx.doi.org/10.1037/0003-066X.45.1.29

Hershberger, W. A. (1986). An approach through the looking-glass. *Animal Learning & Behavior, 14,* 443–451. http://dx.doi.org/10.3758/BF03200092

Holland, P. C. (1979). Differential effects of omission contingencies on various components of Pavlovian appetitive conditioned responding in rats. *Journal of Experimental Psychology: Animal Behavior Processes, 5,* 178–193. http://dx.doi.org/10.1037/0097-7403.5.2.178

Hull, C. L. (1930). Knowledge and purpose as habit mechanisms. *Psychological Review, 37,* 511–525. http://dx.doi.org/10.1037/h0072212

Hull, D. L., Langman, R. E., & Glenn, S. S. (2001). A general account of selection: Biology, immunology, and behavior. *Behavioral and Brain Sciences, 24,* 511–528.

Huxley, J. (1942). *Evolution: The modern synthesis*. London, United Kingdom: Allen & Unwin.

Koepke, A. E., Gray, S. L., & Pepperberg, I. M. (2015). Delayed gratification: A grey parrot (Psittacus erithacus) will wait for a better reward. *Journal of Comparative Psychology, 129,* 339–346. http://dx.doi.org/10.1037/a0039553

Krakauer, J. W., Ghazanfar, A. A., Gomez-Marin, A., MacIver, M. A., & Poeppel, D. (2017). Neuroscience needs behavior: Correcting a reductionist bias. *Neuron, 93,* 480–490. http://dx.doi.org/10.1016/j.neuron.2016.12.041

Krause, M. A., & Domjan, M. (2017). Ethological and evolutionary perspectives on Pavlovian conditioning. In J. Call (Ed.), *APA handbook of comparative psychology* (Vol. 1, pp. 247–266). http://dx.doi.org/10.1037/0000012-012

Laland, K. N., & Rendell, L. (2013). Cultural memory. *Current Biology, 23,* R736–R740. http://dx.doi.org/10.1016/j.cub.2013.07.071

Levis, N. A., & Pfennig, D. W. (2016). Evaluating "plasticity-first" evolution in nature: Key criteria and empirical approaches. *Trends in Ecology & Evolution, 31,* 563–574. http://dx.doi.org/10.1016/j.tree.2016.03.012

Lorenz, K. (1937). Imprinting. *Auk, 54,* 245–273. http://dx.doi.org/10.2307/4078077

Maatsch, J. L. (1959). Learning and fixation after a single shock trial. *Journal of Comparative and Physiological Psychology, 52,* 408–410. http://dx.doi.org/10.1037/h0048310

MacCorquodale, K. M. (1970). On Chomsky's review of Skinner's *Verbal behavior*. *Journal of the Experimental Analysis of Behavior, 13,* 83–99. http://dx.doi.org/10.1901/jeab.1970.13-83

Mayr, E., & Provine, W. B. (1998). *The evolutionary synthesis: Perspectives on the unification of biology*. Cambridge, MA: Harvard University Press.

McNally, R. J. (1992). Disunity in psychology: Chaos or speciation? *American Psychologist, 47,* 1054. http://dx.doi.org/10.1037/0003-066X.47.8.1054.a

Mesoudi, A., Whiten, A., & Laland, K. N. (2006). Towards a unified science of cultural evolution. *Behavioral and Brain Sciences, 29,* 329–347. http://dx.doi.org/10.1017/S0140525X06009083

Mischel, W., Ayduk, O., Berman, M. G., Casey, B. J., Gotlib, I. H., Jonides, J., . . . Shoda, Y. (2011). "Willpower" over the life span: Decomposing self-regulation. *Social Cognitive and Affective Neuroscience, 6,* 252–256. http://dx.doi.org/10.1093/scan/nsq081

Mischel, W., Shoda, Y., & Rodriguez, M. I. (1989, May 26). Delay of gratification in children. *Science, 244,* 933–938. http://dx.doi.org/10.1126/science.2658056

Monterosso, J., & Ainslie, G. (1999). Beyond discounting: Possible experimental models of impulse control. *Psychopharmacology, 146,* 339–347. http://dx.doi.org/10.1007/PL00005480

Moretti, F. (2013). *Distant reading*. London, United Kingdom: Verso.

Morris, E. K., Lazo, J. F., & Smith, N. G. (2004). Whether, when, and why Skinner published on biological participation in behavior. *Behavior Analyst, 27,* 153–169. http://dx.doi.org/10.1007/BF03393176

Naour, P. (2009). *E. O. Wilson and B. F. Skinner: A dialogue between sociobiology and radical behaviorism*. http://dx.doi.org/10.1007/978-0-387-89462-1

Nesse, R. M., & Williams, G. C. (1994). *Why we get sick: The new science of Darwinian medicine*. New York, NY: Vintage.

Neuberg, S. L., & Schaller, M. (2016). An evolutionary threat-management approach to prejudices. *Current Opinion in Psychology, 7,* 1–5. http://dx.doi.org/10.1016/j.copsyc.2015.06.004

Neuringer, A. (2004). Reinforced variability in animals and people: Implications for adaptive action. *American Psychologist, 59,* 891–906. http://dx.doi.org/10.1037/0003-066X.59.9.891

Neuringer, A. (2014). Operant variability and the evolution of volition. *International Journal of Comparative Psychology, 27,* 204–223.

Palmer, D. C., & Donahoe, J. W. (1992). Essentialism and selectionism in cognitive science and behavior analysis. *American Psychologist, 47,* 1344–1358. http://dx.doi.org/10.1037/0003-066X.47.11.1344

Pavlov, I. P. (2003). *Conditioned reflexes* (G. V. Anrep, Trans. & Ed.). Mineola, NY: Dover. (Original work published 1927)

Peterson, G. B. (2004). A day of great illumination: B. F. Skinner's discovery of shaping. *Journal of the Experimental Analysis of Behavior, 82,* 317–328. http://dx.doi.org/10.1901/jeab.2004.82-317

Pinker, S. (1999). *The blank slate: The modern denial of human nature*. New York, NY: Viking.

Pryor, K. (1999). *Don't shoot the dog*. New York, NY: Bantam Books.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago, IL: University of Chicago Press.

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This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Robinson, G. E., & Barron, A. B. (2017, April 7). Epigenetics and the evolution of instincts. *Science, 356,* 26–27. http://dx.doi.org/10.1126/science.aam6142

Ruxton, G. D., & Houston, D. C. (2003). Could Tyrannosaurus rex have been a scavenger rather than a predator? An energetics approach. *Proceedings of the Royal Society of London: Series B. Biological Sciences, 270,* 731–733. http://dx.doi.org/10.1098/rspb.2002.2279

Schlinger, H. D. (2004). Why psychology hasn't kept its promises. *Journal of Mind and Behavior, 25,* 123–144.

Sherrington, C. (1906). *The integrative action of the nervous system*. Cambridge, United Kingdom: Cambridge University Press.

Skinner, B. F. (1935). The generic nature of the concepts of stimulus and response. *Journal of General Psychology, 12,* 40–65. http://dx.doi.org/10.1080/00221309.1935.9920087

Skinner, B. F. (1953). *Science and human behavior*. New York, NY: Free Press.

Skinner, B. F. (1957a). The experimental analysis of behavior. *American Scientist, 45,* 343–371.

Skinner, B. F. (1957b). *Verbal behavior*. East Norwalk, CT: Appleton-Century-Crofts. http://dx.doi.org/10.1037/11256-000

Skinner, B. F. (1966, September 9). The phylogeny and ontogeny of behavior: Contingencies of reinforcement throw light on contingencies of survival in the evolution of behavior. *Science, 153,* 1205–1213. http://dx.doi.org/10.1126/science.153.3741.1205

Skinner, B. F. (1974). *About behaviorism*. New York, NY: Vintage.

Skinner, B. F. (1975). The shaping of phylogenic behavior. *Acta Neurobiologiae Experimentalis, 35,* 409–415.

Skinner, B. F. (1981, July 31). Selection by consequences. *Science, 213,* 501–504. http://dx.doi.org/10.1126/science.7244649

Skinner, B. F. (1983). *A matter of consequences*. New York, NY: Knopf.

Skinner, B. F. (1984). The evolution of behavior. *Journal of the Experimental Analysis of Behavior, 41,* 217–221. http://dx.doi.org/10.1901/jeab.1984.41-217

Skinner, B. F. (1988). Genes and behavior. In G. Greenberg & E. Tobach (Eds.), *Evolution of social behavior and integrative levels* (pp. 77–83). Hillsdale, NJ: Erlbaum.

Smaldino, P. E. (2014). The cultural evolution of emergent group-level traits. *Behavioral and Brain Sciences, 37,* 243–254. http://dx.doi.org/10.1017/S0140525X13001544

Sober, E., & Wilson, D. S. (1998). *Unto others*. Cambridge, MA: Harvard University Press.

Staats, A. W. (1999). Unifying psychology requires new infrastructure, theory, method, and a research agenda. *Review of General Psychology, 3,* 3–13. http://dx.doi.org/10.1037/1089-2680.3.1.3

Staddon, J. E. R. (1983). *Adaptive behavior and learning*. New York, NY: Cambridge University Press.

Stahlman, W. D., Leising, K. J., Garlick, D., & Blaisdell, A. P. (2013). There is room for conditioning in the creative process: Associative learning and the control of behavioral variability. In O. Vartanian, A. S. Bristol, & J. C. Kaufman (Eds.), *The neuroscience of creativity* (pp. 45–68). http://dx.doi.org/10.7551/mitpress/9780262019583.003.0003

Stahlman, W. D., Roberts, S., & Blaisdell, A. P. (2010). Effect of reward probability on spatial and temporal variation. *Journal of Experimental Psychology: Animal Behavior Processes, 36,* 77–91. http://dx.doi.org/10.1037/a0015971

Sternberg, R. J., & Grigorenko, E. L. (2001). Unified psychology. *American Psychologist, 56,* 1069–1079. http://dx.doi.org/10.1037/0003-066X.56.12.1069

Tierney, A. J. (1986). The evolution of learned and innate behavior: Contributions from genetics and neurobiology to a theory of behavioral evolution. *Animal Learning & Behavior, 14,* 339–348. http://dx.doi.org/10.3758/BF03200077

Timberlake, W. (1993). Behavior systems and reinforcement: An integrative approach. *Journal of the Experimental Analysis of Behavior, 60,* 105–128. http://dx.doi.org/10.1901/jeab.1993.60-105

Tinbergen, N. (1951). *The study of instinct*. New York, NY: Clarendon Press.

Todd, J. T., & Morris, E. K. (1992). Case histories in the great power of steady misrepresentation. *American Psychologist, 47,* 1441–1453. http://dx.doi.org/10.1037/0003-066X.47.11.1441

Uttal, W. R. (2007). *The immeasurable mind: The real science of psychology*. Amherst, NY: Prometheus.

Wallace, A. R. (1864). The origin of human races and the antiquity of man deduced from the theory of natural selection. *Journal of the Anthropological Society of London, 2,* clviii–clxxxvii. http://dx.doi.org/10.2307/3025211

Wasserman, E. A. (2012). Species, tepees, scotties, and jockeys: Selected by consequences. *Journal of the Experimental Analysis of Behavior, 98,* 213–226. http://dx.doi.org/10.1901/jeab.2012.98-213

Wasserman, E. A., & Blumberg, M. S. (2010). Designing minds. *American Scientist, 98,* 183–185.

Wasserman, E. A., & Cullen, P. (2016). Evolution of the violin: The law of effect in action. *Journal of Experimental Psychology: Animal Learning and Cognition, 42,* 116–122. http://dx.doi.org/10.1037/xan0000086

Wassermann, G. D. (1984). Neuropsychology vis-à-vis Skinner's behaviouristic psychology. *Behavioral and Brain Sciences, 7,* 700–701. http://dx.doi.org/10.1017/S0140525X00028259

Watrin, J. P., & Darwich, R. (2012). On behaviorism in the cognitive revolution: Myth and reactions. *Review of General Psychology, 16,* 269–282. http://dx.doi.org/10.1037/a0026766

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. New York, NY: Oxford University Press.

Williams, D. R., & Williams, H. (1969). Auto-maintenance in the pigeon: Sustained pecking despite contingent non-reinforcement. *Journal of the Experimental Analysis of Behavior, 12,* 511–520. http://dx.doi.org/10.1901/jeab.1969.12-511

Wilson, D. S., & Sober, E. (1994). Reintroducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences, 17,* 585–608. http://dx.doi.org/10.1017/S0140525X00036104

Wilson, E. O. (1978). *On human nature*. Cambridge, MA: Harvard University Press.

Wixted, J. T., & Gaitan, S. C. (2002). Cognitive theories as reinforcement history surrogates: The case of likelihood ratio models of human recognition memory. *Animal Learning & Behavior, 30,* 289–305. http://dx.doi.org/10.3758/BF03195955

Wynne, C. D. L. (2007). What are animals? Why anthropomorphism is still not a scientific approach to behavior. *Comparative Cognition & Behavior Reviews, 2,* 125–135.

Zilio, D. (2016). Who, what, and when: Skinner's critique of neuroscience and his main targets. *Behavior Analyst, 39,* 197–218. http://dx.doi.org/10.1007/s40614-016-0053-x

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