American Psychologist

© 2025 American Psychological Association
ISSN: 0003-066X

https://doi.org/10.1037/amp0001537

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Beyond the Evolution Versus Learning Fallacy

Laith Al-Shawaf
Department of Psychology, University of Colorado, Colorado Springs
Department of Biology, University of Colorado, Colorado Springs
Center for Cognitive Archaeology, University of Colorado, Colorado Springs
Lyda Hill Institute for Human Resilience, University of Colorado, Colorado Springs
Institute for Advanced Study in Toulouse, Toulouse, France

The behavioral sciences have made a great deal of progress over the last century. They remain stymied, however, by the persistence of the fallacious "evolved vs. learned" dichotomy, in which researchers and students are encouraged to think of evolution and learning as contrasting, conflicting explanations for behavior. This article shows why the evolved versus learned dichotomy is false, suggests a more accurate replacement in the form of evolved learning mechanisms, and illustrates how a deeper understanding of the relation between evolution and learning improves our understanding of key psychological phenomena and removes barriers to progress in the behavioral sciences. The article does not rely on the generic and often-underspecified claim that many behaviors involve both evolution and learning, but instead offers a fine-grained look at the specific, concrete ways that evolution and learning are best conceptualized as explanatory partners rather than competitors. This analysis suggests that a better understanding of the relation between evolution and learning dissolves the false dichotomy in a concrete and substantive way, clearing a path for greater progress and fewer wasted resources in the behavioral sciences.

Public Significance Statement

Progress in the social sciences is stymied by the widespread misconception that evolution and learning are opposing explanations for behavior. This article explains why the "evolution vs. learning" dichotomy is fallacious, replaces it with a more accurate alternative, and illustrates the many ways in which evolution and learning are best conceptualized as explanatory partners rather than explanatory competitors.

Keywords: evolution, learning, levels of analysis, theory, psychology

A Long-Standing Problem in the Social Sciences

Over the last century, the behavioral sciences have grown immensely and illuminated a huge range of behavioral phenomena (Goldstein, 2015; Hunt, 2007; Lilienfeld et al., 2010; Schacter et al., 2017). Despite this, one of the most persistent problems we face is our fields' slow progress due to stagnant debates about whether particular behaviors are biological or cultural, evolved or learned. To quicken the pace of progress and build a more accurate science of mind and behavior, it is time to move past these dichotomies and replace them with a different framework. The answer to the question "is it evolved or learned?" is often "both"—but not in the boring, underspecified sense that the middle is generally a good compromise between two extremes. Instead, it is "both" in a more concrete and scientifically interesting sense. This article argues that a better understanding of the relationship between evolution and learning[1] dissolves the false dichotomy in a specific, concrete, and substantive way, clearing a path for greater progress and fewer wasted resources in the behavioral sciences.

Philip David Zelazo served as action editor.

Laith Al-Shawaf https://orcid.org/0000-0002-8600-0591

The author thanks C. R. Gallistel and Jeremy Bono for their helpful feedback on an earlier draft of this article.

Laith Al-Shawaf conceptualized, wrote, and edited the article.

Correspondence concerning this article should be addressed to Laith Al-Shawaf, Department of Psychology, University of Colorado, Colorado Springs, 1420 Austin Bluffs Parkway, Colorado Springs, CO 80918, United States. Email: lalshawa@uccs.edu

[1] In this article, I use the standard definition of "learning" in psychology: a (relatively stable or permanent) change in knowledge or behavior as a result of experience (e.g., Schacter et al., 2017).

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Laith Al-Shawaf

Consider rats, the quintessential omnivores. Their dietary strategy comes with both pros and cons. The major advantage is that they can extract nutrients from a huge variety of sources, and the major disadvantage is that new food sources might contain toxins that kill them. To solve this problem, rats are equipped with useful adaptive biases: Because sweet things tend to offer energy and bitter things tend to be alkaloid poisons, rats have an innate bias for sweet and against bitter (Gallistel et al., 1991). But this is not good enough, because the matchup is not perfect: Some bitter things are safe, and some sweet things are not. So the rats must learn what is safe and what is dangerous—and rats are indeed master learners (Gallistel et al., 1991; Kalat & Rozin, 1973; Rozin & Kalat, 1971). Their learning is strategic, precise, and well-matched to the problems they face. Rats' food behavior involves four key rules. First, in general, they prefer familiar foods over novel foods. This is called food neophobia, and it helps them avoid toxins because familiar foods have already been shown to be safe, whereas novel foods present an unknown risk (Rozin, 1976). Second, when they eat a new food for the first time, they only eat a small amount of it. This way, they will not eat enough to die, but they might get mildly ill, from which they learn to avoid that food in the future. Third, they do not eat two new foods during the same meal. If they did and they got sick, they would not be able to tell which food caused the sickness. By contrast, they have no objection to eating a new food and a familiar food in the same meal. If this happens and they get sick, they correctly infer that it was the new food and assiduously avoid that food in the future (this is essentially the "manipulate one variable at a time" rule that is so familiar to experimental scientists). Fourth, rats wait a long time between meals (Gallistel et al., 1991). This gives them enough time for an illness—if there is one brewing—to develop. If they were to eat another new meal too soon, and then an illness developed, it would confuse the inference about which food made them sick. By imposing a waiting period, rats give themselves the time they need to extract a meaningful cue that they can use for learning—a cue that would not have existed if they had failed to wait. In other words, rats actively create propitious conditions for their own learning and then harvest valuable information from the experience to guide their future behavior.

Rats' sophisticated food behavior demonstrates several key points. The first and most obvious is that innate biases and learning can coexist harmoniously. There is no reason to regard them as opposed to one another. Beyond this and more importantly, we can see clear evidence that the form and operation of rats' learning mechanisms are adaptively matched to the problem that they confront. The broader principle, which is the central argument of this article, is that evolution and learning are not competing explanations. They are natural explanatory partners that often, and sometimes *must*, go hand in hand in our attempts to explain behavior.

Evolution and Learning Are Not Conflicting Explanations For Behavior

> I sense from the classical debate between Piaget and Chomsky … that at least some of us are all too prone to think of learning and instinct as being virtually antithetical. According to this common view, behavior is one or the other, but it is rarely, if ever, both. … [T]his antithesis is false. (Marler, 1991, p. 37)

Evolution and learning are natural explanatory partners, but few in the social sciences think of them that way (Al-Shawaf, 2024). Instead, they are routinely described as diametric opposites. For example, consider the clear dichotomization in this claim by an established social scientist: "If we have the capacity … to change by learning from example, then our behavior is determined by socialization practices and by our cultural histories, and not by our nature!" (Sussman, 2005, p. 97). In many cases, journals and textbooks in the social sciences describe a behavior as a disjunctive choice: Is it evolved *or* learned, is it nature *or* nurture? (see, e.g., Chapter 2 in Guest, 2013). In some cases, lip service is paid to the notion that both matter, or that a behavior is the product of both evolution and learning at the same time (e.g., Stangor & Walinga, 2014). But these well-intentioned "both matter" statements are often not terribly substantive: They lean away from the concrete; they are typically abstract diplomatic statements that both evolution and learning are important. What is much rarer in the social sciences is (a) a detailed explanation of why evolution and learning are not in conflict as explanations of behavior, (b) a concrete exploration of the relationship between the two, and (c) an illustration of how a solid grasp of this relationship can improve our understanding of learning mechanisms and the behaviors they produce. This article sets out to accomplish these three goals.

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

First, why should we think that evolution and learning are *not* in conflict? The primary answer is that they lie at different levels of analysis (Alcock, 2009; Symons, 1979; Tinbergen, 1963). Evolutionary explanations are located at the "ultimate" or distal level of analysis, which is about why a behavior exists or what function the behavior serves. Learning is at the "proximate" level of analysis, which is about how the behavior is achieved and what underlying mechanisms produce it. A crucial point is that because these levels of analysis have different explanatory targets, it is wrong to assume that there is an automatic conflict between evolutionary and learning explanations (Alcock, 2009; Al-Shawaf, 2024, 2020; Nesse, 2019).

Furthermore, because they lie on different levels of analysis, proximate and ultimate explanations are complementary, and both are needed for a complete explanation of the behavior in question. As one pair of authors put it when discussing proximate and ultimate explanations of anxiety, "even if we knew every connection of every neuron, every action of every transmitter, our understanding would remain inadequate until we also knew the function for which those mechanisms were shaped" (Marks & Nesse, 1994, p. 259). Any behavioral explanation that involves only one of these levels of analysis is necessarily incomplete.

Stated differently, an evolutionary hypothesis about a behavior says "this behavior has an evolutionary basis." It emphatically *does* not imply "this behavior involves no learning." An evolutionary explanation for a behavior is about why it arose over evolutionary time and what survival or reproductive function it serves. This does not automatically commit one to a specific view of how or when it develops during an organism's lifespan. Evolved behaviors can involve some learning, no learning, or a great deal of learning (Alcock, 2009; Gallistel et al., 1991; Marler, 1991). For more details on why evolution and learning are not automatically in conflict, and for a discussion on the specific cases in which they can conflict, see discussion in Al-Shawaf (2024) and Lewis et al. (2017).

A question then arises: If it is true that evolution and learning are not in conflict, then why are they routinely discussed in the social sciences as if they are diametrically opposed explanations? The answer seems to be that people commonly take the claim that "X is evolved" to imply two additional claims: first, that "X does not involve learning" and, second, that "X is present from birth." In reality, neither of these claims follow; to suggest that something is evolved does not imply that it is present from birth, nor does it imply that it is immune to learning or change (Al-Shawaf et al., 2018). Similarly, the claim that a behavior is a product of evolution also does not imply that it is impervious to the influence of culture (e.g., Gaulin & McBurney, 2001). The core problem is that in the social sciences, we often mistake an ultimate-level evolutionary hypothesis for a proximate-level "no learning" statement. Because of this, evolution and learning are erroneously regarded as being locked in an automatic, necessary conflict. This is not true, and it serves as an unnecessary roadblock to progress in the social sciences (Al-Shawaf, 2024).

An accurate understanding of the intimate relationship between evolution and learning enhances our ability to explain behavior. The rest of this article analyzes key aspects of the relationship between evolution and learning, with a view toward replacing their false dichotomization in the behavioral sciences.

But first, there are a few key principles that offer useful background for the rest of the discussion: Learning exists on a continuum, behavior often results from innate templates combined with learned content, and "evolved" does not mean "inflexible."

Basic Principles of Behavior That Weaken the Evolved Versus Learned Dichotomy

Instead of "Evolved Versus Learned," There Is a Continuum of Learning—And Less of One Does Not Mean More of the Other

There is a continuum of learning, ranging from zero learning at one end to a great deal of learning at the other. Specific behaviors can fall anywhere on this learning continuum: present from birth and requiring essentially no learning, or involving a huge amount of learning, or somewhere in between. In some ways this is obvious, but it is a helpful first step in weakening the evolved vs. learned dichotomy. As comparative psychologists Mary Olmstead and Valerie Kuhlmeier put it, "[R]ather than separating innate from learned behaviors, ethologists now view these as traits that vary along a continuum. Inherited mechanisms set up a behavioral response that is then modified by experience; this modification may be minimal or extreme" (Olmstead & Kuhlmeier, 2015, p. 16).

Specific behaviors can even occupy more than one place on this spectrum. For example, rhesus monkeys show a preference for conspecific faces, and this preference is based on two mechanisms: one that is innate and one that involves learning during a sensitive window in development (Olmstead & Kuhlmeier, 2015).

At the less-learning end of the spectrum, we have examples such as Belding's ground squirrels, who can recognize their kin via odor. Biological sisters who are reared apart recognize each other's odors despite never having met before, and they engage in fewer aggressive behaviors than nonsiblings reared apart (Alcock, 2009). Even when juveniles are reared without exposure to their relatives, they can differentiate between the odor of close genetic relatives, distant relatives, and nonrelatives (Mateo, 2002; see also Mateo & Johnston, 2000, for evidence of the same in golden hamsters).

At the same time, the very same squirrels also use the cue of *coresidence* in addition to odor, and they do require learning to use this cue correctly. These squirrels show decreased

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

aggression to others they were reared with, regardless of whether their nestmates are genetically related or not (Holmes & Sherman, 1982). Importantly, you need to learn who you were reared with; you cannot be born knowing this in advance. So in a single example, we have a case in which the same species uses two cues, one that involves learning and one that does not. Both cues—the learned one and the nonlearned one—serve as inputs into an evolved system that processes these cues to figure out (i.e., learn) who the organism's kin are. Right from the first example, the assumption of conflict between evolution and learning as explanations for behavior appears to be on shaky ground.

There are plenty of behaviors in the animal kingdom that fall toward the less-learning end of the spectrum. Kittens and chicks respond to looming stimuli with escape behavior even if they were raised in the dark and have never before been exposed to looming stimuli (Schiff, 1965). Two-day-old human infants discriminate between biological motion and random motion in point-light displays, even when the biological motion comes from nonhuman animals (Simion et al., 2008). Researchers have hypothesized that this ability to detect and to pay more attention to biological motion underlies agency detection and other aspects of social cognition (Olmstead & Kuhlmeier, 2015). But as we will see, just because these abilities appear early in life and require little to no learning, this does not make them "more evolved" than abilities that develop later.

Other behavioral examples involve comparatively more learning. Vervet monkeys give different types of alarm calls for the different types of predators they face in their natural environment: snake, leopard, and eagle (Seyfarth et al., 1980). Infant monkeys need to learn which calls to give to which predators, as they are not born with this knowledge. When infants start to produce alarm calls, their initial calls cast a broad net and are less precisely calibrated to the exact type of predator (Gallistel et al., 1991). For example, they may make an eagle call in response to a different type of bird, or a leopard call in response to an animal that looks vaguely like a leopard. Over time, they learn to narrow their calls, eventually producing the precise fit between predator and alarm type that characterizes adult calls (Seyfarth & Cheney, 1986). However, their learning and their initial performance are both nonrandom: Even as infants, they only provide leopard calls to terrestrial mammals, not to snakes or birds. They only make eagle calls in response to birds, never to snakes or land mammals. And they only make snake calls in response to snakes and long thin things. Over their development, the infants learn to restrict their calls further, eventually hitting the exact target (Gallistel et al., 1991; Seyfarth et al., 1980). This example illustrates three things at once: the fact that the vervet monkeys are born with an innate template, the indisputable importance of learning as they go from broader calls to more precisely calibrated ones, and the fact that the learning process is not random; it is strategic and adaptively structured. More broadly, the example also illustrates the harmonious coexistence of innateness and learning in the same system. There is no reason to construe them as opposing factors; they are partners in service of the same adaptive goal.

Other examples demonstrate a greater degree of learning still. For example, learning to read and write takes years of formal instruction for humans, unlike learning to speak, which develops automatically and without formal instruction as long as the child is exposed to language (Pinker, 2007). Similarly, chimpanzees can learn some elements of sign language, but only after much training, and it never reaches the level of human command of language (Olmstead & Kuhlmeier, 2015; Wynne & Udell, 2020). These examples suggest that it makes more sense to think of learning as a continuum rather than an all-or-nothing counterpart to innateness[2] (Olmstead & Kuhlmeier, 2015).

Evolution Helps Explain Why There Is a Continuum of Learning in the First Place

We might reasonably ask *why* learning exists on a continuum in the first place. Why don't all behavioral outcomes involve the exact same degree of learning, whatever that might be? The answer is that the amount of learning is itself subject to natural selection. The amount of learning required to solve a problem varies as a function of how useful learning is in that particular environment for the particular problem that the organism is facing (Alcock, 2009; Pontes et al., 2020; Symons, 1979). Stochastic dynamic programs show that animals spend less time learning when cues in their environment are either *uninformative* or *highly informative*, and they spend more time learning when cues are moderately informative (Frankenhuis & Panchanathan, 2011).[3] These computational models show that when environmental cues are uninformative, organisms do not gain much by continuing to sample cues, so learning is minimal. And when cues are highly informative, organisms gain a lot in the early stages of sampling, with a steep drop-off in how useful additional learning is—so the learning period is again relatively short. By contrast, when cues are *moderately* informative, the learning period is extended because additional learning continues to pay fitness dividends for a longer period of time (Frankenhuis & Panchanathan, 2011; see also Fenneman & Frankenhuis, 2020). Similarly, other models show that certain environmental conditions—namely, environmental patterns that vary across generations but are reasonably stable within an organism's lifetime—provide circumstances that drive the evolution of learning (Pontes et al., 2020). All of these

---

[2] Again, the concept of a continuum of learning does not imply that behaviors involving less learning are "more evolved" or that those involving more learning are "less evolved." Because evolution and learning are not competing explanations vying for different slices of the explanatory pie, it does not make sense to think of them in this zero-sum analysis of variance way.

[3] And when their Bayesian priors are less informative (Frankenhuis & Panchanathan, 2011)

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

analyses point to the fact that learning is a form of phenotypic plasticity that is produced by evolution under specific circumstances—not an alternative to evolution (Fox et al., 2019; Pontes et al., 2020).

This reflects a key principle: Learning, as with everything else in biology, comes with costs, including opportunity costs. Neurocognitive mechanisms for learning will evolve in contexts where their benefits outweigh their costs (Alcock, 2009).[4] But learning mechanisms are neurally expensive, and learning takes time, and some problems are fatal if they are not solved correctly on the first try (Lima & Dill, 1990).

This means that there are some contexts in which learning mechanisms present a net benefit relative to alternative options and some contexts in which they do not. For example, female banded demoiselle damselflies (*Calopteryx splendens*) learn to differentiate conspecific males from males of other species when they live in areas that overlap with similar-looking species, but never learn to make this differentiation when they do not live in such areas (Olmstead & Kuhlmeier, 2015). The key point is that learning offers both costs and benefits, the degree of which depends on the animal's specific ecology, the specific problems it faces, and how informative the cues it encounters are with respect to the state of the world (Frankenhuis & Panchanathan, 2011). These costs and benefits affect whether animals solve particular problems using a great deal of learning, no learning, or a moderate amount of learning (Alcock, 2009; Frankenhuis & Panchanathan, 2011).

In sum, learning exists on a continuum, not in an innate versus learned dichotomy, and evolution plays an important role in determining where behaviors fall on this continuum. As we will see in the next section, if we start to think of learning *mechanisms* (rather than specific behaviors) as the product of evolution, it becomes even clearer that there is no inherent conflict between evolution and learning.

Behavior Is Often the Product of Innate Templates Combined With Learned Content

The finely graded continuum of learning, and the fact that selection affects where behaviors fall on this continuum, together weaken the "evolved vs. learned" dichotomy. These facts highlight how unhelpful and misleading it is to conceptualize learning and evolution as opposing forces.

The dichotomy is weakened further when we focus on the *mechanisms* that produce behavior. In a great variety of cases, it makes most sense to think of a behavioral outcome as simultaneously innate *and* learned because it is the product of an innate template or algorithm combined with learned content or inputs into that algorithm. This is the model for the well-known phenomenon of imprinting: The "following rule" is innate, but experience supplies the content of which exact object the animal should follow (Mayr, 1974, 2004). This is why you can end up with amusing results like the goslings that famously imprinted on Konrad Lorenz and followed him around everywhere (Lorenz, 1935): The organism learned the "wrong" thing because its innate template received an unexpected or mismatched input.

In many species, organisms inherit innate templates that are combined with learned input to produce behavior. For example, *Polistes* paper wasps inherit systems that implement rules like "Learn [the odor of your nest] soon after you emerge as an adult, and then respond non-aggressively to those individuals that share this odor" (Alcock, 2009, p. 73; Gamboa, 2004). The functional system that specifies this following rule is innate, but the specific odor that the wasp must attend to is learned. It appears that within hours of emerging, wasps learn a nest odor template and compare subsequent odors that they encounter with that template. If the odors are sufficiently similar, the wasp tolerates its conspecific, but if they are not, the wasp rejects its conspecific (Gamboa, 2004). As a result, the behavior involves both an innate component (the rule) and a learned component (the odors). It makes no sense to think of the two components as conflicting with one another. They are individually necessary and jointly sufficient for the adaptive behavior they produce. Take away either the innate or the learned component and you lose the adaptive outcome.

The same is true of song learning in birds (Konishi, 1965; Marler, 1991; Olmstead & Kuhlmeier, 2015)—the outcome involves an innate component and a learned component, both of which are necessary for proper song development. Male sparrows who have been deafened early in life develop abnormal songs that do not have the required auditory characteristics for their species (Marler & Sherman, 1983). Such birds fail to develop normal song regardless of whether they are deafened *before* they ever hear song or *after* they hear it but before they have developed the ability to produce it themselves. This is because, to produce a normal song, these sparrows must not only be able to hear *others' song*—they must also be able to hear *themselves*. Why? Evidence suggests this is because they compare what they are hearing—including what they themselves are producing—with innate templates in their brains. These innate templates process novel inputs to drive the learning process. The combination of innate templates with learned content is key to producing the eventual output of birdsong (Marler, 1991).

A similar interpretation applies to the findings on Belding's ground squirrels discussed earlier. These squirrels learn to identify kin partly by matching the odors of their nestmates (which are learned and not known before birth) to an innate template (e.g., Holmes & Sherman, 1982). Much learning takes place in this way, as a product of learning mechanisms that process novel environmental cues interacting with innate templates.

---

[4] (And when they are not constrained from evolving by other limits on natural selection, e.g., Dawkins, 1982).

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

It is worth stressing again how unhelpful and untrue to reality the *evolved versus learned* or *innate versus learned* dichotomization is. A more accurate formulation would be: evolved systems enable learning. Learning occurs via the combination of evolved systems with environmental inputs, both of which are crucial and indispensable elements of the learning process. In this way, behavioral outcomes are produced by an evolved learning mechanism in which "evolution" and "learning" are deeply intertwined as explanatory complements, not competitors.

Evolved and yet Flexible

The third important background principle is that contrary to widespread misconceptions, "evolved" does not mean "inflexible."

The casual observer of fields like psychology and animal behavior knows that the issue of "flexibility" permeates discussions of evolution and learning. The presumption is that if something is learned, it is flexible, plastic, and capable of changing. By contrast, if something is evolved, it is rigid and inflexible and cannot be changed (Al-Shawaf et al., 2019; Buss, 2019; Marler, 1991). It turns out that this is wrong in both directions: Some learned things become quite fixed after they are learned, and some innate things are quite flexible. (Even the standard definition of "learning" in psychology reflects this: a *relatively stable* or permanent change in knowledge or behavior as a result of experience; Schacter et al., 2017).

As an example of an environmentally driven response that can become fixed, consider certain polyphenisms. A polyphenism is when an organism encounters a key environmental input and consequently undergoes a change, channeling its development into one of two or more discrete types. For example, male dung beetles will develop into either a horned type or a hornless type, based largely on the nutrition available to them as juveniles (Simpson et al., 2011). This change is permanent and irreversible. In tiger salamanders, larvae will either develop into typical morphs that feed on small aquatic invertebrates or cannibal morphs that eat other tiger salamanders. This developmental switch is triggered by having lots of conspecific larvae around (Hoffman & Pfennig, 1999) and is also affected by the extent to which the larva is surrounded by kin (less likely when surrounded by kin; Pfennig et al., 1994). Accent in children appears to be learned during a sensitive window, and it is quite difficult to acquire a native accent in a foreign language if one learns the language as a late adolescent or an adult (Piske et al., 2001; Tahta et al., 1981, but see also Munro & Mann, 2005). In other words, in some cases, environmentally driven changes can result in relatively fixed or difficult-to-reverse outcomes (Frankenhuis & Panchanathan, 2011).[5]

The opposite phenomenon is even more common: Many evolved systems enable flexibility. For example, sensitive windows in many species appear to be innate, but their structure can permit flexibility. In some bird species, if the young are hatched very late in the season, they emerge when singing (which is a seasonal activity) has already ended for the year. In these cases, the sensitive period's closure may be delayed until the next spring. In other cases, when birds are deprived of conspecific models for learning birdsong, this can also delay the closure of the sensitive window. In other words, an innately specified sensitive window can still be labile. And in the case of innate templates for song learning in birds, the learning process sometimes transforms the templates themselves, leading to their modification, elaboration, or enrichment (Marler, 1991). As bird learning expert Marler (1991) puts it: "the invocation of innate influences does not mean sacrifice of the potential for behavioral flexibility; rather, instincts to learn set a species-specific context within which experience operates" (p. 59).

Examples of innate but flexible processes abound. For instance, song sparrows and swamp sparrows have an innate preference for the songs of their own species. If you present male swamp sparrows with simplified songs of either their own species' syllables or those of song sparrows, both of which they have never heard before, they favor the sounds of their own species. The young birds then resing the syllables of their species in the normal syntactical pattern, *even if they have only ever heard these syllables sung in an incorrect, jumbled order* (Marler, 1991).[6] And yet, despite this strong innate influence, sparrows can swerve if necessary: If they are never exposed to conspecific song, they will successfully learn nonpreferred song from another species, especially if they are given additional forms of help such as a live tutor (Marler, 1991).

The point is obviously not that learning always leads to fixed outcomes and innately specified traits are always malleable. Instead, what these examples illustrate is that it is wrong to automatically equate "innate" with "rigid" and "learned" with "flexible." (That would be too rigid and inflexible.) Relatedly, the idea that nonhuman animals respond to stimuli in an automatic or inflexible manner is a misconception (Cesario et al., 2020). Plasticity can be found everywhere, including in plants, animals, and bacteria (Sommer, 2020). An overwhelmingly common setup in animal brains is that innate influences prop up learning systems that have the capacity to flexibly produce outcomes in response to environmental inputs (Alcock, 2009; Marler, 1991). In other words, organisms learn

---

[5] The point is not that all polyphenisms or environmentally driven changes are irreversible, of course. The point is just that some of them are. This, along with the fact that many evolved systems are flexible, highlights how unhelpful and inaccurate it is to equate "evolved" with "rigid and fixed" and "learned" or "environmental" with "flexible."

[6] This is reminiscent in some ways of the creolization of pidgin languages in humans (Bickerton, 1984; Pinker, 1995, 2007) and the finding that deaf children will improve upon their hearing-abled parents' impoverished sign language grammar, fixing it and grammatizing it for them (Pinker, 1995, 2007).

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

because of the combination of environmental regularities with evolved mechanisms that enable them to exploit and benefit from these environmental regularities.[7] Yet again, we see how unhelpful and inaccurate it is to think of "evolved" and "learned" as opposites or as explanatory competitors.

So far, the argument has been that evolution and learning are not conflicting explanations. One key reason for this is that they lie on different levels of analysis—ultimate for evolution and proximate for learning. Moreover, when we looked at specific empirical examples, from birds to vervet monkeys to humans, it quickly became evident that the evolved versus learned dichotomy is on shaky ground. Weakening the dichotomy, the evidence suggests that there is a finely graded continuum of learning, that natural selection influences the amount of learning involved, that examples involving less learning are not "more evolved" than those involving more, that many behaviors are best conceptualized as the product of innate rules combined with learned content, and that evolved systems are often flexible rather than rigid.

This suggests that we need a more nuanced alternative to the evolved versus learned dichotomy. But a basic question remains: Why do learning mechanisms evolve in the first place?

Why Do Learning Mechanisms Evolve in the First Place?

The environment can be variable and unpredictable, and in many cases, it is impossible for an organism to be born knowing everything it needs to know. Some things are unknowable in advance—who will my siblings be? The last time we went to that watering hole, did we encounter any predators? Is this novel food toxic? As a result, evolution shapes learning mechanisms: computational systems in the brain that survey the environment, sampling cues and extracting the information needed to take advantage of the opportunities and solve the problems facing the organism (Tooby & Cosmides, 2005).

The late great behavioral ecologist John Alcock phrased the rule with characteristic clarity: "Natural selection favors […] the mechanisms underlying learning only when there is environmental unpredictability that has reproductive relevance for individuals" (Alcock, 2013, p. 350). For example, sexually deceptive orchids are equipped with flowers that look and smell a bit like female thynnine wasps (Gaskett et al., 2008). These orchids lure male wasps that attempt to copulate with the flower petal (Stoutamire, 1974). After these failed reproductive attempts, male wasps sometimes learn the location of pseudofemale flowers and avoid such trickery and wasted effort again in the future (Alcock, 2009; Peakall, 1990).

The broader point is that the existence of learning mechanisms depends on environmental selection pressures and on the costs and benefits of those learning mechanisms. For example, *P. fuscatus* wasps readily learn to recognize the individual faces of their conspecifics, but *P. metricus* wasps do not (Sheehan & Tibbetts, 2010). Why the difference between these two closely related species? It is because *P. fuscatus* wasps join their peers in founding colonies, and because they compete for dominance, they need to recognize individual conspecifics. By contrast, *P. metricus* wasps are solitary creatures that found their colonies alone (Sheehan & Tibbetts, 2010, 2011). Because there is no need for *P. metricus* wasps to be able to learn to individuate all of their peers, it would be wasteful to build neural mechanisms devoted to this task.

To put it differently: All learning mechanisms are costly. They take time and neural resources to build, maintain, and run. As such, they will evolve only when these substantial costs are sufficiently outweighed by survival or reproductive benefits (Alcock, 2009). If the costs are too high, or there isn't sufficient benefit to learning that particular outcome, the learning system is unlikely to evolve.[8] The social and ecological environment determines the costs and benefits of learning, and only those learning mechanisms with a sensible balance sheet pass through the filter of natural selection.

Bats provide a second example of this principle. Many bats are dietary generalists, such as the big brown bat (*Eptesicus fuscus*), the Antillean fruit-eating bat (*Brachyphylla cavernarum*), and the Jamaican fruit bat (*Artibeus jamaicensis*). This means that they can eat a wide variety of foods. In all three of these species, bats readily learn food aversions: If you give them a food and make them sick, they will quickly learn to avoid that food in the future, and they will only need a single trial to learn this food aversion (Ratcliffe et al., 2003). This makes sense, because like the rats in the example that opened this article, these bats are omnivores. They need to be able to learn which novel foods might be toxic.

Vampire bats, by contrast, are dietary specialists who feed exclusively on blood, and their learning systems are very different. Even if you give vampire bats poisoned blood, they are simply unable to learn food aversions because there was never any selection pressure on them to evolve brain mechanisms capable of learning such a thing—and there was no other food they could switch to anyway (Ratcliffe et al., 2003). You can craft an experiment in which it would benefit vampire bats to be able to learn to avoid a

---

[7] Additionally, learning and plasticity are influenced by genetics and can themselves play a role in driving further evolution (Baldwin, 1896; Bradshaw, 1965; Sommer, 2020; West-Eberhard, 2003).

[8] The same logic applies outside of learning, of course: Any time an organism invests resources in one biological domain, such as building a stronger tail, fewer resources are left over for other allocations, such as to immune function or a better visual system (e.g., Charnov & Krebs, 1974; Charnov et al., 2007; Zera & Harshman, 2001).

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

certain food, and yet they still cannot do it because they never evolved neurocognitive mechanisms capable of learning such a thing.

The neurocognitive mechanisms that enable learning are incredibly useful, and many of them are necessary for survival. But like everything else in the biological world, they are subject to the exacting cost–benefit calculus of natural selection. They evolve only when the hefty costs of building and maintaining an expensive neural learning mechanism are outweighed by the benefits. This is why (and when) learning systems evolve in the first place.

What Characteristics of Learning Mechanisms Are Influenced by Evolution?

So learning mechanisms evolve in response to environmental pressures and are subject to the cost–benefit calculus of natural selection. But in what specific ways does evolution shape learning mechanisms? Do the specific characteristics of learning mechanisms bear the imprint of natural selection?

This section discusses four specific influences of evolution on learning mechanisms: (a) why animals learn some things more easily than others, (b) why different species learn different things when exposed to the same stimuli, (c) specific characteristics of the learning process, such as the presence or absence of a sensitive window, social versus asocial learning, and so on, and (d) why organisms sometimes learn *mal*adaptive behaviors. In each of these four influences, we can see the imprint of evolution on the learning process.

The overall picture that emerges from this body of evidence is that learning mechanisms evolve in concrete and specific ways to fit the environmental problems that drove their evolution. This results in a precise, context-specific, species-specific fit between learning mechanisms and the environmental problems they evolved to solve.

Another way of putting this is that to understand human and animal learning, it helps to remember that "form follows function": Understanding why learning mechanisms evolved helps shed light on how they work, and why they work that way rather than some other way (Al-Shawaf, 2024).

Why Animals Learn Some Things More Easily Than Others

> Animals can form some associations easily, others with some difficulty, and others not at all. (Gallistel et al., 1991, p. 4)

All animals, including humans, learn some things more easily than others (Gallistel, 1990; Seligman & Hager, 1972; Washburn et al., 1965; Wynne & Udell, 2020). To understand why organisms learn some things more readily than others, it helps to pay attention to their evolutionary history, the problems that drove the evolution of their learning mechanisms, and the ecological cues that have repeatedly been associated with those problems.

For example, in Garcia's classic learning experiments, rats easily learned to associate illness with food cues, but not with lights or buzzers (Garcia & Koelling, 1966). Why? Because in the rats' evolutionary history and natural ecology, spoiled food was often associated with illness, but buzzers and lights were not. As a result, there was a strong selection pressure on rat brains to learn the food–illness association, and no comparable selection pressure to learn the irrelevant association between food and buzzers or lights—thus, rats learn the latter association only with great difficulty (Garcia & Koelling, 1966; Olmstead & Kuhlmeier, 2015). Similarly, pigeons find it easy to learn to associate food with visual stimuli, but much more difficult to learn to associate food with auditory stimuli (Olmstead & Kuhlmeier, 2015). The reason is the same: In pigeons' natural environments over the course of their evolution, the presence of food was tightly linked with particular visual cues, but not auditory ones. The pigeon brain is thus equipped with a learning system that privileges ecologically sensible inputs over irrelevant ones (in this case, visual cues over auditory ones), making it easier to learn some things rather than others. Understanding why animals learn some relationships more easily than others requires understanding what they evolved to learn and why.

In a clever experiment, researchers presented pigeons with a *redundant* conditioned stimulus made up of both a light and an auditory tone (LoLordo et al., 1982). Thinking evolutionarily, the researchers reasoned that pigeons would treat sound stimuli as danger-related and visual stimuli as food-related. Consequently, they predicted that during transfer tests, pigeons' escape behavior would be conditioned to the sound, whereas their appetitive, pecking-for-food behavior would be conditioned to the light. This is exactly what they found (LoLordo et al., 1982). This precise pattern of results, which the researchers predicted a priori, only makes sense when you understand that learning mechanisms do not exist in a vacuum; they evolved via natural selection to solve particular environmental problems. The structure of learning mechanisms reflects their function—and their function is tied to how the particular species under investigation solves problems in its natural ecology (Gallistel, 1990). You can see the footprint of selection in the form and operation of these learning mechanisms today.

As pioneer animal learning researcher Charles Gallistel put it:

> Animals behave as if they treat many stimulus-reward, stimulus-response and … stimulus-stimulus pairings as privileged. These privileged relationships cannot always be explained by an animal's conditioning history; instead, they often make sense only when considered in terms of the evolutionary-functional role they play in the animal's life. (Gallistel et al., 1991, p. 8)

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

This is also why the Brelands, students of B.F. Skinner, famously had trouble conditioning animals to do things that did not fit their evolutionary histories or natural behavioral repertoires (Breland & Breland, 1961). Despite being experts in behaviorist principles, the Brelands found that they could not condition animals to engage in “circus tricks” that were incompatible with the animals’ natural behavior (Breland & Breland, 1961). Instead, their research subjects learned some things easily and others only with great difficulty or not at all. For example, their raccoon often failed to do what he was being trained to do with the coins the experimenters gave him, often engaging in “washing behavior” (a natural food preparation behavior) instead. Similarly, their pig drifted away from its conditioned behavior and toward rooting and shaking—both behaviors that are part of its repertoire for obtaining food (Breland & Breland, 1961). The Brelands argued that these anomalies, and the differences between what their animals found easy or difficult to learn, could only be explained by considering the evolutionary history of the animals and the evolved function of their learning mechanisms (Breland & Breland, 1961; Olmstead & Kuhlmeier, 2015; Wynne & Udell, 2020).

Humans show a similar effect: In line with our evolutionary history and the evolved function of our learning mechanisms, we learn some things more easily than others (Mineka & Öhman, 2002; Öhman & Mineka, 2003). Humans and monkeys associate electric shocks with pictures of snakes and spiders more readily than with pictures of flowers or houses (Öhman et al., 1985) or even pictures of guns and electrical outlets (Öhman & Mineka, 2001). Both humans and monkeys will rapidly learn a fear of snakes via observational learning, but it is much more difficult to get them to learn a fear of innocuous stimuli, even if they observe a model being afraid of these stimuli (DeLoache & LoBue, 2009; Mineka & Cook, 1988; Öhman & Mineka, 2001). The claim is not that humans are born with a fear of snakes; the claim is that humans are born with a learning mechanism that finds it easier to learn to fear snakes than stimuli that were not ancestrally dangerous for our species. The neural systems that enable learning “have evolved to serve a particular function [… and they] determine what can be associated with what” (Gallistel et al., 1991, p. 10).

The imprint of selection can also be seen in the extinguishing process: Humans and monkeys have more trouble getting rid of, or overcoming, a fear of snakes and spiders than they do other objects (Mineka & Öhman, 2002; Mystkowski et al., 2002). And in studies with U.S. and Shuar children, researchers found that human children show privileged learning of information about predators compared with other information. Children learned information about predators after a single trial, without any feedback, and recalled it accurately a week later in surprise tests—an impressive feat that they did *not* manage when it came to nonpredator information (Barrett, 2015; Barrett & Broesch, 2012).

Many songbirds show a similar pattern when learning song. They not only *prefer* to learn their own species’ song, they also find it easier (Marler, 1991). Evidence shows that this is not a problem of perception: the birds are not hard of hearing, nor do they have trouble auditorily parsing the sounds made by other species. They can hear and distinguish the songs of other species, sometimes even discriminating between the songs made by different individuals (Marler, 1991). And yet they either fail to learn the songs of other species or, if they do learn them, they forget them easily. The fact that it is not a failure of perception or cognition is important—it’s a feature, not a bug. Songbird brains evolved in such a way that they are less likely to learn the song of another species, and are quicker to forget it, relative to that of their own species. Another way of putting this is that “an open program is by no means a *tabula rasa*; certain types of information are more easily incorporated than others” (Mayr, 1974, p. 652). In other words, neural learning mechanisms are built to privilege some types of information over others, depending on the species and the problems it needs to solve.

In sum, evolution shapes learning mechanisms such that animals learn some things easily and others only with great difficulty. This depends on the function of the learning mechanism and the animals’ evolutionary history. Learning doesn’t just occur by magic; it’s difficult computational work, and it takes complex, metabolically expensive neurocognitive mechanisms to accomplish it. The way these mechanisms evolved—and the reason they evolved—influences the shape of the animal’s learning.

Why Different Species Learn Different Things When Exposed to the Same Stimuli

The same general principle helps explain why different species are capable of learning different things. For example, the cliff swallow is very good at recognizing its own offspring based on their vocal calls. By contrast, the barn swallow is less adept at learning its offspring’s calls and differentiating them from nonoffspring (Alcock, 2009). Why the difference between these two species? Why can the parents of one species learn to differentiate their offspring from unrelated individuals, whereas the parents of another species cannot?

The answer is that in the cliff swallow, it pays fitness dividends to be able to do this, but in the barn swallow, it does not—or at least not enough. This is because the cliff swallow is colonial and social, and offspring sometimes end up in the wrong nest, which makes it important for cliff swallow mothers to be able to differentiate their offspring from strangers (Medvin et al., 1993). By contrast, the barn swallow is less social, and it is much rarer for offspring to accidentally end up in the wrong nest, which means that the selection pressure on barn swallow mothers to evolve neural mechanisms capable of learning the difference between their offspring’s calls and those of other chicks was much

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

weaker (Medvin & Beecher, 1986; Medvin et al., 1993). It is this matrix of costs and benefits that determines whether or not animals evolve neurocognitive mechanisms geared toward learning to solve these problems. Learning mechanisms evolve differently from species to species according to the particular challenges and opportunities they have faced over deep time (Alcock, 2009; Gallistel, 1990; Olmstead & Kuhlmeier, 2015).

For example, consider the obvious—but remarkable—fact that different organisms will learn different things even if they are exposed to the *exact same* inputs and schedules of reinforcement. Given sufficient exposure, a young child will learn Arabic or Tamazight, but a puppy will not (Tooby & Cosmides, 1992, 2005). The puppy will learn other things quite well, though: how to offer the play signal to indicate that apparent aggression is just part of a game, and how to track human gaze, for example (Colbert-White & Kaufman, 2019; Hare et al., 2002). If learning were only about exposure, and not centrally about the evolved systems in the brain that process the inputs from that exposure, then different species would not learn different things when exposed to the same stimuli (Al-Shawaf, 2019; Mayr, 1974; Tooby & Cosmides, 2005). This is why attempts to teach apes language have ended very differently from attempts to teach humans language (Olmstead & Kuhlmeier, 2015; Wynne & Udell, 2020). And as researchers have pointed out, while a 3-pound brain can learn language, game theory, and local moral norms quite well, a 3-pound cauliflower exposed to the exact same instruction and same reinforcement schedules will fail to learn any of the above (Tooby & Cosmides, 2005). Why?

Even though the outcome is obvious—we all know that cruciferous vegetables can't learn language—asking the question still shines a light on an important principle. The principle is that learning is made possible via brain mechanisms whose provenance lies in evolution. These mechanisms enable specific kinds of learning—what the organism needs in its natural environment—in ways that differ from species to species. Because these brain mechanisms were built by evolution, it makes sense that understanding why they evolved would help us better understand how organisms' learning mechanisms work. This point is widely understood and accepted for animals' sensory and perceptual mechanisms (e.g., Goldstein & Cacciamani, 2021; Marr, 1982; Yong, 2022). The exact same point applies to organisms' learning mechanisms (Rozin & Kalat, 1971), but for some reason is much less widely appreciated.

Seligman and Hager famously coined the phrase "biological preparedness" to describe this phenomenon. The key notion is that organisms are "prepared" to learn some things more easily and more quickly than others—and what they are prepared to learn differs predictably from species to species: "[The] preparedness of organisms reflects the selective pressure(s) that their species has faced" (Seligman & Hager, 1972, p. 464). For example, consider how rats and birds learn to avoid poisoned foods. Experimenters offered rats and birds water that had been poisoned, dyed dark blue, and made to taste sour. Both species are obviously motivated to avoid poison, but when given the exact same stimuli and outcomes, they learned different things. The rats learned to avoid sour water in the future, whereas the birds learned to avoid dark blue water. Why? Because rats have evolved to take olfactory and gustatory cues as signs of possible toxins. By contrast, in birds' natural ecology, it is visual cues that are key, so the birds associated the toxins with the dark blue coloration rather than the sourness (Wilcoxon et al., 1971).

The point is that even when exposed to the exact same stimulus (sour, dark blue water) and the exact same outcome (illness), different species learn different things. And crucially, what organisms learn is neither random nor is it a straightforward function of the stimuli to which they are exposed. Out of all the infinite things animals could learn, their learning is laserlike in its focus: It produces the specific outcomes that fit the animals' ecology and the problems that they have recurrently encountered over the course of their evolution.

This message can be humbling for us as humans when we witness the astonishing abilities that other organisms have that we lack. For example, Clark's nutcrackers can remember up to 10,000 locations where they have cached food for up to a whole year (Alcock, 2009; Balda & Kamil, 1992; Kamil & Balda, 1985). Woodrats cache their food for future consumption in a strategic fashion, taking into account a variety of variables such as perishability, larder size, and others (Cosmides & Tooby, 2001). Ants learn to solve astonishingly difficult path integration problems, going out in search of food in a meandering path and returning via the most direct route possible (Gallistel, 1990; Wehner & Srinivasan, 1981). Our inability to do the same as humans is not because we are deficient. Our brains are just structured to learn different things than those of nutcrackers, ants, or bats. Clark's nutcrackers can remember 10,000 locations and humans cannot for the same reason that humans can learn language and rats cannot: Each species is equipped with the learning mechanisms that it needs for the particular environments it evolved in and the tasks it needed to solve (Gallistel, 1990). Learning is sensibly tethered to ecological need in this way. If we are receptive to it, this insight offers a dose of humility and respect for the awesome cognitive capacities of other species.

The Specific Features and Operating Characteristics of Learning Systems

> The structure of the learning mechanism—what information it processes and how—reflects the structure of the problem that has shaped its evolution. (Gallistel et al., 1991, p. 13)

Evolutionary considerations do not just help us understand what animals do and do not learn; they also shed light on the specific characteristics of how learning works in a given

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

species. For example, this might include why an animal responds one way rather than another, whether it engages in social or asocial learning, and what cues it uses to learn. In essence, there is a "fit" between the structure of the learning mechanism and the structure of the environmental problem it is geared toward solving. As a result, understanding what the learning mechanism evolved to do helps us understand how it works and why it works that way.

Why Does an Animal Respond This Way Rather Than That?

To understand learning, we need to understand not just what stimuli an animal responds to, but also *how* it responds. For example, rats will learn to run to avoid electric shocks. By contrast, they will not learn to *rear* to avoid shock. Why? Why does an organism learn one response but not the other? In the case of rats, the answer is that in the natural history and ecology of the species, running is an escape behavior, whereas rearing is an exploratory behavior (Bolles, 1970). Similarly, golden hamsters will easily learn to dig, scrabble, or rear for a food reward. But they will not learn to wash their face, scratch, or scent mark for a food reward. This is because digging, scrabbling, and rearing are hunger-driven behaviors that help the hamsters find food. By contrast, the other three behaviors are suppressed when the hamsters are hungry, as they are not relevant to obtaining food (Shettleworth, 1975). As a result, golden hamsters' neural circuits are not set up to permit an easy association between food and scent marking, the way they are between food and digging. Similarly, pigeons easily learn to peck a key to get food, but have much more trouble learning to peck a key to avoid shock. But learning to flap their wings to avoid shock presents no problem whatsoever (Gallistel et al., 1991; Hineline & Rachlin, 1969).

Why would learning work this way? Without evolutionary considerations, all of these responses would seem equally likely, and there would be no particular reason why specific responses should be tied to specific stimuli. But this is not how pigeon behavior evolved. For pigeons, pecking is an appetitive behavior geared toward obtaining food, whereas flapping one's wings is helpful for flying away and escaping danger (Gallistel et al., 1991).

These examples illustrate that to understand why an animal responds this way rather than that, you need to consider the animal's evolutionary history and the biological function of the type of learning it is engaging in (the problem it is solving). These examples also highlight a surprising irony: Despite the widespread misconception that evolutionary approaches are rigid and insensitive to context (Alcock, 1999; Gaulin & McBurney, 2001; Pratarelli & Mize, 2002; Shackelford & Liddle, 2014; Tooby & Cosmides, 1997, 1992; Waage & Gowaty, 1997), it is actually an evolutionary approach that places context center stage and emphasizes how crucial it is in explaining behavior (e.g., Gallistel et al., 1991; Seligman & Hager, 1972). Purely associationist approaches to learning are devoid of functional context, which robs them of much predictive and explanatory power. By contrast, evolutionary approaches contextualize learning and seek to explain it in relation to ecological context and need, which renders sensible aspects of animal behavior that would otherwise remain inexplicable (Al-Shawaf et al., 2019; Gallistel & King, 2009).

In a classic learning experiment, researchers allowed rats to drink water that had a strange taste and emanated from a spout that produced both light and noise. The rats were then punished by either shock or poisoning. The results were informative (Garcia & Koelling, 1966). When the rats were punished by poisoning, they learned to avoid the weird taste, but made no effort to avoid the noisy and light-emitting spout. By contrast, when they were punished by shock, the rats learned to avoid the loud and bright spout, but not the unusual taste. The researchers also found that learning from punishment followed a different time course in the two cases: In the case of shock, the shock had to come soon after drinking to be effective, but in the case of poisoning, the illness could arrive hours later and it would still be effective (Gallistel et al., 1991; Revusky & Garcia, 1970).

This example illustrates two key principles. First, even if you can show that an animal learns something in response to a stimulus, a key question remains: Why did the animal respond with behavior X rather than behavior Y? Evolutionary considerations help answer this question. Second, different types of learning have different *structures*—in this case, different time courses—that fit the adaptive problem to which the learning is geared. For pain to be useful, it is best for it to be tightly connected in time to the behavior that produced it, but the same is not true for illness, as eating spoiled food can cause illness hours later. The rats' learning mechanisms respect these facts, and thus each learning process is adaptively suited to the problem it evolved to solve.

There is an old view, sometimes attributed to Descartes, of animals as automata that respond automatically and reflexively to stimuli (e.g., Mayr, 1974; Thomas, 2020). On this view, the animal can hardly be said to make any contribution to its own behavior—the response is just an automatic reaction to the stimuli. But this view focuses solely on the environmental inputs and ignores the contribution of the animal's nervous system (Mayr, 1974)—that nervous system evolved to learn certain things in specific contexts and to produce certain behaviors in specific contexts. An evolutionary perspective contextualizes learning and reveals the underlying adaptive fit between the structure of the learning and the structure of the environmental problem that the learning evolved to solve (Gallistel, 1990).

To understand why an animal learns this response rather than that, we must understand both the environmental pressures impinging on the animal *and* the evolved mechanisms in

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

the animal's brain that process those inputs. It is only when we have grasped both the inputs *and* the mechanisms that process them that we can move toward a fuller understanding of the behaviors those learning mechanisms produce.

Social Versus Asocial Learning

Other characteristics of the learning process also show the footprint of evolution. For example, when do animals learn via individual experience, and when do they learn socially from their peers? The choice is not random. Instead, animals learn in a manner that is strategic, adaptive, and well-matched to the problem that they face (Alcock, 2009; Gallistel, 1990; Olmstead & Kuhlmeier, 2015). For example, when ninespine sticklebacks have gleaned useful, up-to-date information from their own personal experience, they prefer individual learning, and they ignore information from their peers about food patches. But when their individual experience leads to unreliable information, they predictably shift to social learning instead (van Bergen et al., 2004). The same is true of kittiwakes (a type of gull): If they have bred successfully in a certain location, they trust individual learning, but if their personal experience was unreliable or yielded failure, they shift to social learning (Danchin et al., 1998).

Studies and models of different types of learning suggest that animals favor social learning when individual experience does not work well or provides unreliable information, when individual learning is costly or dangerous, and when the "demonstrator" is from the same environment as the "observer," and thus the same behaviors are likely to be effective (Boyd & Richerson, 1988; Galef & Whiskin, 2004; Laland, 2004). In other words, animal learning is adaptively structured and nonrandom. The characteristics of this learning process are influenced by the costs and benefits of different learning strategies for the organism in question and for the context under study.

The principle extends further. When organisms learn socially, from whom should they learn? Who should they pay attention to if they are trying to be successful in their local ecologies? Studies show that unsuccessful bats prefer to follow successful bats when it is time to hunt (Wilkinson, 1992). Human children prefer to learn from those who are being attended to rather than those who are being ignored (Chudek et al., 2012). Human children and chimpanzees both prefer to copy the actions of *three* actors who demonstrate the same behavior *once* rather than *one* actor who demonstrates the behavior three times (Haun et al., 2012). Guppies, pigeons, and rats all appear to be more likely to copy a behavior when more conspecifics engage in it (Laland, 2004; Olmstead & Kuhlmeier, 2015). These tendencies, sometimes described as prestige and conformity biases in learning (Boyd & Richerson, 1988; Henrich & Gil-White, 2001), are generally adaptive, although more fine-grained work remains to be done.

What these examples illustrate is that "learning" is not a nebulous monolith. Animals deploy many specific, contextually differentiated learning strategies depending on the costs and benefits of those strategies for the particular problems they need to solve. The strategies they employ, such as whether to learn socially or asocially, and which particular individuals they choose to learn from, can be understood in terms of the costs and benefits of those different learning strategies in those particular environments.

It is not enough to say that something is learned—to really understand it, we want to know *how and why* the animal learns that way in this specific context (Alcock, 2009; Gallistel et al., 1991). This more fine-grained, contextualized look at learning reveals an impressive "fit" between the features of learning and the features of the problem the animal is solving. This fit helps explain why learning mechanisms operate the way that they do (Gallistel, 1990; see also Cosmides & Tooby, 2001; see also Frankenhuis & Panchanathan, 2011, for insights on the presence, absence, and variability in sensitive windows for learning). In other words, the evolved function of the learning mechanism helps us understand how it works—the "why" sheds light on the "how." This approach is often more illuminating than simply describing a behavior as "learned," or "evolved," or indeed any other descriptive, non-explanatory label.

Why Organisms Sometimes Learn Maladaptive Behaviors

Organisms sometimes learn to produce *mal*adaptive behaviors. Just as evolution sheds light on physical diseases and psychological disorders, it can also help explain how and why organisms learn maladaptive behaviors (Gluckman et al., 2016; Gurven et al., 2017; Nesse, 2019; Nesse & Williams, 1994).

A simple example comes from Japanese quail. Male Japanese quail can be easily conditioned to respond sexually to nonsexual cues if those cues were previously associated with copulatory opportunity (Crawford et al., 1993). These cues can be completely arbitrary. For example, if male quail are given an opportunity to learn that artificial bright orange feathers are associated with copulatory opportunity, they will learn to respond sexually to these arbitrary stimuli (Domjan et al., 1988). Humans and rats show similar sexual conditioning effects, which are typically stronger in males and weaker in females (Crawford et al., 1993; Pfaus et al., 2001). What is going on here? The humans, rats, and quail are essentially learning a maladaptive behavioral outcome in that they are responding sexually to arbitrary, nonsexual stimuli (note that "maladaptive" here does not imply any moral judgment). To understand this process, it is important to recognize the key distinction between the *learning mechanism*, which is

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

adaptive, and the *particular outcome learned in this case*, which is not.

Distinguishing Cognitive System From Behavioral Output Helps Explain How and Why Organisms Sometimes Learn to Produce Maladaptive Behaviors

Once you have an adaptive learning mechanism in place, it is possible to supply it with information that will cause it to produce a maladaptive outcome. Some bird species tolerate brood parasite offspring, sometimes even failing to detect that they are parasites (Winfree, 1999). Why? The answer depends on the crucial difference between system and output: The individual outcome is maladaptive, but the cognitive system that produced it is not. Birds are equipped with a cognitive system that must decide whether particular offspring are brood parasites or not. Because there is noise in the system, perfect accuracy is impossible, and some errors are inevitable. There are two types of errors. The first is to tolerate an interloper who is actually a brood parasite. The cost of this can be quite low, especially if brood parasitism is fairly rare in your ecology (Alcock, 2009; Davies et al., 1996). The second error is to reject your own offspring, tossing them out of the nest and killing them.

In line with error management theory (Haselton & Buss, 2000; Haselton & Nettle, 2006), animal brains are equipped with decision-making mechanisms that err on the side of the less costly error (Alcock, 2009; Maier et al., 2004; Maier & Ghazanfar, 2007). In the case of these birds, tolerating a rare parasite chick is (net) less costly than killing your own genetic offspring, so the birds are biased toward tolerance. This adaptive bias produces some errors, but it is much less costly than alternative designs that produce more errors of the catastrophic type. The point is that often, *the output (tolerating an interloper) may be maladaptive even though the system that produces it (the evolved cognitive bias) is adaptive*. When we differentiate clearly between the cognitive system and its behavioral output, much puzzling and maladaptive behavior becomes comprehensible.[9]

Human brains follow a similar “error management” logic. Anxiety alerts us to danger and protects us from threats (Nesse, 2019). It can make two kinds of error: failing to detect a real threat or “detecting” a threat when there is really nothing there (Nesse, 2005). In many individual instances, anxiety will be maladaptive and unnecessary, equivalent to sounding the alarm when there is no threat at the gates. But when we think about why anxiety evolved—and when we focus on the design of the system, not merely individual instances of its outputs—we can see how and why an adaptive system produces some maladaptive outputs *as part of its design*.

For sentry systems like anxiety, failing to detect a real threat is much more dangerous than raising a false alarm. Our brains are therefore equipped with an “adaptively biased” anxiety system that is oriented toward false positives, precisely because this bias reduces the likelihood of the more catastrophic error of missing a real threat (Nesse, 2019; Seixas & Al-Shawaf, 2023). This gives us plenty of opportunities to maladaptively learn that particular stimuli or situations are threatening or anxiety arousing, even when they are not objectively dangerous. The distinction between “system” and “output” helps explain how and why adaptive learning systems sometimes produce maladaptive outcomes.

Addiction provides one last example. Humans and other animals can learn to become addicted to drugs and alcohol (e.g., Durrant, 2024; Siegel, 2005). This is a maladaptive outcome, but it is produced by an adaptive learning mechanism that associates feelings of reward and pleasure with the behavior that generated the reward. Normally, this learning mechanism pushes us toward good food, gratifying friendships, the pursuit of status, fulfilling romantic relationships, and other fitness-enhancing outcomes (Buss, 2019). However, once such a mechanism exists, it can be triggered or hijacked by extremely rewarding-but-damaging stimuli such as opioids. The result is maladaptive outcomes that were produced by an adaptive learning mechanism (Al-Shawaf et al., 2020; Durrant, 2024).

There is more to say on the link between evolution and maladaptive behavior, but it is beyond the scope of this article and deserves a full treatment on its own (see also Del Giudice, 2018; Nesse, 2019). For present purposes, the key point is that integrating evolution and learning in the social sciences can help us understand how and why adaptive learning mechanisms sometimes produce maladaptive behavior in the normal course of their operation.

Summary and Conclusion: Moving Past the Evolution Versus Learning Fallacy

This article has argued that evolution and learning are not in conflict, and that it makes no sense to think of them as explanatory competitors. We can avoid false conflicts and speed up progress in the behavioral sciences if we replace the “evolved vs. learned” fallacy with the concept of evolved learning mechanisms, which are neurocognitive mechanisms in the brain that evolved to enable learning in specific contexts and for specific problem domains. See Table 1 for a summary of some key principles.

What This Does, and Does Not, Mean

The operation of these learning mechanisms—how they work, and why they work like that rather than some other way—is influenced by their evolved function. Understanding their evolved function will therefore shed light on how they work. This does not *at all* imply that evolution will cannibalize

---

[9] Indeed, reed warblers take into account the probability of parasitism in their ecology, and this affects their tolerance or rejection of parasite eggs (Davies et al., 1996).

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Table 1
A Summary of Some Key Principles Pertaining to Evolution and Learning

Key principle	Explanation or subprinciple
Evolution and learning are not conflicting explanations for behavior	Evolution and learning are located at different levels of analysis (proximate for learning, ultimate for evolution). • Both levels of analysis—proximate and ultimate—are necessary for a complete explanation. They are complementary, not conflicting. The statement “X is evolved” is erroneously taken to mean “X is present from birth” and “X doesn’t involve learning.” • In reality, evolved traits often involve learning, and they do not need to be present at birth.
Basic principles of behavior that weaken the evolved versus learned dichotomy	Rather than “evolved vs. learned,” there is a continuum of learning. • More learning does not mean less evolved, and less learning does not mean more evolved. They are not conflicting slices of a zero-sum explanatory pie. • Evolution helps explain why there is a continuum of learning in the first place. Behavior is often the product of innate templates combined with learned content. • Examples provided in text. Evolved does not mean “inflexible.” • Many evolved systems are flexible. • Some environmentally driven outcomes are not flexible.
Why do learning mechanisms evolve in the first place?	Learning mechanisms evolve when there is environmental unpredictability that affects survival or reproduction. Environmental selection pressures drive the evolution of learning mechanisms. Costs and benefits both matter. • For learning mechanisms to evolve, the benefits of building and running the expensive neural machinery that enables learning must outweigh the costs. In some cases, the benefits do outweigh the costs, but in others, they do not.
What characteristics of learning mechanisms are influenced by evolution?	Why animals learn some things more easily or readily than others • Examples provided in text. Why different species learn different things when exposed to the exact same stimuli • Examples provided in text. Specific features of how the learning mechanism works • For example: social versus asocial learning, why an animal responds one way rather than another, and so on Why organisms sometimes learn maladaptive behaviors • Examples provided in text.
Conclusion: To build a more accurate science of behavior, the social sciences must move past the “evolution versus learning” fallacy.	What this does (and does not) mean • This does not mean that learning is unimportant. It *does* mean that learning is not an alternative to evolution; learning mechanisms are a product of evolution. Descriptions versus explanations • “Learned” and “evolved” are mere labels, not explanations. They do not illuminate much on their own unless more detail is added. Uniting evolution and learning into one explanatory framework • Learning is a rich, complex process made possible by neurocognitive mechanisms that were shaped by evolution. To adequately explain behavior, we will often have to reference evolution and learning in the same analysis. • Evolutionary and sociocultural researchers can make great progress by working together to uncover the proximate and ultimate basis of evolved learning systems.

learning, or that learning will “reduce” to evolution, or that learning is unimportant. Quite the contrary: A great variety of behaviors in a wide range of species involve learning, and to explain behavior, we will often need to invoke learning in detail.

What it *does* mean is that learning is not an alternative to evolution. It is a type of adaptive mechanism crafted by natural selection in response to specific environmental pressures (Alcock, 2009; Al-Shawaf, 2024; Gallistel, 1990; Marler, 1991; Pontes et al., 2020; Symons, 1979; Tooby & Cosmides, 1992). In our mission to explain behavior, we will therefore often need to reference evolution and learning in concert. Hopefully, we will eventually reach the point where this explanatory mode will no longer be an anomaly in a science otherwise dominated by the tired, old, false dichotomy. It will become the norm.

Descriptions Versus Explanations

It is worth remembering that slapping the label “learned” on a behavior does not explain it. It merely describes one thing about the behavior in a vague and underspecified way. The same is true of slapping the label “evolved” on something. Such one-word labels are descriptive rather than explanatory, and badly underspecified.

To truly understand a behavior, we must understand how the learning mechanism that produced it works—what inputs

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

it takes, whether it has a sensitive period, how it organizes and integrates different cues, whether it is social or asocial or both, and so on. And to understand the structure of the learning mechanism, it pays to understand why it evolved that way. As ever, the "why" sheds light on the "how" (Al-Shawaf, 2024).

In many cases, the holy grail for a comprehensive explanation of behavior might look something like this: Which environmental pressures led to the evolution of this learning mechanism, and what is its function? How does this learning mechanism work in the present and how does it develop during the organism's life? What information does this learning mechanism privilege, and what are its operating rules? These questions reflect the natural integration of evolution and learning in trying to explain behavior.

Uniting Evolution and Learning Into One Explanatory Framework

Hopefully, it is clear that this is not a call to abandon learning as an explanation of behavior–in fact, this framework raises learning to a place of paramount importance. Learning is everywhere. But this approach simultaneously stresses that learning does not occur by magic or divine intervention; it is a rich, complex process that is made possible by neurocognitive circuits that were shaped by natural selection to *be* learning mechanisms. And it suggests, in line with a great deal of evidence (e.g., Alcock, 2009; Gallistel, 1990; Marler, 1991; Tooby & Cosmides, 1992), that understanding how and why these learning mechanisms evolved will shed light on how they work, which will in turn give us a deeper understanding of how humans and other animals learn to solve the problems they face.

This article has argued that to explain behavior, we will need to invoke both learning and evolution in the form of evolved learning mechanisms. Learning is not an alternative to evolution, it is a *product* of evolution. We will often need to reference both in the same breath to successfully explain behavior. Researchers from different backgrounds—evolutionary, sociocultural, and others—can take great strides by working together to uncover the ultimate and proximate basis of evolved learning mechanisms.

It is time for the social and behavioral sciences to move past the "evolution versus learning" fallacy and replace it with a more accurate framework for behavior—one that views evolution and learning as explanatory partners rather than explanatory competitors. This will yield a great predictive and explanatory harvest for psychology and the social sciences, nudging us toward a better integrated, less fragmented science of mind and behavior.

References

Al-Shawaf, L. (2019). Seven key misconceptions about evolutionary psychology. *Areo Magazine*.

Al-Shawaf, L. (2020, July 10). *The why is not the same as the how: Levels of analysis and scientific progress in psychology*. https://areomagazine.com/2020/07/20/the-why-is-not-the-same-as-the-how-levels-of-analysis-and-scientific-progress-in-psychology/

Al-Shawaf, L. (2024). Levels of analysis and explanatory progress in psychology: Integrating frameworks from biology and cognitive science for a more comprehensive science of the mind. *Psychological Review*. Advance online publication. https://doi.org/10.1037/rev0000459

Al-Shawaf, L., Lewis, D. M., Barbaro, N., & Wehbe, Y. S. (2020). The products of evolution: Conceptual distinctions, evidentiary criteria, and empirical examples. In T. K. Shackleford (Ed.), *The SAGE handbook of evolutionary psychology* (pp. 70–95). SAGE Publications.

Al-Shawaf, L., Lewis, D. M., Wehbe, Y. S., & Buss, D. M. (2019). Context, environment, and learning in evolutionary psychology. In T. Shackelford & V. Weekes-Shackelford (Eds.), *Encyclopedia of evolutionary psychological science* (pp. 1–12). Springer. https://doi.org/10.1007/978-3-319-16999-6_227-1

Al-Shawaf, L., Zreik, K., & Buss, D. M. (2018). Thirteen misunderstandings about natural selection. In T. Shackelford & V. Weekes-Shackelford (Eds.), *Encyclopedia of evolutionary psychological science* (pp. 1–14). Springer. https://doi.org/10.1007/978-3-319-16999-6_2158-2

Alcock, J. (1999). The myth of genetic determinism—Again. *Behavioral and Brain Sciences*, *22*(5), 885–886. https://doi.org/10.1017/S0140525X99222200

Alcock, J. (2009). *Animal behavior: An evolutionary approach*. Sinauer.

Alcock, J. (2013). *Animal behavior: An evolutionary approach* (10th ed.). Sinauer Associates.

Balda, R. P., & Kamil, A. C. (1992). Long-term spatial memory in Clark's nutcracker, *Nucifraga Columbiana*. *Animal Behaviour*, *44*(4), 761–769. https://doi.org/10.1016/S0003-3472(05)80302-1

Baldwin, J. M. (1896). A new factor in evolution. *American Naturalist*, *30*(354), 441–451. https://doi.org/10.1086/276408

Barrett, H. C. (2015). Adaptations to predators and prey. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 200–223). Wiley. https://doi.org/10.1002/9780470939376.ch7

Barrett, H. C., & Broesch, J. (2012). Prepared social learning about dangerous animals in children. *Evolution and Human Behavior*, *33*(5), 499–508. https://doi.org/10.1016/j.evolhumbehav.2012.01.003

Bickerton, D. (1984). The language bioprogram hypothesis. *Behavioral and Brain Sciences*, *7*(2), 173–188. https://doi.org/10.1017/S0140525X00044149

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

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

Bradshaw, A. D. (1965). Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, *13*, 115–155. https://doi.org/10.1016/S0065-2660(08)60048-6

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

Buss, D. M. (2019). *Evolutionary psychology: The new science of the mind*. Routledge. https://doi.org/10.4324/9780429061417

Cesario, J., Johnson, D., & Eisthen, H. (2020). Your brain is not an onion with a tiny reptile inside. *Current Directions in Psychological Science*, *29*(3), 255–260. https://doi.org/10.1177/0963721420917687

Charnov, E. L., & Krebs, J. R. (1974). On clutch-size and fitness. *Ibis*, *116*(2), 217–219. https://doi.org/10.1111/j.1474-919X.1974.tb00241.x

Charnov, E. L., Warne, R., & Moses, M. (2007). Lifetime reproductive effort. *The American Naturalist*, *170*(6), E129–E142. https://doi.org/10.1086/522840

Chudek, M., Heller, S., Birch, S., & Henrich, J. (2012). Prestige-biased cultural learning: Bystander's differential attention to potential models influences children's learning. *Evolution and Human Behavior*, *33*(1), 46–56. https://doi.org/10.1016/j.evolhumbehav.2011.05.005

Colbert-White, E. N., & Kaufman, A. B. (2019). *Animal cognition101*. Springer.

Cosmides, L., & Tooby, J. (2001). Unraveling the enigma of human intelligence. In R. J. Sternberg & J. C. Kaufman (Eds.), *The evolution of intelligence* (pp. 145–198). Lawrence Erlbaum.

Crawford, L. L., Holloway, K. S., & Domjan, M. (1993). The nature of sexual reinforcement. *Journal of the Experimental Analysis of Behavior*, *60*(1), 55–66. https://doi.org/10.1901/jeab.1993.60-55

Danchin, E., Boulinier, T., & Massot, M. (1998). Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. *Ecology*, *79*(7), 2415–2428. https://doi.org/10.1890/0012-9658(1998)079[2415:CRSABH]2.0.CO;2

Davies, N. B., Brooke, M. L., & Kacelnik, A. (1996). Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proceedings of the Royal Society B: Biological Sciences*, *263*(1372), 925–931. https://doi.org/10.1098/rspb.1996.0137

Dawkins, R. (1982). *The extended phenotype*. Oxford University Press.

Del Giudice, M. (2018). *Evolutionary psychopathology: A unified approach*. Oxford University Press. https://doi.org/10.1093/med-psych/9780190246846.001.0001

DeLoache, J. S., & LoBue, V. (2009). The narrow fellow in the grass: Human infants associate snakes and fear. *Developmental Science*, *12*(1), 201–207. https://doi.org/10.1111/j.1467-7687.2008.00753.x

Domjan, M., O'Vary, D., & Greene, P. (1988). Conditioning of appetitive and consummatory sexual behavior in male Japanese quail. *Journal of the Experimental Analysis of Behavior*, *50*(3), 505–519. https://doi.org/10.1901/jeab.1988.50-505

Durrant, R. (2024). Addiction and substance use. In L. Al-Shawaf & T. K. Shackelford (Eds.), *The Oxford handbook of evolution and the emotions* (pp. 1218–1237). Oxford University Press. https://doi.org/10.1093/oxfordhb/9780197544754.013.61

Fenneman, J., & Frankenhuis, W. E. (2020). Is impulsive behavior adaptive in harsh and unpredictable environments? A formal model. *Evolution and Human Behavior*, *41*(4), 261–273. https://doi.org/10.1016/j.evolhumbehav.2020.02.005

Fox, R. J., Donelson, J. M., Schunter, C., Ravasi, T., & Gaitán-Espitia, J. D. (2019). Beyond buying time: The role of plasticity in phenotypic adaptation to rapid environmental change. *Philosophical Transactions of the Royal Society B*, *374*(1768), Article 20180174. https://doi.org/10.1098/rstb.2018.0174

Frank, R. H. (1988). *Passions within reason: The strategic role of the emotions*. W.W. Norton.

Frankenhuis, W. E., & Panchanathan, K. (2011). Balancing sampling and specialization: An adaptationist model of incremental development. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1724), 3558–3565. https://doi.org/10.1098/rspb.2011.0055

Galef, B. G., Jr., & Whiskin, E. E. (2004). Effects of environmental stability and demonstrator age on social learning of food preferences by young Norway rats. *Animal Behaviour*, *68*(4), 897–902. https://doi.org/10.1016/j.anbehav.2003.10.029

Gallistel, C. R. (1990). *The organization of learning*. MIT Press.

Gallistel, C. R., Brown, A., Carey, S., Gelman, R., & Keil, F. (1991). Lessons from animal learning. In R. Gelman & S. Carey (Eds.), *The epigenesis of mind* (pp. 3–37). Lawrence Erlbaum.

Gallistel, C. R., & King, A. P. (2009). *Memory and the computational brain: Why cognitive science will transform neuroscience*. Wiley-Blackwell.

Gamboa, G. J. (2004). Kin recognition in eusocial wasps. *Annales Zoologici Fennici*, *41*(6), 789–808. https://www.jstor.org/stable/23736143?casa_token=RR5wlRBd2NMAAAAA%3A3h2V3oTXrprpwsjpxEJxnO9yTx-3APZ7n88pJRxGlol-0VF30VgCdMVJoUY1QevVBXtTecjhWyZ4iW-umBmCKCffv38vHlNktr2TJJyj7Ov3QTRSZDs

Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science*, *4*(1), 123–124. https://doi.org/10.3758/BF03342209

Gaskett, A. C., Winnick, C. G., & Herberstein, M. E. (2008). Orchid sexual deceit provokes ejaculation. *American Naturalist*, *171*(6), E206–E212. https://doi.org/10.1086/587532

Gaulin, S. J. C., & McBurney, D. (2001). *Psychology: An evolutionary approach*. Prentice Hall.

Gluckman, P., Beedle, A., Buklijas, T., Low, F., & Hanson, M. (2016). *Principles of evolutionary medicine*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199663927.001.0001

Goldstein, E. B. (2015). *Cognitive psychology: Connecting mind, research, and everyday experience* (4th ed.). Cengage Learning.

Goldstein, E. B., & Cacciamani, L. (2021). *Sensation and perception* (11th ed.). Cengage Learning.

Guest, K. J. (2013). *Cultural anthropology: A toolkit for a global age*. W.W. Norton.

Gurven, M., Stieglitz, J., Trumble, B., Blackwell, A. D., Beheim, B., Davis, H., Hooper, P., & Kaplan, H. (2017). The Tsimane Health and Life History Project: Integrating anthropology and biomedicine. *Evolutionary Anthropology*, *26*(2), 54–73. https://doi.org/10.1002/evan.21515

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, *298*(5598), 1634–1636. https://doi.org/10.1126/science.1072702

Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology*, *78*(1), 81–91. https://doi.org/10.1037/0022-3514.78.1.81

Haselton, M. G., & Nettle, D. (2006). The paranoid optimist: An integrative evolutionary model of cognitive biases. *Personality and Social Psychology Review*, *10*(1), 47–66. https://doi.org/10.1207/s15327957pspr1001_3

Haun, D. B. M., Rekers, Y., & Tomasello, M. (2012). Majority-biased transmission in chimpanzees and human children, but not orangutans. *Current Biology*, *22*(8), 727–731. https://doi.org/10.1016/j.cub.2012.03.006

Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, *22*(3), 165–196. https://doi.org/10.1016/S1090-5138(00)00071-4

Hineline, P. N., & Rachlin, H. (1969). Escape and avoidance of shock by pigeons pecking a key. *Journal of the Experimental Analysis of Behavior*, *12*(4), 533–538. https://doi.org/10.1901/jeab.1969.12-533

Hoffman, E. A., & Pfennig, D. W. (1999). Proximate causes of cannibalistic polyphenism in larval tiger salamanders. *Ecology*, *80*(3), 1076–1080. https://doi.org/10.1890/0012-9658(1999)080[1076:PCOCPI]2.0.CO;2

Holmes, W. G., & Sherman, P. W. (1982). The ontogeny of kin recognition in two species of ground squirrels. *American Zoologist*, *22*(3), 491–517. https://doi.org/10.1093/icb/22.3.491

Hunt, M. M. (2007). *Story of psychology*. Anchor.

Kalat, J. W., & Rozin, P. (1973). "Learned safety" as a mechanism in long-delay taste-aversion learning in rats. *Journal of Comparative and Physiological Psychology*, *83*(2), 198–207. https://doi.org/10.1037/h0034424

Kamil, A. C., & Balda, R. P. (1985). Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes*, *11*(1), 95–111. https://doi.org/10.1037/0097-7403.11.1.95

Konishi, M. (1965). The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Zeitschrift für Tierpsychologie*, *22*(7), 770–783. https://doi.org/10.1111/j.1439-0310.1965.tb01688.x

Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, *32*(1), 4–14. https://doi.org/10.3758/BF03196002

Lewis, D. M. G., Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2017). Evolutionary psychology: A how-to guide. *American Psychologist*, *72*(4), 353–373. https://doi.org/10.1037/a0040409

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Lilienfeld, S. O., Lynn, S. J., Ruscio, J., & Beyerstein, B. L. (2010). *50 great myths of popular psychology: Shattering widespread misconceptions about human behavior*. Wiley-Blackwell.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

LoLordo, V. M., Jacobs, W. J., & Foree, D. D. (1982). Failure to block control by a relevant stimulus. *Animal Learning & Behavior*, *10*(2), 183–192. https://doi.org/10.3758/BF03212268

Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels; die Artgenosse als auslosendes Moment sozialer Verhaltungsweisen [The companion in the bird's environment; the conspecific as a triggering moment of social behavior]. *Journal of Ornithology*, *83*, 137–213. https://doi.org/10.1007/BF01905355

Maier, J. X., & Ghazanfar, A. A. (2007). Looming biases in monkey auditory cortex. *The Journal of Neuroscience*, *27*(15), 4093–4100. https://doi.org/10.1523/JNEUROSCI.0330-07.2007

Maier, J. X., Neuhoff, J. G., Logothetis, N. K., & Ghazanfar, A. A. (2004). Multisensory integration of looming signals by rhesus monkeys. *Neuron*, *43*(2), 177–181. https://doi.org/10.1016/j.neuron.2004.06.027

Marks, I. M., & Nesse, R. M. (1994). Fear and fitness: An evolutionary analysis of anxiety disorders. *Ethology and Sociobiology*, *15*(5–6), 247–261. https://doi.org/10.1016/0162-3095(94)90002-7

Marler, P. (1991). Song-learning behavior: The interface with neuroethology. *Trends in Neurosciences*, *14*(5), 199–206. https://doi.org/10.1016/0166-2236(91)90106-5

Marler, P., & Sherman, V. (1983). Song structure without auditory feedback: Emendations of the auditory template hypothesis. *The Journal of Neuroscience*, *3*(3), 517–531. https://doi.org/10.1523/JNEUROSCI.03-03-00517.1983

Marr, D. (1982). *Vision: A computational investigation into the human representation and proceedings of visual information*. Freeman.

Mateo, J. M. (2002). Kin-recognition abilities and nepotism as a function of sociality. *Proceedings of the Royal Society B: Biological Sciences*, *269*(1492), 721–727. https://doi.org/10.1098/rspb.2001.1947

Mateo, J. M., & Johnston, R. E. (2000). Kin recognition and the 'armpit effect': Evidence of self-referent phenotype matching. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1444), 695–700. https://doi.org/10.1098/rspb.2000.1058

Mayr, E. (1974). Behavior programs and evolutionary strategies. *American Scientist*, *62*(6), 650–659. https://www.jstor.org/stable/27845170?casa_token=Fij2n55IjDgAAAAA%3AGRx4LGxeMID3VgBEoTXI_bkLHqy5sOzmJMwHNLi967RzXtzHWZn15vH48PpnLsN8wdvBd09adEvc0on20nkqWD0Lx7JQbX2Sk_FyME3KxeVN6Ko3Be8&seq=1

Mayr, E. (2004). *What makes biology unique? Considerations on the autonomy of a scientific discipline*. Cambridge University Press. https://doi.org/10.1017/CBO9780511617188

Medvin, M. B., & Beecher, M. D. (1986). Parent–offspring recognition in the barn swallow (*Hirundo rustica*). *Animal Behaviour*, *34*(6), 1627–1639. https://doi.org/10.1016/S0003-3472(86)80251-2

Medvin, M. B., Stoddard, P. K., & Beecher, M. D. (1993). Signals for parent–offspring recognition: A comparative analysis of the begging calls of cliff swallows and barn swallows. *Animal Behaviour*, *45*(5), 841–850. https://doi.org/10.1006/anbe.1993.1105

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys. In T. Zentall & B. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 51–73). Lawrence Erlbaum.

Mineka, S., & Öhman, A. (2002). Phobias and preparedness: The selective, automatic, and encapsulated nature of fear. *Biological Psychiatry*, *52*(10), 927–937. https://doi.org/10.1016/S0006-3223(02)01669-4

Munro, M., & Mann, V. (2005). Age of immersion as a predictor of foreign accent. *Applied Psycholinguistics*, *26*(3), 311–341. https://doi.org/10.1017/S0142716405050198

Mystkowski, J. L., Craske, M. G., & Echiverri, A. M. (2002). Treatment context and return of fear in spider phobia. *Behavior Therapy*, *33*(3), 399–416. https://doi.org/10.1016/S0005-7894(02)80035-1

Nesse, R. M. (2005). Natural selection and the regulation of defenses: A signal detection analysis of the smoke detector principle. *Evolution and Human Behavior*, *26*(1), 88–105. https://doi.org/10.1016/j.evolhumbehav.2004.08.002

Nesse, R. M. (2019). *Good reasons for bad feelings: Insights from the frontier of evolutionary psychiatry*. Dutton.

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

Öhman, A., Dimberg, U., & Öst, L. G. (1985). Animal and social phobias: Biological constraints on learned fear responses. In S. Reiss & R. R. Bootzin (Eds.), *Theoretical issues in behavior therapy* (pp. 123–175). Academic Press.

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295X.108.3.483

Öhman, A., & Mineka, S. (2003). The malicious serpent: Snakes as a prototypical stimulus for an evolved module of fear. *Current Directions in Psychological Science*, *12*(1), 5–9. https://doi.org/10.1111/1467-8721.01211

Olmstead, M. C., & Kuhlmeier, V. A. (2015). *Comparative cognition*. Cambridge University Press. https://doi.org/10.1017/CBO9780511894787

Peakall, R. (1990). Responses of male zaspilothynnus trilobatus turner wasps to females and the sexually deceptive orchid it pollinates. *Functional Ecology*, *4*(2), 159–167. https://doi.org/10.2307/2389335

Pfaus, J. G., Kippin, T. E., & Centeno, S. (2001). Conditioning and sexual behavior: A review. *Hormones and Behavior*, *40*(2), 291–321. https://doi.org/10.1006/hbeh.2001.1686

Pfennig, D. W., Sherman, P. W., & Collins, J. P. (1994). Kin recognition and cannibalism in polyphenic salamanders. *Behavioral Ecology*, *5*(2), 225–232. https://doi.org/10.1093/beheco/5.2.225

Pinker, S. (1995). Language is a human instinct. In J. Brockman (Ed.), *The third culture: Beyond the scientific revolution* (pp. 223–236). Simon & Schuster.

Pinker, S. (2007). *The language instinct: How the mind creates language*. Harper.

Piske, T., MacKay, I. R. A., & Flege, J. E. (2001). Factors affecting degree of foreign accent in an L2: A review. *Journal of Phonetics*, *29*(2), 191–215. https://doi.org/10.1006/jpho.2001.0134

Pontes, A. C., Mobley, R. B., Ofria, C., Adami, C., & Dyer, F. C. (2020). The evolutionary origin of associative learning. *American Naturalist*, *195*(1), E1–E19. https://doi.org/10.1086/706252

Pratarelli, M. E., & Mize, K. D. (2002). Biological determinism/fatalism: Are they extreme cases of inference in evolutionary psychology? *Theory and Science*, *3*(1). https://theoryandscience.icaap.org/content/vol003.001/pratarelli-mize.html

Ratcliffe, J. M., Fenton, M. B., & Galef, B. G., Jr. (2003). An exception to the rule: Common vampire bats do not learn taste aversions. *Animal Behaviour*, *65*(2), 385–389. https://doi.org/10.1006/anbe.2003.2059

Revusky, S., & Garcia, J. (1970). Learned associations over long delays. In G. H. Bower (Ed.), *Psychology of learning and motivation* (Vol. 4, pp. 1–84). Academic Press.

Rozin, P. (1976). The selection of foods by rats, humans, and other animals. *Advances in the Study of Behavior*, *6*, 21–76. https://doi.org/10.1016/S0065-3454(08)60081-9

Rozin, P., & Kalat, J. W. (1971). Specific hungers and poison avoidance as adaptive specializations of learning. *Psychological Review*, *78*(6), 459–486. https://doi.org/10.1037/h0031878

Schacter, D. L., Gilbert, D. T., Nock, M. K., & Wegner, D. M. (2017). *Psychology* (4th ed.). Worth Publishers. https://www.amazon.com/Psychology-Daniel-L-Schacter/dp/1464155461/ref=sr_1_7?crid=3N4IMWPZFC1RR&dib=eyJ2IjoiMSJ9.7vKyLaaMPO2IfgWx8Lo0F9zJyyj5EioBGGI_

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

sFaCEEToH-JyfjSE2PJdayzK4YX8Qdxalnn1ggpRRvylibJit3IOeG9v6hN1WM6lOITXPkhhFy4Anvvw0ris9mFBh9pgrJaSERNVnzXUA-hWAPSJ675qz4Chkt-YLSdgCMTuFXzqJHqOM0hpI2hPBEKPx4UbJsTHJOnR4UqMqDCm8VWxdOG1K6XPLq7nN5iwftkgpqs.KuqCKu12sjfpg4sWPyb4kW9ez3UUJaHNm3PGklpH-qs&dib_tag=se&keywords=schacter+psychology&qid=1743362849&sprefix=schacter%2Caps%2C240&sr=8-7

Schiff, W. (1965). Perception of impending collision: A study of visually directed avoidant behavior. *Psychological Monographs: General and Applied*, *79*(11), 1–26. https://doi.org/10.1037/h0093887

Seixas, B. U., & Al-Shawaf, L. (2023). Error management theory and the evolution of cognitive bias. In T. K. Shackelford (Ed.), *Encyclopedia of sexual psychology and behavior* (pp. 1–5). Springer. https://doi.org/10.1007/978-3-031-08956-5_83-1

Seligman, M. E. P., & Hager, J. L. (Eds.). (1972). *Biological boundaries of learning*. Appleton-Century-Crofts.

Seyfarth, R. M., Cheney, D. L, & Marler, P. (1980). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, *210*(14), 801–803. https://doi.org/10.1126/science.7433999

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, *34*(6), 1640–1658. https://doi.org/10.1016/S0003-3472(86)80252-4

Shackelford, T. K., & Liddle, J. R. (2014). Understanding the mind from an evolutionary perspective: An overview of evolutionary psychology. *Wiley Interdisciplinary Reviews: Cognitive Science*, *5*(3), 247–260. https://doi.org/10.1002/wcs.1281

Sheehan, M. J., & Tibbetts, E. A. (2010). Selection for individual recognition and the evolution of polymorphic identity signals in Polistes paper wasps. *Journal of Evolutionary Biology*, *23*(3), 570–577. https://doi.org/10.1111/j.1420-9101.2009.01923.x

Sheehan, M. J., & Tibbetts, E. A. (2011). Specialized face learning is associated with individual recognition in paper wasps. *Science*, *334*(6060), 1272–1275. https://doi.org/10.1126/science.1211334

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

Siegel, S. (2005). Drug tolerance, drug addiction, and drug anticipation. *Current Directions in Psychological Science*, *14*(6), 296–300. https://doi.org/10.1111/j.0963-7214.2005.00384.x

Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(2), 809–813. https://doi.org/10.1073/pnas.0707021105

Simpson, S. J., Sword, G. A., & Lo, N. (2011). Polyphenism in insects. *Current Biology*, *21*(18), R738–R749. https://doi.org/10.1016/j.cub.2011.06.006

Sommer, R. J. (2020). Phenotypic plasticity: From theory and genetics to current and future challenges. *Genetics*, *215*(1), 1–13. https://doi.org/10.1534/genetics.120.303163

Stangor, C., & Walinga, J. (2014). *Introduction to psychology—1st Canadian edition*. BCcampus. https://opentextbc.ca/introductiontopsychology/

Stoutamire, W. P. (1974). Relationships of the purple-fringed orchids *Platanthera psycodes* and *P. grandiflora*. *Brittonia*, *26*(1), 42–58. https://doi.org/10.2307/2805919

Sussman, R. W. (2005). Exploring our basic human nature: Are humans inherently violent? In M. A. Park (Ed.), *Biological anthropology: An introductory reader (pp. 92-98)*. McGraw-Hill.

Symons, D. (1979). *The evolution of human sexuality*. Oxford University Press.

Tahta, S., Wood, M., & Loewenthal, K. (1981). Age changes in the ability to replicate foreign pronunciation and intonation. *Language and Speech*, *24*(4), 363–372. https://doi.org/10.1177/002383098102400405

Thomas, E. (2020). Descartes on the animal within, and the animals without. *Canadian Journal of Philosophy*, *50*(8), 999–1014. https://doi.org/10.1017/can.2020.44

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, *20*(4), 410–433. https://doi.org/10.1111/j.1439-0310.1963.tb01161.x

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). Oxford University Press.

Tooby, J., & Cosmides, L. (1997). *Letter to the Editor of The New York Review of Books on Stephen Jay Gould's 'Darwinian Fundamentalism' (June 12, 1997) and 'Evolution: The Pleasures of Pluralism'(June 26, 1997)*. http://cogweb.ucla.edu/Debate/CEP_Gould.html

Tooby, J., & Cosmides, L. (2005). Evolutionary psychology: Conceptual foundations. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 5–67). Wiley.

van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1542), 957–962. https://doi.org/10.1098/rspb.2004.2684

Waage, J. K., & Gowaty, P. A. (1997). Myths of genetic determinism. In P. A. Gowaty (Ed.), *Feminism and evolutionary biology: Boundaries, intersections and frontiers* (pp. 585–613). Springer. https://doi.org/10.1007/978-1-4615-5985-6_29

Washburn, S. L., Jay, P. C., & Lancaster, J. B. (1965). Field studies of Old World Monkeys and Apes. *Science*, *150*(3703), 1541–1547. https://doi.org/10.1126/science.150.3703.1541

Wehner, R., & Srinivasan, M. V. (1981). Searching behaviour of desert ants, genus *Cataglyphis* (*formicidae, hymenoptera*). *Journal of Comparative Physiology*, *142*(3), 315–338. https://doi.org/10.1007/BF00605445

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press. https://doi.org/10.1093/oso/9780195122343.001.0001

Wilcoxon, H. C., Dragoin, W. B., & Kral, P. A. (1971). Illness-induced aversions in rat and quail: Relative salience of visual and gustatory cues. *Science*, *171*(3973), 826–828. https://doi.org/10.1126/science.171.3973.826

Wilkinson, G. S. (1992). Information transfer at evening bat colonies. *Animal Behaviour*, *44*(3), 501–518. https://doi.org/10.1016/0003-3472(92)90059-I

Winfree, R. (1999). Cuckoos, cowbirds and the persistence of brood parasitism. *Trends in Ecology & Evolution*, *14*(9), 338–343. https://doi.org/10.1016/S0169-5347(99)01643-2

Wynne, C. D. L., & Udell, M. A. R. (2020). *Animal cognition: Evolution, behavior and cognition* (3rd ed.). Bloomsbury Academic.

Yong, E. (2022). *An immense world: How animal senses reveal the hidden realms around us*. Random House.

Zera, A. J., & Harshman, L. G. (2001). The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics*, *32*(1), 95–126. https://doi.org/10.1146/annurev.ecolsys.32.081501.114006

Received October 21, 2024
Revision received March 3, 2025
Accepted March 4, 2025 ■