THEORETICAL ARTICLE

The behavioral origins of phylogenic responses and ontogenic habits

W. David Stahlman[1] | **Kenneth J. Leising**[2]

[1]University of Mary Washington—Department of Psychological Science, Fredericksburg, VA, USA

[2]Texas Christian University, Fort Worth, TX, USA

Correspondence
W. David Stahlman, University of Mary Washington—Department of Psychological Science, 1301 College Ave. Fredericksburg, Virginia, 22401, USA.
Email: wdstahlm@umw.edu

Editor-in-Chief: Mark E. Bouton
Handling Editor: Eric Thrailkill

Abstract

An examination of innate behavior and its possible origins suggests parallels with the formation of habitual behavior. Inflexible but adaptive responses—innate reflexive behavior, Pavlovian conditioned responses, and operant habits—may have evolved from variable behavior in phylogeny and ontogeny. This form of "plasticity-first" scientific narrative was unpopular post-Darwin but has recently gained credibility in evolutionary biology. The present article seeks to identify originating events and contingencies contributing to such inflexible but adaptive behavior at both phylogenic and ontogenic levels of selection. In ontogeny, the development of inflexible performance (i.e., habit) from variable operant behavior is reminiscent of the genetic accommodation of initially variable phylogenic traits. The effects characteristic of habit (e.g., unresponsiveness to reinforcer devaluation) are explicable as the result of a conflict between behaviors at distinct levels of selection. The present interpretation validates the practice of seeking hard analogies between evolutionary biology and operant behavior. Finding such parallels implies the validity of a claim that organismal behavior, both innate and learned, is a product of selection by consequences. A complete and coherent account of organismal behavior may ultimately focus on functional selective histories in much the same way evolutionary biology does with its subject matter.

KEYWORDS

canalization, consequences, evolution, genetic assimilation and accommodation, selection, Skinner

"Strict repetition and recurrence decrease relatively to the novel. … [H]abit-forming wears grooves; behavior is confined to channels established by prior behavior. In so far the tendency is toward monotonous regularity."
—John Dewey (1958/1925, p. 280), *Experience and Nature*.

Habitual behavior is characterized by reduced flexibility of action. Under circumstances in which contingencies are invariant, operant behavior becomes more regular, impervious to revaluation of its consequences and resistant to degradation of the contingency between behavior and reinforcing consequences. Although operant behavior early in training may be characterized by relative flexibility and adaptiveness to dynamic contingencies, with more training it can become comparatively inflexible and resistant to change (for a general overview of habit, see, e.g., Lingawi et al., 2016).

One may observe an analogy between the formation of habit and the development of rigid behavioral "strategies" in evolutionary history. Animals behave in adaptive, species-specific ways in response to environmental demands, ones requiring little to no learning. To invoke a metaphor, these behaviors are hard-wired into the organism by virtue of an evolutionary history. Stable contingencies relating to biological fitness—at least with respect to the behavior of interest—have produced relative invariance of some behavioral forms. Some behaviors are so consistently adaptive they become stimulus bound across evolutionary time and thus nearly automatic.

The present article is an interpretation of habit learning by way of an analogy with instinctual responding and Pavlovian conditioning. What follows is aligned with a

functional selectionist perspective (Skinner, 1953, 1966, 1981) in which behavior is a product of three levels of selection. Skinner extended Darwinian selection to account for adaptive behavior in operant learning and cultural domains. His account treats behavior in much the same way as Darwin's does biological traits. New forms of learned behavior are reproduced as a function of differential reinforcement. All behavior is explicable as the product of some combination of contingencies in evolution, learning, and cultural transmission. A spider builds a web largely as a function of an evolutionary history; a primitive human invented the fishing net largely as a function of a personal history; and net-building in humans proliferated largely because of imitation, modeling, and the adaptive consequences following the use of fishing nets.

Readers unconvinced that behavior represents grist for the selective mill in a Darwinian fashion will likely not be convinced by this article. They may consider what follows to be of limited use. They may not "change their minds." But there are readers of this journal who see the topics in evolutionary biology and behavior as *particular instances* of a more fundamental process (i.e., selection by consequences). These folks may find utility in this article's contents. Biology and behavior may be linked via a hard analogy, helping us identify real corresponding entities and their respective functions. Skinner's (e.g., 1981) stance, and the position of the present article, is that biology and behavior share more than surface features (see also Catania, 2001, 2013; Stahlman & Leising, 2018). Like all selectionist sciences, behavior analysis is concerned with histories of a particular sort (e.g., Donahoe, 2003, 2012).

Skinner's framework is supported by identifying similarities across biological and behavioral sciences. If selective systems operate in distinctive ways, they will show distinctive effects (e.g., Schneider, 2012; Wasserman, 2012; Wasserman & Cullen, 2016). The substrate is in this sense irrelevant: Observations in phylogeny will have ontogenic parallels and vice versa. Our proper study may be variation and selection themselves, with biology, behavior, and culture forming convenient subdisciplines within the broader science (e.g., Hull et al., 2001). The present article approaches these topics in this light.

We will begin by introducing a pair of plasticity-first accounts of biological evolution. The topic has deep roots in seminal literature. Within a century of the *Origin* (Darwin, 1859), Baldwin and Waddington had each offered means—genetic accommodation and genetic assimilation, respectively—by which innate or instinctual behavior could be selected from variable and learned ancestral behavior. This history has not been well represented in the pages of *JEAB*. According to Google Scholar, in the journal's history, the phrase *Baldwin effect* appears only once (Hayes & Sanford, 2014). The proper name *Waddington* appears in eight articles, equating to once every 8 years. (To give a sense for the range of possible values, *Skinner* appears in about 2,200 papers in the journal's history, an average of

approximately 34 articles per year.) The words *canalized* and *canalization*, critical to Waddington's account, appear in one article each (Killeen, 1992; Schneider, 2003). Neither *genetic accommodation* nor *genetic assimilation* appears a single time.

At the least, it seems worthwhile to bring these topics to *JEAB* as matters pertaining to the adaptive behavior of organisms. Further, in accordance with well-established behavioristic practice (e.g., Donahoe, 2012; Skinner, 1975, 1984; Stahlman & Catania, 2020, 2023; Wasserman, 2012), we will draw from the philosophy of biology in reinterpreting Pavlovian responses and operant behavior.

The behavioral origins of instincts: A very brief history

In a classic paper, Skinner (1966) examined the various origins of adaptive behavior. In so doing, he continued to draw parallels between Darwinian (1859) natural selection and reinforcement in operant behavior. In a note appended to the republished article, Skinner (1969, chap. 7) identified the potential behavioral origins of some phylogenic behavior. It is worth reading the majority of a relevant passage:

> Let us assume that a dog possesses no instinctive tendency to turn around as it lies down but that lying down in this way is reinforced as an operant by the production of a more comfortable bed. *If there are no phylogenic advantages, presumably the readiness with which the response is learned will not be changed by selection. But phylogenic advantages can be imagined*: such a bed may be freer of vermin, offer improved visibility with respect to predators or prey, permit quick movement in an emergency, and so on. *Dogs in which the response was most readily conditioned must have been most likely to survive and breed.* … Turning around when lying down may have become so readily available as an operant that it eventually appeared without reinforcement. It was then 'instinctive.' *Ontogenic contingencies were responsible for the topography of an inherited response.*
>
> (emphasis added)

Many might consider these musings forbidden, as they suggest the genetic inheritance of acquired characteristics, the so-called Lamarckian heresy (Dawkins 1982; see also Mayr & Provine, 1998; Weismann, 1891, 1893). But within evolutionary biology, there is a long history in which scientists offered non-Lamarckian mechanisms for the plastic behavioral origins of innate action. Darwin himself thought instincts could be constructed from the behavior of ancestors, though he thought Lamarck's mechanism of evolutionary change to be "nonsense" (Darwin, 1892, p. 174).

Baldwin (1896, 1902, see also Morgan 1896, Osborn 1896) is credited with an early proposal for the construction of instincts. Organisms in an evolving population may learn to perform a particular adaptive response at earlier and earlier points in development. Over generations, such a directional effect may proceed until the behavior requires little to no learning. Variously called genetic accommodation and the Baldwin effect (Simpson, 1953) this suggests a means by which instinct may be built (see also, e.g., Avital & Jablonka, 2000; Badyaev, 2009; Bateson, 2006; West-Eberhard, 2003). There are three necessary components for the Baldwin effect to occur. First, ontogenic behavioral plasticity must relate to biological fitness; second, there must be hereditary factors that contribute to this initially plastic behavior; and third, these genetic factors, by virtue of Darwinian selection, proliferate over generations. After this process, one may call such behavior *prepared* (Dunlap & Stephens, 2014; Lolordo, 1979; Seligman, 1970; Shettleworth, 1972). One example of prepared learning has been demonstrated in rhesus monkeys, which only respond with fear to snakes following snake-relevant experience. This fear response is much more rapidly acquired to snakes than to other stimuli and can even be learned via observation of other monkeys' fear responses (e.g., Cook & Mineka, 1989, 1990). This suggests an evolved propensity, one with obvious adaptive value in environments where snakes are a threat.

Waddington (e.g., 1942, 1953, 1957, 1959; see Crispo, 2007, and Gottlieb, 1997, for reviews) introduced the concept of *canalization*. Over generations, an adaptive developmental program may become increasingly robust to environmental perturbation (e.g., Waddington & Robertson, 1966). In a novel or changing environment, variability in development may increase fitness. But in stable environments, selection may act over generations to increase the (genetic) fixedness of an adaptive phenotype. This process has been referred to as genetic assimilation (see also Hallgrímsson et al., 2019; Loison, 2019; Nijhout et al., 2021; Pigliucci et al., 2006; Warburton, 1956). The variability in the original population may be lost in the same way other costly features are expunged by iterative natural selection (e.g., the loss of eyes in the Mexican cave tetra; Protas et al., 2007). Following canalization, slight or brief environmental perturbations are unlikely to result in large differences in gene expression (e.g., Meiklejohn & Hartl, 2002). A phenotype may thus become genetically fixed or swiftly acquired under usual developmental conditions for the species (Gottlieb, 1991a, 1991b).

Baldwin's and Waddington's accounts are not mutually exclusive. Indeed, they seem likely to work in parallel when conditions demand (Crispo, 2007, Figure 2). It is not the goal of the present article to disentangle them or to resolve the many disputes (see, e.g., Loison, 2019) over their relative importance in biological evolution. These specifics by which initial plasticity may evolve into a hard-wired, inflexible, and/or innate phenotype are not crucial for the purposes of this article. Thus, we will favor the more general term *genetic accommodation*, but we will refer to *canalization* as well. For our purposes, it is enough to highlight that these two accounts have well-established histories in the evolutionary biology literature and are plausible "phenotype-first" drivers of evolutionary change.

On innate behavior

Behavior primarily due to natural selection has many familiar names: instinct (Beach, 1955; Tinbergen, 1951), modal and fixed action patterns (Barlow, 1977), reflexes (Sherrington, 1906), and unconditional responses (Pavlov & Anrep, 1927/2003) are but a few. These terms all refer to adaptive behavior that is dependent on particular kinds of ancestral history rather than a personal history. The controlling variables for innate behavior are to be found in an ancestral history, not in a personal one. Behavior may be "released" by prevailing environmental variables, but doing so reflects nothing called learning (but see, e.g., Chittka & Rossi, 2023).

The origins of innate responding may lie in the behavioral flexibility of ancestral organisms. Specific propensities to behave in given ways may well have become fixed because of their relation to the consequences of reproductive success in ancient environments. This represents an inversion of the prevailing view that instincts are ancestral to acquired behavior (e.g., Laland et al., 2015; Levis & Pfennig, 2016). Bell and Robinson (2011, p. 1161) write,

> When circumstances change, *an organism's first response is often behavioral*. But how does adaptive behavior evolve, given that it requires constant and often instantaneous interactions between an individual and its environment? The dominant view emphasizes new random DNA mutation as the starting point. … [But] an alternative theory proposes environmentally induced change in an organism's behavior as the starting point, and "phenotypic plasticity" that is inherited across generations through an unspecified process of "genetic assimilation." [. . .] *[B]ehavioral genetics and genomics, especially for animals in natural populations, lend some plausibility to the phenotypic plasticity view*.
>
> (emphasis added)

Much evidence supports the possibility that initial phenotypic variation may become fixed in an evolving population (e.g., Badyaev, 2009; Ginsburg & Jablonka, 2010; Haig, 2007; Heyes et al., 2020; Jablonka & Lamb, 2005; Moray & Connolly, 1963; Portera & Mandrioli, 2021; Tierney, 1986). Robinson & Barron (2017) point to the possibility that instinct and learning share cellular and molecular mechanisms. They write, "[e]volutionary 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). Such a program requires a shift in behavioral control from recent and prevailing contingencies to ancestral ones. They conclude, tantalizingly, as follows: "Considering an instinct as an 'ancestral memory' of a specific response to the environment may help to guide efforts to understand the physical basis of memory" (p. 27).

On Pavlovian behavior

Pavlovian conditioning is said to be a process by which animals learn the relations between stimulus events (Rescorla, 1988). To a greater extent than with innate behavior, the variables of interest in conditioned behavior are found in the animal's personal history. But like with innate behavior, Pavlovian conditioned responses are non-arbitrary and inflexible. Their characteristics are largely determined by an evolutionary history. Pavlovian responses may thus be considered innate responses to fitness-related predictive stimuli (e.g., Timberlake, 1993, 1994). We will suggest that Pavlovian conditioned responses are not categorically distinct from instinctual behaviors. They are to be found on the same continuum as innate behavior but differ quantitatively in their degree of fixedness.

A plausible narrative for the origins of conditioned behavior

Pavlovian conditioning is evolutionarily ancient, and thus it is difficult to be certain of its deep origins. What follows is merely a plausible narrative. But as it adheres to established principles of evolutionary biological thought, it may be helpful.

Suppose a population of organisms exists with variance in efficiency of eating. Some members are passive feeders, merely consuming food they happen to contact. In an aquatic, nutrient-rich environment, this may suffice. But when conditions are worse and there is competition for limited resources, an active organism has the advantage. Organisms that move through space may move away from especially nutrient-poor locations and are more likely to encounter nutrient-rich oases. This confers a selective advantage for movers. Of these, those organisms that take advantage of fitness-related regularities in their environment—those that move nonrandomly, in the direction of food—have a greater advantage still. Some of these regularities may be stable over evolutionary time. For example, aquatic photosynthetic bacteria are always found close to the ocean's surface, not at depth. Organisms that primarily feed on these bacteria may benefit from staying near the surface. Such conditions are ripe for the full genetic accommodation of behavior. Other regularities in

feeding opportunities may be less stable—new seafloor vents open, ocean currents change, or organisms venture into novel territory. A prepared response to these kinds of variable, punctate events would confer an advantage, but the relative unpredictability of the events themselves means adaptive behavior cannot become fully canalized.

Pavlovian conditioning is adaptive across systems. It has a direct role in foraging and feeding, courtship, prevention and removal of external irritants, and predator evasion. If the foregoing account is correct, it suggests Pavlovian conditioning—rooted in the plasticity of ancestral organisms vis-à-vis specific fitness-related events—emerged many times, in concert with the evolution of reflexive behavior in each system.

Pavlovian conditioning as a general process

Different varieties of conditioning share apparent features. But a plasticity-first view suggests these evolved separately and converged on a similar terminal solution. Conditioning is a process, not a mechanism (e.g., Fanselow & Wassum, 2016; Krause & Domjan, 2017). Different forms of conditioned behavior could have emerged independently as they were shaped by biological contingencies. An analogous biological concept is *homoplasy*, or convergent evolution. A bat's wings and a pigeon's wings may have similar behavioral functions, but they are not classically homologous—so too with the many independent emergences of the eye (though deep genetic homologies may well exist; Shubin et al., 2009). The term *anticipation* and similar others (e.g., *expectation*) may refer to a collection of effects with similar form, but with dissimilar selective histories rendering them distinct in a functional account. Therefore, organisms may not *generally* anticipate events. Animals approach stimuli that are predictive of food, and they also approach stimuli that are predictive of safety, but this does not entail that *approach* is the same in each case. Overshadowing occurs in both conditioned salivation and fear preparations, but this does not entail the two cases having a shared origin.

There are many specific differences between the varieties of conditioning; these are consistent with independent origins. One example is evidence that different standard preparations are differentially able to produce cue competition (e.g., Maes et al., 2018); another is the radical disparity in optimal interstimulus intervals across forms (e.g., Garcia et al., 1966; Hawkins et al., 1986). These do not unambiguously support a plasticity-first view because selection could have shaped these differences from a common ancestral form of conditioned behavior. More convincing is the vastly different neural systems mediating each Pavlovian response. For example, the conditioned eyeblink response is mediated by the cerebellum (see, e.g., Kim et al., 1998), whereas conditioned fear is mediated by nuclei in the amygdala (see, e.g., Fanselow & LeDoux, 1999). Pavlovian conditioned behavior reflects

acquisition of adaptive behavior to *particular* stimuli as a function of their necessary relation to fitness-related events in phylogeny. This agrees with Fanselow & Wassum (2016, p. 14), who write,

> [c]onditioning is embedded in the neural systems that evolved for very different functions (e.g., defense, reproduction, feeding). There is no Pavlovian learning system per se; rather, because of the adaptive value of anticipating events, Pavlovian conditioning appears to have evolved independently within each of these systems. … There is little overlap in the circuitry of functionally distinct classes of conditioning. Thus, at a mechanistic level each type of conditioning needs to be considered on its own.

The role of behavioral consequences

Pavlovian responses are a product of the juncture of stimulus relations and a deep evolutionary history. They are not a function of their current consequences. A conditioned response will predictably occur when stimulus relations dictate, even if its occurrence has aversive consequences for the organism.

For example, if a tone reliably precedes the delivery of sucrose at a food niche (i.e., Tone→Sucrose), a hungry rat will come to approach the niche during the tone. An omission contingency can then be arranged so that sucrose is contingent on avoiding the niche during the tone. Conditioned approach is maintained even though it costs the rat many feeding opportunities (Holland, 1979). There are countless analogous examples (e.g., Hershberger, 1986; Williams & Williams, 1969).

The ontogenic history and the current consequences of a Pavlovian response are irrelevant to its expression; this entails that it cannot change in response to prevailing contingencies that conflict with ancestral ones. Pavlovian behavior reflects long-standing stable evolutionary contingencies, the conditions under which genetic accommodation could occur. Early ancestral flexibility may have given way to modern rigidity.

There is another class of adaptive behavior, however, allowing for rapid and flexible adjustment in dynamic environments. This behavior may reflect the early variability required by a plasticity-first view of behavioral evolution. Operants are largely a function of their consequences and are accordingly more arbitrary with respect to evolutionary history. But within operant behavior, there too is a sequence by which flexibility is replaced by rigidity. Such a progression may be a shared property of selective systems. We will suggest the transition from flexible "goal-directed" behavior to inflexible "habit" constitutes an ontogenic analogue for genetic accommodation in biological evolution.

On operant behavior

Under some circumstances, the consequences following behavior have the effect of changing the future probability of similar actions. Behavior in this category is called *operant* (Catania, 1973; Skinner, 1938).

The arbitrariness of operant behavior

As a rule, operants more strictly reflect recent contingencies than do instinctual or Pavlovian responses. The latter are the largely the consequence of stable ancestral histories that promote the genetic accommodation of behavior; in contrast, operant behavior reflects control by more capricious environmental relations that need not be similar to those in ancestral history. Thus, compared with phylogenic behavior, operant behavior appears to be more arbitrary. Contingent sucrose may make food-restricted rats' lever-pressing more likely in part because related motor behavior (e.g., orienting, rearing) has few phylogenic commitments. Contingent sugar can also increase the probability of pole pushing, string pulling, digging, open rearing, and wheel running, among other behaviors[1] (e.g., Shettleworth, 1975). Contingent omission of sucrose has the opposite effect in that any of those behaviors may be made less likely (e.g., Uhl, 1973).

Given these clear behavioral differences between operants and Pavlovian conditioned responses, one would expect divergence in their neural mechanisms. And in this respect, operant behavior is indeed dissimilar to conditioned behavior. Pavlovian behavior is subdivided across systems distributed throughout the brain—perhaps evidence for their independent behavioral origins. In contrast, operant behavior appears to be generally mediated by specific neural pathways. In mammals, the dorsolateral striatum and infralimbic prefrontal cortex are implicated in stimulus-driven operant behavior; the dorsomedial striatum, prelimbic prefrontal cortex, and the ventral orbitofrontal cortex are linked to the sensitivity of behavior to its consequences (Dolan & Dayan, 2013). And in invertebrates, the neural structures contributing to operant behavior are homologous with those of the vertebrate basal ganglia (Strausfeld & Hirth, 2013; Tomer et al., 2010). Neural circuitry provides no indication that different operants have different phylogenic origins.[2]

---

[1]Like with humans, technology has expanded the potential repertoire of the rat today as compared with the past.

[2]We note that phylogenic history clearly does matter for operant behavior, in a sense. Presentation of stimuli with evolutionary importance (e.g., food, sexual opportunities) modifies the probability of contingent, if arbitrary, behavior. What makes something food or a sexual partner is largely the product of an ancestral history. Also, actions that are physically impossible can never be reinforced and can thus never be made more probable. A child will never take flight by flapping her arms, no matter how she might strain. But this is why we have airplanes.

The development of habit

Because operant behavior is responsive to its consequences, it may change as a function of changing environmental circumstances. Actions yielding positive outcomes will be repeated, whereas those yielding aversive consequences will not be. To the extent this remains true, operant behavior remains adaptive.

A standard case is seen when a single operant response is first established via positive reinforcement and is then followed by a change in the hedonic value of the consequence (e.g., Balleine & Dickinson, 1998; Colwill & Rescorla, 1985; Dickinson et al., 1983; Thrailkill & Bouton, 2015). For example, in a food-restricted rat, one might establish lever pressing by delivering contingent chocolate pellets. Subsequently, chocolate is paired with gastric illness via the intraperitoneal injection of lithium chloride; a small number of pairings generates aversion to chocolate. Following this, in an extinction test, the rat may show a reduction in lever pressing. This may suggest the operant behavior is "goal directed." It is as though the organism considers the outcome of its behavior prior to acting. But operant behavior does not always conform so neatly to prevailing conditions. *Habit* represents a category of operant behavior that does not show this sensitivity to its consequences. As an example, let's posit another food-restricted rat pressing a lever and receiving contingent chocolate pellets but with greatly extended operant training. After overtraining the behavior, we can again devalue the chocolate by pairing it with lithium chloride. In a subsequent extinction test, we may see no decrease in lever pressing—the rat presses the lever as rapidly as it did before the devaluation. This rat's behavior is stimulus bound and automatic. By mere virtue of additional operant training, the rat no longer appears to consider the consequences of its behavior. As Bouton (2021, p. 349) writes,

> [i]t is now customary to imagine that the rodent is more cognitively engaged than classic behaviorists like Hull and Skinner assumed. … [Actions] are apparently performed—and this is the "cognitively engaged" part—with a representation of the goal in memory. Habits, in contrast, as behaviors that may eventually get us to a goal, but are performed more automatically, without the goal in memory or "mind." Actions can become habits with extended repetition and practice.

We will return later to matters of "cognitive engagement," goal representation, and memory.

Researchers have examined the neurobiological correlates of habit formation. There is evidence for a shift from dorsomedial to dorsolateral basal ganglia pathways during operant learning (Balleine et al., 2009; Belin et al., 2009; Graybiel, 2005; Graybiel & Grafton, 2015; O'Doherty et al., 2004; Thorn et al., 2010; Yin

et al., 2004, 2009). Comparative analysis (e.g., Balleine & O'Doherty, 2010; Brembs, 2009, 2011; Wood & Rünger, 2016) suggests this transition generally mediates the formation of habit (see also Corbit, 2018; de Wit, 2012). Many (e.g., Adams & Dickinson, 1981; Balleine, 2019; Bouton, 2021; Dickinson et al., 1983; Thrailkill & Bouton, 2015) suggest that the development of habit reflects a shift not only in the neurobiological correlates but also in the associative structure of behavior. Behavior that is sensitive to reinforcer devaluation may be said to reflect control by a response–outcome (R-O) association. An operant no longer sensitive to reinforcer devaluation may be said to reflect control by stimulus–response (S-R) associations. But this is not the only way of considering the matter.

A different way of thinking about habit

Let us consider a case in which a naïve rat is placed into a free-operant learning experiment. The animal is confronted with a new environment and a novel set of contingencies. A single lever protrudes from the side wall. There is a practical unpredictability at this early stage. It is adaptive for behavior first to be a function of its consequences, to be flexible. Lever presses that produce sucrose are at first incidental and sporadic as the animal does other things (e.g., "exploring") that are characteristic of behavior in a new environment. These latter forms of behavior drop away as the experiment continues. The regularity of the contingencies yields ever-more regular lever pressing, which progressively becomes less sensitive to its consequences. The behavior becomes habitual. This effect in operant learning resembles in no small way the reduction in flexibility observed in the genetic accommodation of behavior. In each, initial variability gives way to inflexibility by virtue of stable consequences for adaptive behavior. One might say that habit represents *ontogenic canalization*.

If one considers this example to be a behavioral analogue to the development of prepared learning in evolution, a question emerges: What if the canalized behaviors produced by evolutionary and behavioral contingencies are in mutual conflict?

There are many cases of conflict between phylogenic and ontogenic behavior. A classic example is found in *misbehavior* (Breland & Breland, 1961). Delivery of food reinforcers may activate species-specific behavioral repertoires that interfere with the operant response. A raccoon receives food contingent on picking coins and dropping them into a metal box, but the behavior is resistant to shaping, as the animal spends many minutes rubbing the coins together and dipping them into the box but not releasing them. The characteristic food-handling behavior, elicited by food delivery, prevents the occurrence of the operant behavior. This example of "instinctive drift" (p. 684) is but one among many. Another example is in

the well-established difficulty of training certain kinds of actions as avoidance responses. Rats do not readily learn to lever press to avoid strong footshocks because the delivery of shocks results in species-specific, threat-related behavior that conflicts with execution of the avoidance response (e.g., Bolles, 1970; Bouton & Bolles, 1980; D'Amato & Schiff, 1964). Intrusions in the other direction are also possible; operant behavior may interfere with evolved, species-specific behavior. The discipline of soldiers in battle may be one such example. Prepared, canalized, species-specific behavior cannot always co-occur with operant behavior (Stahlman & Leising, 2018). We may extend some implications to the treatment of habit as a behavioral analogue of genetic accommodation.

The behavioral effects of food poisoning are dramatic and have a rapid onset. A rat falls ill after consuming of a food item and quickly learns an aversion. Taste aversion requires very little learning (e.g., a trial or two) to manifest and is robust. The rapidity by which conditioning proceeds is an indicator of its preparedness; the behavior of avoiding poison has long been under strong selective pressure. Animals that do not eat poisonous substances a second time should have a fitness advantage over those that do. Likewise, animals that do not spend their resources *working for* and *returning* to poisonous food sources should have a fitness advantage over those that do. Across evolutionary time, such regularities have provided the proper conditions for the genetic accommodation of behavior of flavor aversion. Critically, the canalized behavior encompasses both the reduced consumption of the poisonous food *and* the reduction of behavior that produces the poisonous food. Of course, the animal would be expected to continue to work for untainted food.

Overtraining a positively reinforced operant produces a different form of long-lasting stability and results in a different kind of fixedness. Selection by consequences works not only to increase the probability of lever pressing but also to make lever-pressing more secure in the rat's repertoire (Nevin & Grace, 2000). Conflict may occur between the evolutionary tendency to avoid responses that yield poisoned food and the habitual tendency to behave. One observed result is that lever pressing continues unabated and so reinforcer devaluation appears to be ineffective. Here, ontogeny wins. Entries to the food magazine, however, are immediately reduced following reinforcer devaluation (Nelson & Killcross, 2006). These results at first seem paradoxical, but they may be explicable in terms of their relative proximity to fitness-related events. Magazine entry is more proximal to food handling (i.e., an event directly related to evolutionary history) and is less arbitrary than lever pressing. Here, phylogeny wins.

If this analysis is correct, the evolution of response fixedness in natural selection bears a hard analogical relationship to the development of fixedness in operant behavior by reinforcement. One should expect other common effects. As mentioned, the genetic accommodation of behavior should be greatest when environmental contingencies are stable over evolutionary time. Complete accommodation of adaptive behavior is unlikely, however, when contingencies are unstable or dynamic. If the analogy to operant behavior is valid, one must expect unpredictable operant contingencies will prevent the development of habit.

This is precisely what is observed. Changes in exigences—for example, in the contextual antecedents to operant behavior or in the predictability of contingent reinforcers—render behavior sensitive to its consequences and thus prevent the development of habit. Simply interleaving different training contexts during operant learning is enough to maintain the goal directedness of behavior (e.g., Bouton et al., 2020; Steinfeld & Bouton, 2021; Trask et al., 2020). A wealth of evidence (Bouton et al., 2020; Bouton, 2021; Olton, 1979; Thrailkill et al., 2018, 2021) indicates the shift from goal-directed to habitual behavior is directly related to reinforcer's predictability. Free-operant behavior on a single lever, in a single, invariant context, and delivering consistent reinforcers is likely to become habitual. Discriminated operant behavior, on the other hand, appears to resist becoming habitual even with large amounts of training, but this resistance is eliminated when parameters are established to ensure that the reinforcer is delivered predictably (Thrailkill et al., 2018).

Concluding comments on a unified framework

The transition from goal-directed to habitual operant responding may be considered one distinct example of a general process. Stable contingencies produce the development of fixedness from more variable origins. This may be true for any type of selection (Skinner, 1981). It may simply be something selection does, whether in a Darwinian substrate or an operant one.

This article presents an interpretation, the validity of which should be subject to scrutiny. The literature of habit is rich and associative interpretations well established. Scientists have customary ways of speaking about habit, including ways in conflict with the present narrative.

A predictive stimulus (i.e., a CS) may elicit a conditional response, but is said to do so because it activates a *representation* of the unconditioned stimulus. An animal may *expect* the occurrence of the unconditioned stimulus. The conditional response may be due to the animal possessing a corresponding stimulus–stimulus (S-S) association. In operant behavior, the experimental evidence suggests to some the existence of *associations* [i.e., R-O, O-R, and S(R-O)] governing *goal-directed* organismal behavior. Operant behavior is also said to reflect *anticipation* or *expectation*, in this case of the outcome or consequence of behavior (e.g., Bouton, 2021). Habitual behavior, less sensitive to its consequences, is said to be a

function of stimulus–response (S-R) *associations*. The present article, in contrast, does not depend on such terms to account for differential effects of reinforcer devaluation. It explains the same facts as associative accounts, but it does not appeal to hypothetical explanatory constructs. It instead appeals only to selection by consequences in evolution and operant learning. Thus, it aligns well with modern evolutionary biology. As Skinner ([1985](), p. 295) notes,

> [w]e say that we have eyes in order to see, but biologists have long since learned to say only that eyes have evolved because variations that enabled organisms to see better were selected. A similar mistake is made when cognitive psychologists call operant behavior purposive or goal directed. The goal … has no effect upon the organism's behavior. Only past arrivals at the goal can have had any effect.

The arguments presented here are aligned with a philosophy of science emphasizing path dependence and the determinative role of histories. Although one might suggest "actions that have become habitual and reflexive *relieve cognitive and attentional load*" (Lingawi et al., [2016](), p. 411; emphasis added), the adaptive origins of habit may be found elsewhere. They may instead be a fundamental adaptive character of a stable, selective system.

Behavior is not a mere symptom, the product of events "taking place somewhere else, at some other level of observations, described in different terms, and measured, if at all, in different dimensions" (Skinner, [1950](), p. 193). Behavior is a subject matter on its own merits (Catania, [2013](); Watson, [1913]()). This article sought to draw some parallels across observations of the phylogeny and ontogeny of behavior as suggested by a plasticity-first account of origins. Selection may be sufficient to explain the parallel establishment of inflexible adaptive behavior at multiple levels. Such an account is necessarily incomplete, but it is hoped the present narrative will draw attention to the relevant biological arguments and illuminate features regarding the development of habit and of adaptive behavior generally. When we ask about the origins of instincts, of Pavlovian responses, and of habit, maybe we will find behavior does indeed "always come first" (Catania, [2000](), [2017](), p. 3).

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest to declare.

ETHICS APPROVAL

No human or animal subjects were used to produce this article.

REFERENCES

Adams, C. D., & Dickinson, A. (1981). Instrumental responding following reinforcer devaluation. *Quarterly Journal of Experimental Psychology: B*, *33*(2b), 109–121. https://doi.org/10.1080/14640748108400816

Avital, E., & Jablonka, E. (2000). *Animal traditions: Behavioural inheritance in evolution*. Cambridge.

Badyaev, A. V. (2009). Evolutionary significance of phenotypic accommodation in novel environments: An empirical test of the Baldwin effect. *Philosophical Transactions of the Royal Society B*, *364*, 1125–1141. https://doi.org/10.1098/rstb.2008.0285

Baldwin, J. M. (1896). A new factor in evolution. In R. K. Belew & M. Mitchell (Eds.), *Adaptive individuals in evolving populations: Models and algorithms* (pp. 59–80). Addison-Wesley.

Baldwin, J. M. (1902). *Development and evolution*. Macmillan.

Balleine, B. W. (2019). The meaning of behavior: Discriminating reflex and volition in the brain. *Neuron*, *104*(1), 47–62. https://doi.org/10.1016/j.neuron.2019.09.024

Balleine, B. W., & Dickinson, A. (1998). The role of incentive learning in instrumental outcome revaluation by sensory-specific satiety. *Animal Learning & Behavior*, *26*, 46–59. https://doi.org/10.3758/BF03199161

Balleine, B. W., Liljeholm, M., & Ostlund, S. B. (2009). The integrative function of the basal ganglia in instrumental conditioning. *Behavioural Brain Research*, *199*, 43–52. https://doi.org/10.1016/j.bbr.2008.10.034

Balleine, B. W., & O'Doherty, J. P. (2010). Human and rodent homologies in action control: Corticostriatal determinants of goal-directed and habitual action. *Neuropsychopharmacology*, *35*, 48–69. https://doi.org/10.1038/npp.2009.131

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

Bateson, P. (2006). The adaptability driver: Links between behavior and evolution. *Biological Theory*, *1*, 342–345. https://doi.org/10.1162/biot.2006.1.4.342

Beach, F. A. (1955). The descent of instinct. *Psychological Review*, *62*(6), 401–410. https://doi.org/10.1037/h0049138

Belin, D., Jonkman, S., Dickinson, A., Robbins, T. W., & Everitt, B. J. (2009). Parallel and interactive learning processes within the basal ganglia: Relevance for the understanding of addiction. *Behavioural Brain Research*, *199*(1), 89–102. https://doi.org/10.1016/j.bbr.2008.09.027

Bell, A. M., & Robinson, G. E. (2011). Behavior and the dynamic genome. *Science*, *332*(6034), 1161–1162. https://doi.org/10.1126/science.1203295

Bolles, R. C. (1970). Species-specific defense reactions and avoidance learning. *Psychological Review*, *77*(1), 32–48. https://doi.org/10.1037/h0028589

Bouton, M. E. (2021). Context, attention, and the switch between habit and goal-direction in behavior. *Learning & Behavior*, *49*(4), 349–362. https://doi.org/10.3758/s13420-021-00488-z

Bouton, M. E., & Bolles, R. C. (1980). Conditioned fear assessed by freezing and by the suppression of three different baselines. *Animal Learning & Behavior*, *8*(3), 429–434. https://doi.org/10.3758/BF03199629

Bouton, M. E., Broomer, M. C., Rey, C. N., & Thrailkill, E. A. (2020). Unexpected food outcomes can return a habit to goal-directed action. *Neurobiology of Learning and Memory*, *169*, Article 107163. https://doi.org/10.1016/j.nlm.2020.107163

Breland, K., & Breland, M. (1961). The misbehavior of organisms. *American Psychologist*, *16*(11), 681–684. https://doi.org/10.1037/h0040090

Brembs, B. (2009). Mushroom bodies regulate habit formation in Drosophila. *Current Biology*, *19*(16), 1351–1355. https://doi.org/10.1016/j.cub.2009.06.014

Brembs, B. (2011). Spontaneous decisions and operant conditioning in fruit flies. *Behavioural Processes*, 87(1), 157–164. https://doi.org/10.1016/j.beproc.2011.02.005

Catania, A. C. (1973). The concept of the operant in the analysis of behavior. *Behaviorism*, 1(2), 103–116. https://www.jstor.org/stable/27758804

Catania, A. C. (2000). From behavior to brain and back again: Review of Orbach on Lashley-Hebb. *Psycholoquy*, 11(27), Article 14.

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

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

Catania, A. C. (2017). *The ABCs of behavior analysis*. Sloan.

Chittka, L., & Rossi, N. (2023). Bees learn to dance: Experience yields precision in the waggle dance of honey bees. *Science*, 379(6636), 985–986. https://doi.org/10.1126/science.adg6020

Colwill, R. M., & Rescorla, R. A. (1985). Postconditioning devaluation of a reinforcer affects instrumental responding. *Journal of Experimental Psychology: Animal Behavior Processes*, 11(1), 120–132. https://doi.org/10.1037/0097-7403.11.1.120

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. https://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 Experimetnal Psychology: Animal Behavior Processes*, 34, 101–122. https://doi.org/10.1037/0097-7403.16.4.372

Corbit, L. H. (2018). Understanding the balance between goal-directed and habitual behavioral control. *Current Opinion in Behavioral Sciences*, 20, 161–168. https://doi.org/10.1016/j.cobeha.2018.01.010

Crispo, E. (2007). The Baldwin effect and genetic assimilation: Revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. *Evolution*, 61(11), 2469–2749. https://doi.org/10.1111/j.1558-5646.2007.00203.x

D'Amato, M. R., & Schiff, D. (1964). Long-term discriminated avoidance performance in the rat. *Journal of Comparative and Physiological Psychology*, 57(1), 123–126. https://doi.org/10.1037/h0046678

Darwin, C. (1859). *On the origin of species*. John Murray.

Darwin, C. (1892). *Charles Darwin: His life told in an autobiographical chapter, and in a selected series of published letters* (F. Darwin, Ed.). John Murray.

Dawkins, R. (1982). Replicators and vehicles. In K. S. C. Sociobiology & Group (Eds.), *Current problems in sociobiology* (pp. 45–64). Cambridge University Press.

Dewey, J. (1958). *Experience and nature*. Dover. (Original work published in 1925)

de Wit, S., Watson, P., Harsay, H. A., Cohen, M. X., van de Vijver, I., & Ridderinkhof, K. R. (2012). Corticostriatal connectivity underlies individual differences in the balance between habitual and goal-directed action control. *Journal of Neuroscience*, 32(35), 12066–12075. https://doi.org/10.1523/JNEUROSCI.1088-12.2012

Dickinson, A., Nicholas, D. J., & Adams, C. D. (1983). The effect of the instrumental training contingency on susceptibility ro reinforcer devaluation. *Quarterly Journal of Experimental Psychology*, 35(1), 35–51. https://doi.org/10.1080/14640748308400912

Dolan, R. J., & Dayan, P. (2013). Goals and habits in the brain. *Neuron*, 80, 312–325. https://doi.org/10.1016/j.neuron.2013.09.007

Donahoe, J. W. (2003). Selectionism. In Lattal, K. A. & Chase, P. N. (Eds.), *Behavior theory and philosophy*. Kluwer Academic Publishers. https://doi.org/10.1007/978-1-4757-4590-0_6

Donahoe, J. W. (2012). Reflections on behavior analysis and evolutionary biology: A selective review of "Evolution since Darwin—The first 150 years." *Journal of the Experimental Analysis of Behavior*, 97(2), 249–260. https://doi.org/10.1901/jeab.2012.97-249

Dunlap, A. S., & Stephens, D. W. (2014). Experimental evolution of prepared learning. *Proceedings of the National Academy of Sciences*, 111(32), 11750–11755. https://doi.org/10.1073/pnas.1404176111

Fanselow, M. S., & LeDoux, J. E. (1999). Why we think plasticity underlying Pavlovian fear conditioning occurs in the basolateral amygdala. *Neuron*, 23(2), 229–232. https://doi.org/10.1016/S0896-6273(00)80775-8

Fanselow, M. S., & Wassum, K. M. (2016). The origins and organization of vertebrate Pavlovian conditioning. *Cold Spring Harbor Perspectives in Biology*, 8, Article a021717. https://doi.org/10.1101/cshperspect.a021717

Garcia, J., Ervin, F. R., & Kölling, R. A. (1966). Learning with prolonged delay of reinforcement. *Psychonomic Science*, 5(3), 121–122. https://doi.org/10.3758/BF03328311

Ginsburg, S., & Jablonka, E. (2010). The evolution of associative learning: A factor in the Cambrian explosion. *Journal of Theoretical Biology*, 266(7), 11–20. https://doi.org/10.1016/j.jtbi.2010.06.017

Gottlieb, G. (1991a). Experiential canalization of behavioral development: Results. *Developmental Psychology*, 27(1), 35–39. 10/1037/0012-1649.27.1.35

Gottlieb, G. (1991b). Experiential canalization of behavioral development: Theory. *Developmental Psychology*, 27(1), 4–13. https://doi.org/10.1037/0012-1649.27.1.4

Gottlieb, G. (1997). *Synthesizing nature-nurture: Prenatal roots of instinctive behavior*. Lawrence Erlbaum Associates.

Graybiel, A. M. (2005). The basal ganglia: Learning new tricks and loving it. *Current Opinion in Neurobiology*, 15, 638–644. https://doi.org/10.1016/j.conb.2005.10.006

Graybiel, A. M., & Grafton, S. T. (2015). The striatum: Where skills and habits meet. *Cold Spring Harbor Perspectives in Biology*, 7, Article a021691. https://doi.org/10.1101/cshperspect.a021691

Haig, D. (2007). Weismann rules! OK? Epigenetics and the Lamarckian temptation. *Biology and Philosophy*, 22, 415–428. https://doi.org/10.1007/s10539-006-9033-y

Hallgrímsson, B., Green, R. M., Katz, D. C., Fish, J. L., Bernier, F. P., Roseman, C. C., Young, N. M., Cheverud, J. M., & Marcucio, R. S. (2019). The developmental-genetics of canalization. *Seminars in Cellular Developmental Biology*, 88, 67–79. https://doi.org/10.1016/j.semcdb.2018.05.019

Hawkins, R. D., Carew, T. J., & Kandel, E. R. (1986). Effects of inter-stimulus interval and contingency on classical conditioning of the Aplysia siphon withdrawal reflex. *Journal of Neuroscience*, 6(6), 1695–1701. https://doi.org/10.1523/jneurosci.06-06-01695.1986

Hayes, S. C., & Sanford, B. T. (2014). Cooperation came first: Evolution and human cognition. *Journal of the Experimental Analysis of Behavior*, 101(1), 112–129. https://doi.org/10.1002/jeab.64

Hershberger, W. A. (1986). An approach through the looking-glass. *Animal Learning & Behavior*, 14(4), 443–451. https://doi.org/10.3758/BF03200092

Heyes, C., Chater, N., & Dwyer, D. M. (2020). Sinking in: The peripheral Baldwinisation of human cognition. *Trends in Cognitive Sciences*, 24(11), 884–899. https://doi.org/10.1016/j.tics.2020.08.006

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(2), 178–193. https://doi.org/10.1037/0097-7403.5.2.178

Hull, D. L., Langman, R. E., & Glenn, S. S. (2001). A general account of selection: Biology, immunology, and behavior. *Behavioral and Brain Sciences*, 24, 511–573. https://doi.org/10.1017/S0140525X01004162

Jablonka, E., & Lamb, M. J. (2005). *Evolution in four dimensions: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. MIT Press.

Killeen, P. R. (1992). Mechanics of the animate. *Journal of the Experimental Analysis of Behavior*, 57(3), 429–463. https://doi.org/10.1901/jeab.1992.57-429

Kim, J. J., Krupa, D. J., & Thompson, R. F. (1998). Inhibitory cerebello-olivary projections and blocking effect in classical conditioning. *Science*, 279(5350), 570–573. https://doi.org/10.1126/science.279.5350.570

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). American Psychological Association.

Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczek, A., Jablonka, E., & Odling-Smee, J. (2015). The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proceedings of the Royal Society B*, *282*, Article 20151019. https://doi.org/10.1098/rspb.2015.1019

Levis, N. A., & Pfennig, D. W. (2016). Evaluating 'plasticity-first' evolution in nature: Key criteria and empirical approaches. *Trends in Ecology and Evolution*, *31*(7), 563–574. https://doi.org/10.1016/j.tree.2016.03.012

Lingawi, N. W., Dezfoui, A., & Balleine, B. W. (2016). The psychological and physiological mechanisms of habit formation. In R. A. Murphy & R. C. Honey (Eds.), *The Wiley Handbook on the Cognitive Neuroscience of Learning* (pp. 409–441). Wiley.

Loison, L. (2019). Canalization and genetic assimilation: Reassessing the radicality of the Waddingtonian concept of inheritance of acquired characters. *Seminars in Cell & Developmental Biology*, *88*, 4–13. https://doi.org/10.1016/j.semcdb.2018.05.009

Lolordo, V. M. (1979). Selective associations. In A. Dickinson & R. A. Boakes (Eds), *Mechanisms of learning and motivation: A memorial volume to Jerzy Konorski* (pp. 367–398). Routledge.

Maes, E., Krypotos, A. M., Boddez, Y., Alfei Palloni, J. M., D'Hooge, R., de Houwer, J., & Beckers, T. (2018). Failures to replicate blocking are surprising and informative—Reply to Soto. *Journal of Experimental Psychology: General*, *147*(4), 603–610. https://doi.org/10.1037/xge0000413

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

Meiklejohn, C. D., & Hartl, D. L. (2002). A single mode of canalization. *Trends in Ecology & Evolution*, *17*(10), 468–473. https://doi.org/10.1016/S0169-5347(02)02596-X

Moray, N., & Connolly, K. (1963). A possible case of genetic assimilation of behaviour. *Nature*, *199*(4891), 358–360. https://doi.org/10.1038/199358a0

Morgan, C. L. (1896). *Habit and instinct*. Arnold.

Nelson, A., & Killcross, S. (2006). Amphetamine exposure enhances habit formation. *Journal of Neuroscience*, *26*(14), 3805–3812. https://doi.org/10.1523/JNEUROSCI.4305-05.2006

Nevin, J. A., & Grace, R. C. (2000). Behavioral momentum and the law of effect. *Behavioral and Brain Sciences*, *23*(1), 73–90. https://doi.org/10.1017/S0140525X00002405

Nijhout, H. F., Kudla, A. M., & Hazelwood, C. C. (2021). Genetic assimilation and accommodation: Models and mechanisms. *Current Topics in Developmental Biology*, *141*, 337–369. https://doi.org/10.1016/bs.ctdb.2020.11.006

O'Doherty, J., Dayan, P., Schultz, J., Deichmann, R., Friston, K., & Dolan, R. J. (2004). Dissociable roles of ventral and dorsal striatum in instrumental conditioning. *Science*, *304*(5669), 452–454. https://doi.org/10.1126/science.1094285

Olton, D. S. (1979). Mazes, maps, and memory. *American Psychologist*, *34*(7), 583–596. https://doi.org/10.1037/0003-066X.34.7.583

Osborn, H. F. (1896). A mode of evolution requiring neither natural selection nor the inheritance of acquired characters. *Transactions of the New York Academy of Sciences*, *15*, 141–142, 148.

Pavlov, I. P., & Anrep, G. V. (2003). *Conditioned reflexes*. Dover. (Original work printed in 1927)

Pigliucci, M., Murren, C. J., & Schlichting, C. D. (2006). Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, *12*, 2362–2367. https://doi.org/10.1242/jeb.02070

Portera, M., & Mandrioli, M. (2021). Who's afraid of epigenetics? Habits, instincts, and Charles Darwin's evolutionary theory. *History and Philosophy of the Life Sciences*, *43*, Article 20. https://doi.org/10.1007/s40656-021-00376-9

Protas, M., Conrad, M., Gross, J. B., Tabin, C., & Borowsky, R. (2007). Regressive evolution in the Mexican cave tetra, *Astyanax mexicanus*. *Current Biology*, *17*(5), 452–454. https://doi.org/10.1016/j.cub.2007.01.051

Rescorla, R. A. (1988). Pavlovian conditioning: It's not what you think it is. *American Psychologist*, *43*(3), 151–160. https://doi.org/10.1037/0003-066X.43.3.151

Robinson, G. E., & Barron, A. B. (2017). Epigenetics and the evolution of instincts. *Science*, *356*(6333), 26–27. https://doi.org/10.1126/science.aam6142

Schneider, S. M. (2003). Evolution, behavior principles, and developmental systems: A review of Gottlieb's *Synthesizing Nature-Nurture: Prenatal roots of instinctive behavior*. *Journal of the Experimental Analysis of Behavior*, *79*(1), 137–152. https://doi.org/10.1901/jeab.2003.79-137

Schneider, S. M. (2012). *The science of consequences: How they affect genes, change the brain, and impact our world*. Prometheus.

Seligman, M. E. (1970). On the generality of the laws of learning. *Psychological Review*, *77*(5), 406–418.

Sherrington, C. (1906). *The integrative action of the nervous system*. CUP Archive.

Shettleworth, S. J. (1972). Constraints on learning. In D. S. Lehrman, R. A. Hinde, & E. Shaw (Eds.), *Advances in the Study of Behavior* (Vol. 4, pp. 1–68). Academic Press.

Shettleworth, S. J. (1975). Reinforcement and the organization of behavior in golden hamsters: Hunger, environment, and food reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes*, *1*(1), 56–87. https://doi.org/10.1037/0097-7403.1.1.56

Shubin, N., Tabin, C., & Carroll, S. (2009). Deep homology and the origins of evolutionary novelty. *Nature*, *457*(7231), 818–823. https://doi.org/10.1038/nature07891

Simpson, G. G. (1953). The Baldwin effect. *Evolution*, *7*(2), 110–117. https://doi.org/10.2307/2405746

Skinner, B. F. (1938). *The behavior of organisms: An experimental analysis*. Appleton-Century.

Skinner, B. F. (1950). Are theories of learning necessary? *Psychological Review*, *57*(4), 193–216. https://doi.org/10.1037/h0054367

Skinner, B. F. (1953). *Science and human behavior*. Free Press.

Skinner, B. F. (1966). The phylogeny and ontogeny of behavior. *Science*, *153*(3741), 1205–1213. https://doi.org/10.1126/science.153.3741.1205

Skinner, B. F. (1969). *Contingencies of reinforcement*. Appleton-Century-Crofts.

Skinner, B. F. (1975). The shaping of phylogenic behavior. *Journal of the Experimental Analysis of Behavior*, *24*(1), 117–120. https://doi.org/10.1901/jeab.1975.24-117

Skinner, B. F. (1981). Selection by consequences. *Science*, *213*(4507), 501–504. https://doi.org/10.1126/science.7244649

Skinner, B. F. (1984). The evolution of behavior. *Journal of the Experimental Analysis of Behavior*, *41*(2), 217–221. 10.1901%2Fjeab.1984.41-217

Skinner, B. F. (1985). Cognitive science and behaviourism. *British Journal of Psychology*, *76*, 291–301. https://doi.org/10.1111/j.2044-8295.1985.tb01953.x

Stahlman, W. D., & Catania, A. C. (2020). Evolutionary biology and the natural selection of behavior. In S. Hupp & J. D. Jewell (Eds.), *The encyclopedia of child and adolescent development* (pp. 1–13). Wiley.

Stahlman, W. D., & Catania, A. C. (2023). Faustian bargains: Short-term and long-term contingencies in phylogeny, ontogeny, and sociogeny. *Journal of the Experimental Analysis of Behavior*, *119*(1), 192–202. https://doi.org/10.1002/jeab.812

Stahlman, W. D., & Leising, K. J. (2018). The coelacanth still lives: Bringing selection back to the fore in a science of behavior. *American Psychologist*, *73*(7), 918–929. https://doi.org/10.1037/amp0000261

Steinfeld, M. R., & Bouton, M. E. (2021). Renewal of goal direction with a context change after habit learning. *Behavioral Neuroscience*, *135*(1), 79–87. https://doi.org/10.1037/bne0000422

Strausfeld, N. J., & Hirth, F. (2013). Deep homology of arthropod central complex and vertebrate basal ganglia. *Science*, *340*(6129), 157–161. https://doi.org/10.1126/science.1231828

Thorn, C. A., Atallah, H., Howe, M., & Graybiel, A. M. (2010). Differential dynamics of activity changes in dorsolateral and dorsomedial striatal loops during learning. *Neuron*, *66*(5), 781–795. https://doi.org/10.1016/j.neuron.2010.04.036

Thrailkill, E. A., & Bouton, M. E. (2015). Contextual control of instrumental actions and habits. *Journal of Experimental Psychology: Animal Learning & Cognition*, *41*(1), 69–80. https://doi.org/10.1037/xan0000045

Thrailkill, E. A., Michaud, N. L., & Bouton, M. E. (2021). Reinforcer predictability and stimulus salience promote discriminated habit learning. *Journal of Experimental Psychology: Animal Learning and Cognition*, *47*(2), 183–199. https://doi.org/10.1037/xan0000285

Thrailkill, E. A., Trask, S., Vidal, P., Alcalá, J. A., & Bouton, M. E. (2018). Stimulus control of actions and habits: A role for reinforcer predictability and attention in the devlopment of habitual behavior. *Journal of Experimental Psychology: Animal Learning and Cognition*, *44*(4), 370–384. https://doi.org/10.1037/xan0000188

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*(4), 339–348. https://doi.org/10.3758/BF03200077

Timberlake, W. (1993). Behavior systems and reinforcement: An integrative approach. *Journal of the Experimental Analysis of Behavior*, *60*(1), 105–128. https://doi.org/10.1901/jeab.1993.60-105

Timberlake, W. (1994). Behavior systems, associationism, and Pavlovian conditioning. *Psychonomic Bulletin & Review*, *1*(4), 405–420. https://doi.org/10.3758/BF03210945

Tinbergen, N. (1951). *The study of instinct*. Clarendon Press.

Tomer, R., Denes, A. S., Tessmar-Raible, K., & Arendt, D. (2010). Profiling by image registration reveals common origin of annelid mushroom bodies and vertebrate pallium. *Cell*, *142*, 800–809. https://doi.org/10.1016/j.cell.2010.07.043

Trask, S., Shipman, M. L., Green, J. T., & Bouton, M. E. (2020). Some factors that restore goal-direction to a habitual behavior. *Neurobiology of Learning and Memory*, *169*, Article 107161. https://doi.org/10.1016/j.nlm.2020.107161

Uhl, C. N. (1973). Eliminating behavior with omission and extinction after varying amounts of training. *Animal Learning & Behavior*, *1*(3), 237–240. https://doi.org/10.3758/BF03199082

Waddington, C. H. (1942). Canalization of development and genetic assimilation of acquired characters. *Nature*, *183*, 1654–1655. https://doi.org/10.1038/150563a0

Waddington, C. H. (1953). Genetic assimilation of an acquired character. *Evolution*, *7*(2), 118–126. https://doi.org/10.2307/2405747

Waddington, C. H. (1957). *The strategy of the genes: A discussion of some aspects of theoretical biology*. Allen & Unwin.

Waddington, C. H. (1959). Evolutionary adaptation. *Perspectives in Biology and Medicine*, *2*(4), 379–401. https://doi.org/10.1353/pbm.1959.0027

Waddington, C. H., & Robertson, E. (1966). Selection for developmental canalisation. *Genetics Research*, *7*(3), 303–312. https://doi.org/10.1017/S0016672300009769

Warburton, F. E. (1956). Genetic assimilation: Adaptation versus adaptability. *Evolution*, *10*(3), 337–339. https://doi.org/10.2307/2406018

Wasserman, E. A. (2012). Species, tepees, scotties, and jockeys: Selected by consequences. *Journal of the Experimental Analysis of Behavior*, *98*(2), 213–226. https://doi.org/10.1901/jeab.2012.98-213

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. https://doi.org/10.1037/xan0000086

Watson, J. B. (1913). Psychology as the behaviorist views it. *Psychological Review*, *20*(2), 158–177. https://doi.org/10.1037/h0074428

Weismann, A. (1891). *Essays upon heredity and kindred biological problems*, Vol. 1. Clarendon Press.

Weismann, A. (1893). The all-sufficiency of natural selection: A reply to Herbert Spencer. *The Contemporary Review*, *64*, 309–338.

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. 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*(4), 511–520. https://doi.org/10.1901/jeab.1969.12-511

Wood, W., & Rünger, D. (2016). Psychology of habit. *Annual Review of Psychology*, *67*, 289–314. https://doi.org/10.1146/annurev-psych-122414-033417

Yin, H. H., Knowlton, B. J., & Balleine, B. W. (2004). Lesions of dorsolateral striatum preserve outcome expectancy but disrupt habit formation in instrumental learning. *European Journal of Neuroscience*, *19*, 181–189. https://doi.org/10.1111/j.1460-9568.2004.03095.x

Yin, H. H., Mulcare, S. P., Hilário, M. R. F., Clouse, E., Holloway, T., Davis, M. I., Hansson, A. C., Lovinger, D. M., & Costa, R. M. (2009). Dynamic reorganization of striatal circuits during the acquisition and consolidation of a skill. *Nature Neuroscience*, *12*(3), 333–341. https://doi.org/10.1038/nn.2261