

INTRODUCTION

Perspectives on the Evolution of Learning and Memory Mechanisms

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The capacity to learn and remember exists in most known animal species, which raises fascinating questions about the role of evolutionary processes. Logic suggests that processing and storing information for future use is likely to be fundamental for an animal's survival and reproductive success. Foraging for food requires capacities to respond to cues that signal its availability and location, and store memories for future excursions; successful reproduction requires capacities to locate and choose a suitable mate; and, evading predators requires learning about and remembering cues associated with survival threats, such as the presence and location of predators; all of these capacities, either directly or indirectly, enhance reproductive success. Although logical deduction plays an important role in science, empirical tests are needed to confirm, in this case, evolutionary hypotheses about learning and memory. This book is about the ways in which evolutionary hypotheses inform the design of experiments on learning and memory, the empirical methods and tests that have been developed, and the knowledge derived from research programs that reveal relationships between learning, memory, and evolution. The contributors to each chapter provide unique insights into how evolution has influenced a broad array of learning and memory mechanisms across a diverse representation of invertebrate and vertebrate species.

How learning and memory work has been at the center of inquiry in comparative psychology since the earliest days of the field. However, comparative psychologists and biologists share an interest in *why* learning and memory occur. As a result, we find approaches that converge on Tinbergen's four aims of inquiry (Tinbergen, 1963). That is, to understand the capacity for learning and memory fully, researchers have explored its underlying neural and molecular mechanisms (causation), its genetic and developmental bases (ontogeny), its adaptive function (survival and reproductive fitness), and its phylogenetic distribution across species (evolution). Although no single approach will tell us *why* learning and memory evolved, their integration gives us fascinating clues. And, as it turns out, approaching learning and

memory from an evolutionary perspective has yielded important insights that further our understanding of the fundamental questions of *how* they occur. Each contributor to this volume (whose names are cited in **bold**) offers an important empirical and theoretical view toward advancing our understanding of the relationships between learning, memory, and evolution.

We assembled this volume because so much fascinating research on the evolutionary basis of learning and memory has been conducted by psychologists and biologists. We felt it was time to bring together researchers approaching evolutionary questions from diverse viewpoints, behavior systems, and study species, and, in doing so, create a single volume that represents not only how the field has changed in recent decades, but also the directions in which it is headed. Our aim in this introduction is to provide a brief overview of the major questions and issues that provide context for the book, and, hopefully, offer a rationale for why we believe such a book is an important contribution to our field.

I.1 GENERAL PROCESS, ADAPTIVE SPECIALIZATION, OR BOTH?

Adaptation by natural selection is a major concept driving our understanding of learning and memory. As an evolutionary concept, adaptation is usually invoked when a character exhibits a complexity in organization that defies alternatives, such as other forces of nature or the product of random processes. Williams (1966) warned that adaptation should not be invoked when more basic processes provide an explanation. To use his own example, it is apparently adaptive for flying fish to return to water because they cannot survive outside of it; however, an adaptive explanation is not needed because the return to the water can be explained more parsimoniously by gravity. Some clues that a character is an adaptation, when measures of reproductive success are not available, involve the complexity of the character and the presence of intermediate forms of that character. For example, the eye of vertebrates can be traced to a basal form in living lampreys from which the complex eye of jawed classes evolved over the last 500 million years (Lamb et al., 2007). Regarding learning and memory, the intricacies of processes involved in the encoding and retrieval of information strongly suggest that their evolution was shaped by natural selection. Moreover, studies on animals with few neurons may help us understand how these components have evolved to produce the complexity that we observe today in terms of incentive representations, spatial mapping, episodic memories, and metacognition, to name some functions described in this volume. But how is adaptation to be incorporated into our understanding of learning and memory in an evolutionary context?

Since the 1960s, comparative psychologists have been struggling with these two questions: Are learning and memory all-purpose mechanisms common to many species? Or has selection acted upon learning and memory mechanisms such that they are either constrained or specialized by the attentional, sensory/perceptual, or learning capacities of the study species? The answer to which alternative best summarizes the current state of knowledge regarding the evolution of learning and memory may depend on the scope of the question. At a macro level, Pavlovian conditioning, for example, occurs across a wide range of organisms (Ginsberg & Jablonka, 2010; Hollis, 1997; Hollis & Guillette, 2011, 2015; Krause & Domjan, 2017; Papini, 2021). Signature effects such as acquisition and extinction are found across species, and across aversive and appetitive response systems. However, unique ecological and evolutionary circumstances may give rise to adaptively specialized forms of this learning, and empirical findings of this effect have laid challenges for the principle of *equipotentiality*. According to this tenet of the general process view of learning, learning is unaffected by the nature of the stimuli that organisms experience, and responses to stimuli are unaffected by stimulus properties. This principle is contradicted in various Pavlovian conditioning phenomena (**Blaisdell & Seitz**), including taste aversions (Garcia & Koelling, 1966; Miller & Domjan, 1981), antipredator behavior (Griffin et al., 2001), and sexual responses (Domjan & Krause, 2017; **Krause & Domjan**). The behavior systems framework synthesizes disparate “anomalies” that contradict general process theories of learning into a coherent structure (**Silva & Silva**). But even when equipotentiality does not apply, the efficient stimuli and reinforcers for learning seem to exhibit some familiar phenomena, including acquisition, extinction, discrimination, generalization, and others.

The capacity to learn can lead to adaptive outcomes; the question is how general the trait is. The tension between general processes and adaptive specializations applies to other traits beyond learning and memory, as demonstrated by the following example involving temperature regulation in vertebrates (Bicego et al., 2007). Within some limits, living birds and mammals are endothermic, that is, they are able to maintain a constant internal temperature by means of behavioral and physiological mechanisms. Living reptiles, however, are ectothermic, able to regulate their internal temperature only by behavioral means. This ability to regulate temperature, albeit by different means, is true for these classes of vertebrates despite adaptations to a broad range of environments (think of penguins in the Antarctic and ostriches in the African savannah). Occasionally, however, some animals have evolved mechanisms for endothermy, including some fish species of the family Scombroidei, like tuna and mackerel (Block & Finnerty, 1994), and temperature regulation may underlie the evolution of fish species with large body size, like some sharks, as well as sea turtles (Ferrón, 2017;

Sato, 2014). A high surface-to-volume ratio in large animals makes preserving constant core temperature more likely. Similarly, as far as we know, all animals with neurons exhibit habituation, sensitization, and conditioning phenomena, with similar behavioral properties and similar mechanisms of synaptic plasticity. The type of functional and neural stability exhibited by the role of the hippocampus in spatial learning in vertebrates, and perhaps epigenetic mechanisms, warn us of the limits of adaptation as a local process. One way to understand these stable properties of learning and memory is that the selective pressures behind their evolution are factors common to a wide range of ecological conditions, such as time and space (Dickinson, 1980). But examples of local adaptations in learning and memory also are possible, and may be restricted to a relatively small set of species, as illustrated in this volume in such research areas as sexual conditioning and metacognition. General adaptations would be consistent with a general-process view, whereas local adaptations would be consistent with constraints on learning, associative selectivity, or preparedness (Papini, 2002). This framework leads to a treatment of all forms of learning as adaptations, namely, the products of natural selection.

I.2 EVOLUTION AND GENERAL LEARNING PROCESSES

Since the advent of the modern synthesis of evolution (Huxley, 1942) – a unification of Mendelian genetics and Darwinian theory – evolution has been recognized as an opportunistic process affecting gene frequencies, a process that was sometimes interpreted as leading to constant change, even at the genetic level. For example, as Mayr (1963, p. 609) proposed, “Much that has been learned about gene physiology makes it evident that the search for homologous genes is quite futile except in very close relatives.” However, in an insightful article, Simpson (1964, pp. 1536–1537) suggested that

Behavior is subject to particularly strong selection, and it is probably farthest removed from the genes and also most elaborately polygenic as a rule. [...] Convergence to the point of identity or of seriously confusing similarity would appear to be more likely in a single kind of molecule, even one as complicated as a protein, than in such phenotypic characters of a very large number of such molecules.

These passages, produced by two major proponents of the modern synthesis, illustrate the tension between the notion that natural selection is constantly changing the genome (so that similarities, when found, are unlikely to be examples of homologies) and the notion that deep similarities in complex biological characters are likely to be the result of homology, rather than homoplasy. But these evolutionary biologists also recognized character stability, without which taxonomy would be impossible. As we emphasize

in greater detail later in this introduction, this same tension in the study of learning and memory, namely, between local adaptations and deep homologies, forms the background to the constraints-on-learning debate, the question of whether all learning must be an evolutionary response to local selective pressures or a result of a more general learning process.

During the past few decades, advances in evolutionary developmental biology have uncovered an impressive degree of conservation in gene sequence and function, again emphasizing general mechanisms. Hox genes provide a striking example (e.g., Ferrier, 2016; Raff, 1996). First discovered in *Drosophila*, they are present in every animal studied thus far and are characterized by a sequence of 180 bases, the *homeobox*, that is stable across vertebrates, arthropods, annelids, nematodes, and flat worms. Hox genes are expressed in the anterior-posterior axis in the same sequence across animal phyla that have evolved independently at least since the Cambrian Period, about 640 million years ago. This stability at the cellular-molecular level across widely divergent lineages also provides a basis for general process views of learning and memory. For example, the role of CREB (the cAMP response-element-binding protein) in gene expression, which is related to synaptic plasticity and important for learning and long-term memory, has been identified in species from at least four animal phyla: nematodes, mollusks, arthropods, and vertebrates (e.g., Bozorgmehr et al., 2013; Kandel 2012). Such stability is so specific that explaining it in terms other than homology is difficult. Of course, learning and memory go beyond this cellular-molecular level, also involving neurochemical (synaptic transmission) and neurobiological (circuit architecture) levels, which provide room for further homologies, but also for homoplasy (parallel and convergent evolution) and divergent evolution.

Although learning and memory are nearly ubiquitous across animal taxa, the early decades of comparative psychology, in particular, yielded discoveries about a relatively small number of study species. The reason that species diversity in studies of learning and memory has historically been low is not exclusively because rats and pigeons, for example, are just easier to acquire and keep in a laboratory. It is also because researchers were pursuing the types of questions that would not necessitate comparing multiple species. Clearly, a single “model” species and some good hypotheses to test have made significant contributions to the field. Similar concentrations on a few species were a common research strategy in other experimental disciplines, including *Drosophila* in genetics, the sea urchin and chick embryo in developmental biology, and currently mice in cellular and molecular studies. However, in recent decades comparative psychologists and biologists have greatly expanded the diversity of study species. Studying multiple species enables researchers to test adaptive hypotheses about the evolution of behavioral and physical traits, for example, to determine whether a mechanism of

learning and memory is restricted to a particular taxonomic group, or whether it is common to a group of species because of homoplasy (common function independently evolved) or homology (common function inherited from common ancestors) (**Schnell & Clayton; Kriete & Hollis**). Pavlovian conditioning, for example, is widely distributed across all major animal lineages (Hollis, 1997; Hollis & Guillette, 2011, 2015; Papini, 2021). By contrast, episodic memory may occur only within a relatively small group of animals. Depending on one's definition, particularly if that definition includes the capacity for language, episodic memory may be restricted to humans (Suddendorf & Corballis, 2007), or alternatively exists in a mosaic of species (Clayton, 2017; Crystal, 2018; Krause, 2015a) (**Crystal**).

Exploration of the neurobiological basis that supports learning and memory has been particularly useful to comparative evolutionary analyses, and again emphasizes the evolution of general processes. For example, habituation and sensitization to chemical cues in nematode worms (*Caenorhabditis elegans*) involve acquired changes in behavior that can be accomplished with a subset of the 302 total available neurons (**Yu & Rankin**). Spatial cognition in amphibians, as in animals of other taxa, is accomplished using egocentric, beacon-guided cues, as well as, quite possibly, “cognitive mapping” involving activation of the medial pallium (hippocampus) in toads (**Muzio & Bingman**). We see a similar neurobiological approach to the hippocampus in studies of the hippocampal pallium and its role in relational memory in teleost fish (**Gómez, Ocaña, del Águila, Rodríguez, & Salas**) and in research exploring the phylogenetic distribution of neural processes supporting nonassociative learning and Pavlovian conditioning in gastropod mollusks (**Wright**) and incentive learning in vertebrates (**Papini**). Finally, researchers continue to reveal what are still much underappreciated epigenetic mechanisms that contribute to long-term memory consolidation (**Guan**). Ultimately, we need a combination of a broader comparative base and systematic research on specific model species to test for general learning and memory capacities. To this end, we have invited contributors who work with a wide diversity of animal species, including nematodes, gastropod mollusks, insects, amphibians, actinopterygian fish, birds, and mammals, including rats, bears, monkeys, apes, and humans, among others.

1.3 EVOLUTION AND ADAPTIVE SPECIALIZATIONS

The term “adaptive specialization” represents an empirical claim about the evolution of a trait, in this case learning. Thus, if the term is used to explain empirical data derived from learning experiments, then we should expect that an adaptive hypothesis has been tested using established methods. Testing the adaptive nature of a trait, physical or behavioral, requires that certain methods have been employed to rule out alternative explanations

(e.g., random mutation, exaptation, or by-product). We all recognize that spinning a story about how data fit an evolutionary interpretation based on local adaptations is not sufficient as a scientific practice (e.g., Gould & Lewontin, 1979). Specific methods must first be implemented and put to empirical test. Current evolutionary theory provides several options for testing adaptive hypotheses. Traditional methods include, but are not limited to, comparative methods (e.g., systematics), measures of reproductive success, quantitative and molecular genetics, common garden survival experiments, and examination of fossil specimens and records. The late twentieth century witnessed a surge of additional methodologies, such as genomics, bioinformatics, and evolutionary developmental biology (Pigliucci, 2009; Rose & Oakley, 2007). Krause (2015b) examined the degree to which traditional methods for testing adaptive hypotheses have been applied to studies reporting adaptively specialized fear learning in primates (e.g., “prepared” conditioning to biological threats, Öhman & Mineka, 2003) and conditioned sexual behavior in birds (Domjan et al., 2004), and reports that both research programs have made significant efforts to formally test adaptive hypotheses of Pavlovian conditioning. Moreover, in each program, experimental results confirm adaptive hypotheses.

Direct tests of how prepared – and, thus, adaptively specialized – learning can evolve over multiple generations are possible in laboratory experiments (Dunlap & Stephens, 2014) and reveal evidence that natural selection acting on free-living organisms can result in altered phenotypic expression of learning (**Dunlap & Dexheimer**). Indeed, free-living organisms show measurable phenotypic change, including learning capacity, in response to environmental changes (**Griffin & Diquelou**), and both laboratory and naturalistic studies of species that are less represented tell us about the complex ways in which selection can act upon learning and memory (**Vonk**). However, as behavioral ecologists discovered many years ago, just because something is specialized does not mean it performs at a theoretical optimum (**Anselme**).

This same issue concerning adaptive specialization versus general mechanism closely parallels ongoing debate in the field of human memory, where many researchers have been addressing evolutionary questions. A major issue concerns the *survival processing effect* (**Nairne & Coverdale**). The survival processing effect, a phenomenon that involves episodic memory, refers to repeatable observations of superior recall for words evoking survival scenarios in comparison to scenarios that are matched on all characteristics but survival. A central theme in research on the survival processing effect, which also carries through much of the literature on animal learning and memory, concerns whether the effect is an outcome of evolutionary processes, thus making it adaptive memory, or whether general memory processes can account for it without requiring an evolutionary

interpretation (Nairne & Pandeirada, 2016). A similar contrast of views on the evolution of human memory concerns other potentially adaptive functions, such as enhanced memory for cheaters (**Kroneisen**). The lively debate over the evolutionary implications of human memory processing made it clear to us that this volume needed to represent researchers from this sphere.

Related to the question of adaptive specializations is why animals appear to possess so many separate types of learning and memory mechanisms, each adaptively specialized for a particular function, given that such mechanisms are behaviorally and physiologically costly. One possibility is that learning and memory capacities are fine-tuned because such fine-tuning is more efficient, in evolutionary terms, than highly generalized capacities (**Lind, Ghirlanda, & Endquist**). In addition, social learning, yet another form of learning and memory, may be favorable, in evolutionary terms, when the benefits of learning from others outweigh the costs. However, contemporary research on social learning (**Kendal**) suggests that we should not overstate its uniqueness as a separate mechanism. That is, both domain-specific and domain-general capacities underlie social learning, and these may not be distinct from the same associative processes that also guide individual learning. One advantage of a mechanism for social learning is that it can afford rapid and widespread changes in behavior among populations. The plasticity that allows widespread changes to occur can itself be selected upon through genetic accommodation. Furthermore, culturally transmitted behavior can result in environmental changes that actually alter the effects of natural selection on populations (**Laland, Oudman, & Toyokawa**). Thus, learning has a bidirectional relationship with natural selection.

The capacity for explicit-declarative cognition in humans, yet another capacity that appears to be adaptively specialized, particularly when examined in tasks that require symbolic language, creates a sense that humans are qualitatively unique in some aspects of learning and memory. For example, studying episodic memory in nonhumans would be a dead end if it was universally held that it cannot exist without language (e.g., Tulving, 2005). This view has changed among many researchers of animal behavior (Krause & Sanz, 2019). The challenge for comparative psychologists and biologists has been to devise tests for memory and cognition that circumvent the need for language. In so doing, complex cognition can appear in surprising ways (**Schnell & Clayton**). For example, both implicit and explicit rule-following in dimensional categorization can occur in monkeys as well as humans and, although monkeys require a multitude of trials to learn explicit rules, the capacity nonetheless exists (**Church, Jackson, & Smith**). Moreover, monkeys appear to know *that* they know, exhibiting what is called *meta-memory*, a capacity that has been cleverly demonstrated by offering monkeys the opportunity to opt out of taking a challenging test, which they readily choose to do (**Hampton**). Further evidence of complex learning and memory

processes in nonhumans comes from studies of choice, namely, situations in which animals can exercise self-control by choosing to wait, or expend greater effort, to acquire a more valuable reward at a later time (**Beran & Parrish**).

Laboratory studies allow researchers to test specific hypotheses about the underlying processes involved in learning and memory (**Fanselow**). A fundamental issue concerns learning and memory as they occur naturally among free-living organisms. Although adaptive specializations of learning and memory promote survival and reproduction in numerous species, testing hypotheses about how they might have evolved in natural populations is a difficult endeavor, involving quantifying phenotypic variation, its heritable basis, and the direction and strength of selection on that trait. Phenotypic variation in learning and memory capacities has been documented extensively, though mostly on captive animals (see Morand-Ferron, 2017, for a review). Heritable performance of learning ability in wild populations is challenging to measure for a variety of logistical reasons, including the challenge of calculating repeatability. However, although heritability estimates may apply only to the population from which they are drawn, they still provide key background information about how learning for a given species is under selective pressures within corresponding natural populations, especially if the cognitive capacities of individuals in natural populations are quantified. An experimental evolutionary approach, in which the reliability of biologically relevant cues is manipulated directly, demonstrates the evolution of specialized learning phenotypes in *Drosophila* (**Dunlap & Dexheimer**). Similarly, phenotypic change in associative learning in parasitic wasps (*Nasonia*) also responds to selective pressures (**Liefting**). Indeed, ontogenetic change that occurs through learning does not work in opposition to generational change through natural selection. Their interaction is dynamic, complex, and merits a volume of its own in which to explore it.

I.4 ORGANIZATION OF THE BOOK

The organization of this book has taken us on a long road of individual contemplation and collaborative discussion, a road with many twists and turns. Because in many categorical schemes, three is often a magical number, we began with a three-part scheme in mind. However, as the chapters arrived and we attempted to group them, placing each one into its appropriate section, the three themes began to shift, and then reform and shift again. Our organizational road seemed to be made of beach sand. At some point, however, a point that was disconcertedly near our publisher's deadline, we made the final decision to divide the book into two sections, one emphasizing basic conditioning processes and another emphasizing memory. Readers might be tempted to think that they recognize this dichotomy as the same

one that many older texts follow, an unfortunate, and scientifically flawed, dichotomy that separates “animal learning” from “human memory.” However, as we hope to have already convinced readers in the previous pages of this introduction, many of the same questions – for example, homology vs. homoplasy, general process vs. adaptive specialization – drive research in both learning and memory. Our organizational goal, then, has not been to separate human and nonhuman animal research but, rather, to emphasize researchers’ similar focus on the ways in which animals, both human and nonhuman alike, learn and remember. We describe these sections thusly:

- * **Part I: Evolution of Learning Processes.** Chapters in this part examine the evolution of learning based on conditioning and basic associative processes. Chapters focus on functional considerations, such as learning and its relationship to survival, reproduction, and ecological adaptation, and also on the underlying mechanisms, whether at the psychological, neurobiological, neurochemical, or cellular-molecular level.
- * **Part II: Evolution of Memory Processes.** Chapters in this part examine the evolution of learning based on different memory processes, including spatial, emotional, episodic, prospective, recognition, and working memory, as well as metamemory. Whereas most of these chapters deal with behavioral data, the seeds for an understanding of memory at lower levels of analysis are also present.

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