

THEORETICAL NOTES

Pattern and Process in the Evolution of Learning

Mauricio R. Papini
Texas Christian University

A century after E. L. Thorndike's (1898) dissertation on the comparative psychology of learning, the field seems ready for a reassessment of its metatheoretical foundations. The stability of learning phenotypes across species is shown to be similar to that of other biological characters, both genotypic (e.g., Hox genes) and phenotypic (e.g., vertebrate brain structure). Moreover, an analysis of some current lines of comparative research indicates that researchers use similar strategies when approaching problems from either an ecological view (emphasizing adaptive significance) or a general-process view (emphasizing commonality across species). An integration of learning and evolution requires the development of criteria for recognizing and studying the divergence, homology, and homoplasy of learning mechanisms, much as it is done in other branches of biological research.

The study of learning has been influenced in recent decades by an adaptationist view in which learned behavior is part of the organism's biological equipment that allows for an adaptive fit to its environment. This *ecological view* is a central aspect of several approaches to the study of learning, including the constraints-on-learning approach, prompted by discoveries in taste-aversion learning, avoidance training, and autoshaping during the late 1960s; the more contemporary behavior systems approach, seeking explanations of learned behavior as resulting from preorganized systems evolved by natural selection; and the application of optimal foraging theory to learning, according to which natural selection shapes decision rules so that behavior maximizes resource value, minimizes behavioral costs, or both, within certain constraints (see Domjan, 1998). These lines of research follow from a view of learning mechanisms as adaptations shaped by natural selection to achieve outcomes that represent the best solutions to specific environmental problems, within certain constraints. According to this view, the species to be compared in terms of learning tasks must be chosen "on the basis of adaptation and biological function" (Kamil & Clements, 1990, p. 25).

This ecological approach to learning stands in contrast to the so-called *general-process view*, which posits that learning pro-

cesses are basically the same in all animals that exhibit some form of learning. Generality of learning processes can best be shown by comparisons involving distantly related species, such as insects and mammals. However, such comparisons have been criticized on the grounds that they are "extremely difficult to apply to behavior in a biologically meaningful way" (Kamil & Clements, 1990, p. 25). Shettleworth (1998), for example, asked about "what, if anything, results from this kind of selection of species and problems can reveal about 'the evolution of intelligence'" (p. 19). Comparisons among widely divergent species also have been interpreted as attempts to revive the misleading notion of *scala naturae*, first suggested by Aristotle, according to which living organisms can be ordered in a unidimensional scale with humans at the top (Hodos & Campbell, 1969).

I show below that despite their widespread influence, these criticisms are incorrect: Comparisons among distantly related species in terms of learning or any other biological character can be biologically meaningful. Such comparisons can also provide historical information about the evolution of learning mechanisms when the phenotypes are extremely stable. Failure to recognize that many biological phenomena are stable has led to the view that only an adaptationist approach to learning makes biological sense. In addition, despite the fact that the general-process view rests on an impressive body of empirical evidence pointing to generality in learning phenomena, its evolutionary basis has not progressed beyond interesting, but limited, notions. For example, Dickinson (1980) pointed out that general processes might represent a solution to ecological dimensions common to many different niches, such as time and causality, and Macphail's (1982) null hypothesis implies that natural selection has affected learned performance indirectly by altering sensory, motor, and motivational mechanisms while leaving learning mechanisms relatively unmodified. What additional notions and findings from evolutionary biology can contribute to an understanding of the evolutionary basis of learning?

Recent progress in phylogenetic analysis is providing new information with bearing on the history of life that was not available

This article is the result of a talk given at several Japanese universities during 1997. I am grateful to Masato Ishida for hosting my stay in Japan; to colleagues and students at the Universities of Hiroshima, Kanazawa, Kwansai Gakuin, Nagoya, Osaka, Osaka Kyoiku, and Tsukuba for encouraging comments and discussion; and to the Japan Society for the Promotion of Science for their support (Grant S-97165). I am indebted to Jeff Bitterman for valuable comments and criticisms on the original manuscript, as well as for years of stimulating conversation and guidance. Bob Brush, Michael Domjan, Karen Hollis, Steven Stout, Brian Thomas, and Bill Wright made helpful criticisms that improved the original manuscript. Bill Wright kindly provided the material for Figure 5.

Correspondence concerning this article should be addressed to Mauricio R. Papini, Department of Psychology, Texas Christian University, TCU Box 298920, Fort Worth, Texas 76129. E-mail: m.papini@tcu.edu

just a few years ago (Benton, 1990; Doolittle, Feng, Tsang, Cho, & Little, 1996; Valentine, 1995). Phylogenies—that is, hypotheses about the evolutionary relationships among taxa—can now be expanded from comparisons of morphological characters (i.e., the traditional database of phylogenies) to comparisons of DNA sequences in specific genes. Such methods allow not only an independent view for comparison with more traditional approaches but also permit comparisons among taxa with few or no common morphologies, such as plants, fungi, and animals—indeed, more distantly related than any species used in comparative learning research. In addition, cladistic methods of classification combined with computer algorithms are placing taxonomy on more objective grounds by reducing the influence of the biologist's personal biases in characterizing the importance of various traits for classification (Harvey & Pagel, 1991). Molecular techniques have also led to some surprising discoveries connecting evolution and development. For example, animals with vastly different body plans, including jellyfish (Cnidaria), worms (Annelida), insects (Arthropoda), and humans (Chordata), share a set of genes called the *Hox* cluster (see examples of evolutionary stasis below) that determines the head–tail positional axis of body organization (Ruddle et al., 1994). Stability in evolution is not only a feature of the fossil record (Gould & Eldredge, 1977) but also a property of highly conserved developmental pathways. Are there some implications of this revolutionary knowledge for the way we think about animal learning?

I propose here to take another look at the relationship between evolution and learning. The occasion seems appropriate to celebrate the centennial of Edward Lee Thorndike's (1898) doctoral dissertation, a publication that has enjoyed a pervasive and lasting influence in the comparative analysis of learning. This exercise will show that a general-process view can have just as sound an evolutionary basis as the ecological view that has dominated comparative research on learning over the past 20 years. Furthermore, this exercise will uncover how much still remains to be done to fully integrate evolutionary thinking into the study of learning. Basic evolutionary problems, such as the determination of homologies and homoplasies (see below), are almost totally absent from comparative research on learning. In trying to accomplish such a level of integration, learning researchers must adopt a multidisciplinary approach and make efforts to uncover relationships between their findings and advances in such fields as comparative neurology, molecular developmental biology, and cladistic analysis, among others.

This article is divided into four sections. The first section introduces several major concepts in evolutionary theory, including a definition of *evolution* that emphasizes change as well as stasis, and the key concepts of divergence, homology, and homoplasy. The second section provides a brief review of biological traits that exhibit impressive evolutionary stability; there I argue that generality in learning processes is not so dramatic when seen in the context provided by other biological traits. The third section provides a brief review of three lines of research on animal learning that incorporate modern evolutionary ideas. They involve species comparisons at various taxonomic levels; nonetheless, there are major common themes, including the application of cladistic analysis, the integration of behavioral and neurological information, and the problem of distinguishing between the contribution of learning processes and that of nonlearning or context-

tual factors (e.g., species differences in perceptual, motivational, and motor processes) to the behaviors under analysis. These research examples also illustrate the application of such basic concepts as homology, homoplasy, and divergence to comparative research on learning. The fourth and final section provides a new framework for the study of the evolution of learning mechanisms on the basis of concepts derived from the study of other biological traits. It is argued that the notions of modularity (that traits can be decoupled in evolution) and co-option (that evolution may be achieved by changes in regulatory mechanisms) provide an evolutionary basis for the traditional general-process view of learning.

Evolution: Some Key Concepts

Change and Stasis

Evolution is generally associated with notions of change and transformation. Typical postmodern-synthesis definitions emphasize changes in allele frequencies in a population of genetically variable individuals (Futuyma, 1979). Such genotypic changes are driven by natural selection—that is, the differential reproductive success of alternative phenotypic traits. However correct, these are only partial aspects of evolution. Evolution is just as much characterized by stasis as it is characterized by change. The reason for this apparent paradox is illustrated in Figure 1. In the figure's left panel, various forms substitute for each other at different points in time. Imagine, for example, that you are viewing pictures of your kitchen table taken at three different times; the objects on the table may change from picture to picture without themselves being connected in any deep sense. This is an example of nonevolutionary change. Evolutionary change, on the other hand, implies shared ancestry. "Pictures" of a particular fauna taken at three different times may show a type of change that allows for the establishment of genealogical relationships between ancestors and descendants. An important property of shared ancestry is that it can only be detected on the basis of *character similarity*, that is, evolutionary stasis. Character similarities have provided a major basis for evolutionary thinking, as demonstrated ultimately in the sharing of a

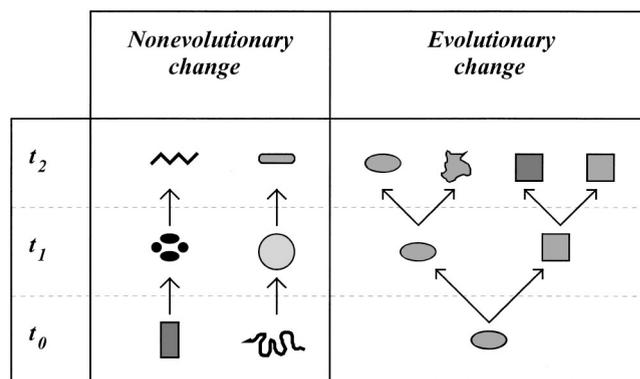


Figure 1. Lineal transformations representing nonevolutionary change (left panel) and evolutionary change (right panel). Diversity in form, shape, and shade at t_1 or t_2 can be traced to a common ancestor only in the case of evolutionary change. However, common ancestors can only be detected on the basis of character similarities, represented here in terms of equal shape or shading. $t =$ time.

genetic code by organisms as diverse as plants, fungi, animals, and unicellulars. Change is evolutionary only when it occurs in the context of shared ancestry. In Figure 1, right panel, diversity in morphology at any point in time can ultimately be traced to a common ancestor on the basis of character similarity (i.e., common shape or shading). Stasis is, therefore, as important a part of evolutionary theory as change.

In evolutionary theory, change is accomplished by a variety of mechanisms, including natural selection, correlation or allometry, and genetic drift, collectively referred to as *evolutionary processes*. Natural selection is critical for understanding the evolution of relatively complex traits, whether in morphology (e.g., organs) or in function (e.g., metabolic, physiological, or behavioral processes). It is unlikely that the assembly of parts necessary to build complex organs (e.g., the vertebrate eye) or to develop complex functions (e.g., echolocation in bats) has occurred by chance alone. Such traits, called *adaptations*, are assumed to have evolved by natural selection. Traits may also change not as a result of specific selective pressures but because they are correlated with some other character, which is itself being selected for by differential fitness. Such correlations are based on the pleiotropic effects of genes—that is, that individual genes contribute to the development of more than one character. For example, natural selection for increased body size will passively drive other organs, such as the brain, to increase in size by correlated growth (Aboitiz, 1996). Moreover, in relatively small populations, random sexual recombination may lead to the loss of some alleles, a process known as genetic drift (Futuyma, 1979). Evolutionary processes responsible for changes in allelic frequencies in evolving populations can be thought of as “creative” forces that lead to evolutionary divergence, novelty, and progressive or regressive change.

Evolutionary processes operate on genetic variation. Inherited information imposes a cascade of constraints, including genetic, developmental, cellular, metabolic, and functional constraints, in addition to the obvious physicochemical limits within which living organisms must exist (Hall, 1992). Because these constraints are the product of the historical trajectory of a lineage, they are referred to as *phylogenetic constraints*. Phylogenetic constraints determine the *evolutionary pattern*—that is, the specific pathways that are open for evolutionary change—and can thus be thought of as “conservative” forces. The estimated 5–50 million extant species provide an estimate of the potential for change within the limits imposed by phylogenetic histories (e.g., six-limbed mammals such as the Centaur and Pegasus only “evolved” in human mythology). However, the fact that an even greater number of species seem to have followed the path of extinction suggests that the limits to creativity in evolutionary change are real and tangible (Benton, 1995).

Evolution is therefore defined as an outcome resulting from the interaction of process and pattern. This is by no means a novel definition; it is clearly recognizable in Darwin’s writings, in which processes are referred to as “the conditions of existence” (i.e., natural selection) and patterns as “the unity of type” (i.e., phylogenetic constraints). Darwin (1859/1993) wrote:

It is generally acknowledged that all organic beings have been formed on two great laws—Unity of Type, and the Conditions of Existence. By unity of type is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is quite

independent of their habits of life. On my theory, unity of type is explained by unity of descent. The expression of conditions of existence, so often insisted on by the illustrious Cuvier, is fully embraced by the principle of natural selection. (pp. 261–262)

Divergence, Homology, and Homoplasy

There are essentially two major outcomes in evolutionary change. Evolved species either show similarities or they show differences as far as some biological character is concerned. The process of biological adaptation leads to the evolution of differences in trait morphology or function. This phenomenon is referred to as *divergence*. One of the clearest examples of divergence is found in the evolution of beak size and shape in birds that have colonized various archipelagos, including the Hawaiian honeycreepers, shown in Figure 2, and the Galápagos finches. In finches, beak properties and body size correlate with the size and hardness of available seeds. In a long-term study of *Geospiza fortis* on Daphne Major Island between 1975 and 1978, Grant (1986) found that a drought during 1977 caused a relative abundance of larger and harder seeds. Concomitantly, population averages for both body size and beak depth increased as a result of differential survival. Such morphological changes seem functionally appropriate for dealing with scarce food resources (i.e., a large body size might confer an advantage in competition for food) and harder seeds (i.e., a deeper beak allows for faster tearing of the seed coating). The rapidity of the population’s response to the environmental change was striking, as was the fact that population trends in body size and beak depth were reversed after years of exceptionally high humidity, as in 1983–1984 (Gibbs & Grant, 1987).

Variation in beak shape, such as that shown in Figure 2, is so noticeable and so obviously related to a natural resource (i.e., food) that it has served as an inspiring theme in the field of learning. Perhaps there is a similar variation in learning processes resulting from the different information-processing demands imposed by the ecological resources driving divergent evolution (Sherry & Schacter, 1987). On the assumption that each species is adapted to a unique ecological niche, adaptations should be specific to single species. Such a claim seems to justify the argument that learning researchers should select behaviors that are part of the organism’s natural repertoire, and what is most clearly an instance of an ecologically relevant character than one that is unique to a single species, as beaks are in Figure 2? In the field of learning, for example, the food-storing behavior of corvids and parids is easily perceived as an adaptation because of its restricted taxonomic distribution (see below). In fact, Coddington (1988) suggested that the concept of adaptation should refer exclusively to traits that are both unique to a single species and correlated with selective pressures also unique to the species. The problem with this argument, as it applies to both biological characters in general and learning phenotypes in particular, is that selective pressures can be general enough to affect characters distributed above the species level (Stearns, 1992). For example, in addition to species variations in beak morphology, the Hawaiian honeycreepers depicted in Figure 2 exhibit features that are far more stable, including feathers (common to class Aves), bony jaws (common to superclass Gnathostomata), and a pair of eyes (common to subphylum Vertebrata). Similarly, the feeding behaviors most typically exploited in learning experiments are probably quite general in their organiza-

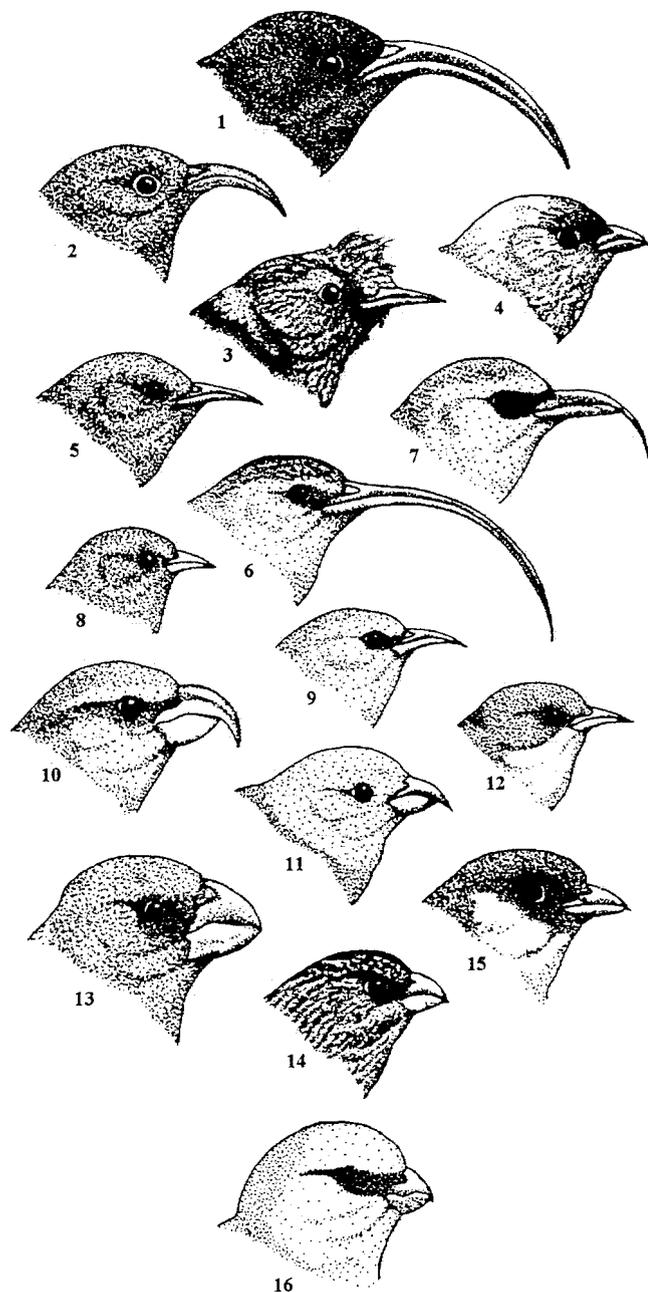


Figure 2. Adaptive radiation of a group of honeycreeper birds in the Hawaiian islands. The following genera are shown in this drawing: *Drepanis* (1), *Vestiaria* (2), *Palmeria* (3), *Ciridops* (4), *Himatione* (5), *Hemignathus* (6–7), *Loxops* (8–9), *Pseudonestor* (10), *Loxioides* (11, 13, 16), *Paroreomyza* (12), *Telespiza* (14), and *Melamprosops* (15). Peter R. Grant; *Ecology and Evolution of Darwin's Finches*. Copyright © 1986 by Princeton University Press. Reprinted by permission of Princeton University Press.

tion and thus less conspicuously seen as adaptations, but it would be clearly a mistake to say that feathers, jaws, and eyes lack adaptive significance because of their supraspecies taxonomic distribution. A similar argument can be made for the behaviors typically used in learning experiments, such as running, manipu-

lating a lever, pecking, or freezing, among others that do not stand out as adaptations because they are common to many species.

But where is such an impressive similarity coming from? The origin of character similarity is a complex issue in evolutionary theory because resemblance can be based on inheritance from a common ancestor or on common selective pressures (see Hall, 1994; Sanderson & Hufford, 1996). These two sources of character similarity, shared ancestry and shared selective pressures, are distinguished as *homology* and *homoplasy*, respectively. The homology of characters is usually established by their common position, architecture, embryology, and functional properties. For example, the basic division of the vertebrate telencephalon into a dorsal pallium and a ventral subpallium is widely thought to be derived from a common ancestor and thus to be homologous (Northcutt, 1995; Striedter, 1997). Comparative research on the relative position of these large divisions, as well as on their internal structure, afferent and efferent connections, distribution of neurotransmitters, and embryological origin, provides support for homology. By contrast, the body shape and mode of locomotion of marine mammals and fish are similar by homoplasy (i.e., adaptation to similar selective pressures). The immediate common ancestor of all marine mammals was a quadruped animal. Moreover, clear evidence of homoplastic evolution is seen at the behavioral level. Whereas marine mammals propel themselves by dorsoventral movements of the tail, fish swim by lateral movements of the tail. As Figure 3 shows, homoplasies are further subdivided into three different outcomes: *convergence* (as in the example just given), *parallelism* (see section on food-storing behavior), and *reversal* (see section on learning in molluscs). Homoplasy implies, therefore, that no matter how similar two characters might be on first appearance, deep comparative analysis of both form and function should establish important distinctions. The reason should be obvious: Homoplasies based on exactly the same underlying processes should evolve only by chance, and the probability that exactly the same set of genes would evolve by chance in independent lineages, and that they would lead to exactly the same developmental trajectory, is negligible.

Concepts such as divergence, homology, and homoplasy play a central role in evolutionary theory. Could they be of some application to understanding the evolution of learning?

Evolutionary Stasis: Some Examples

Learning phenomena appear, at least on the surface, to be extremely stable across a wide variety of animals. Some of the most basic phenomena known from research with a few selected species of mammals and birds have been reported in analogous experiments with other vertebrates (Macphail, 1982), notably teleost fish (Bitterman, 1984), and with a variety of species from various other phyla, including molluscs, arthropods, annelids, and nematodes (Bitterman, 1996; Carew & Sahley, 1986; Wen et al., 1997). Although comparative research on learning is far from covering the known 35 or so animal phyla, the sample is wide enough to attempt some generalizations. Figure 4 presents a view of the phylogeny of the most common metazoan phyla in the format of a *cladogram*, which is a depiction of the pattern of divergence of a set of monophyletic taxa grouped on the basis of unique derived traits. Some of such shared derived traits, or synapomorphies, are also included in this cladogram (e.g., a ner-

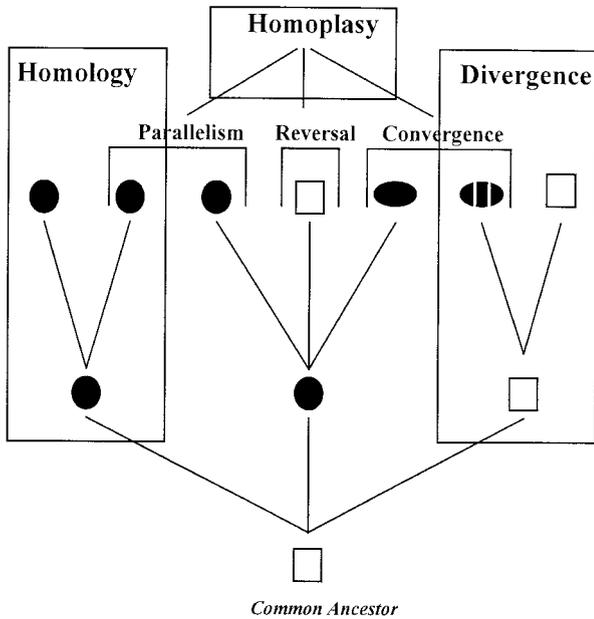


Figure 3. A simplified representation of major evolutionary outcomes. Phenotypic similarities and differences are represented in terms of the shape and shade of geometric forms. The three main concepts are *homology* (similarity resulting from shared ancestry), *homoplasy* (similarity resulting from shared ecological pressures), and *divergence* (dissimilarity in descendants from a common ancestor). Homology implies similarity in outcome (e.g., behavior) based on the same underlying mechanism. Three cases of homoplasy can be distinguished. In parallelism, relatively closely related lineages independently evolve similar characters. In reversal, a character in a descendant recovers features of a remote ancestor. In convergence, similarity occurs in relatively distantly related species. Parallel and convergent evolution imply similarity in outcome (e.g., behavior) but not in process (e.g., underlying mechanism). Divergence implies different outcomes (e.g., behavior) resulting from the operation of different underlying mechanisms.

vous system characterizes all phyla except the sponges [Porifera]. This cladogram assumes monophyly (i.e., a single common ancestor), although the matter of metazoan origins is far from settled, as are some of the phylogenetic relationships among the phyla (e.g., Brusca & Brusca, 1990; Willmer, 1990). Nonetheless, certain features are reasonably well established, including the position of the Porifera and Cnidaria (e.g., jellyfish, coral, sea anemones) at the basis of the cladogram. Most of the animal phyla exhibit bilateral symmetry as a primitive condition (true also for equinoderms such as the starfish, in which the pentamer symmetry is a derived feature of the adult form). Bilateral animals are usually segregated into two broad superphyla known as protostomes and deuterostomes, differentiated on the basis of their embryology (described below; see also examples of evolutionary stasis below).

Figure 4 sets the phylogenetic stage for a consideration of learning in a comparative framework. Most of the invertebrates used in experimental research on learning are protostomes (insects such as honeybees and fruit flies, molluscs such as *Aplysia* and *Hermisenda*, and annelids such as the leech *Hirudo medicinalis*; e.g., Carew & Sahley, 1986). The performance of these animals is often compared with that of deuterostome vertebrates, with whom

they share a very remote common ancestor. The protostome–deuterostome divergence is evident in fossils from the early and mid Cambrian period (544–520 million years ago), so it must have occurred well before that time, during the Proterozoic eon; indeed, according to one estimate based on molecular data, the divergence could have occurred as far back as 1.2 billion years ago (Wray, Levinton, & Shapiro, 1996). The Cambrian fauna include such protostomes as arthropods and molluscs and such deuterostomes as equinoderms and the presumed chordate *Pikaia gracilens* (Briggs, Erwin, & Collier, 1994). Therefore, these lineages have undergone extensive independent evolution; evidence of conservation in learning processes would be particularly revealing if it could be interpreted in terms of the homology-versus-homoplasy distinction (Walters, 1994).

There is evidence of nonassociative, short-term learning in cnidarian species (e.g., Haralson & Haralson, 1988; Johnson & Wuensch, 1994). Cnidarians display radial symmetry and possess the simplest nervous systems of all animals, consisting of a diffuse nerve net (i.e., no central nervous system is present). It is interesting to note that cnidarian neurons exhibit familiar physiological properties, including excitatory and inhibitory postsynaptic poten-

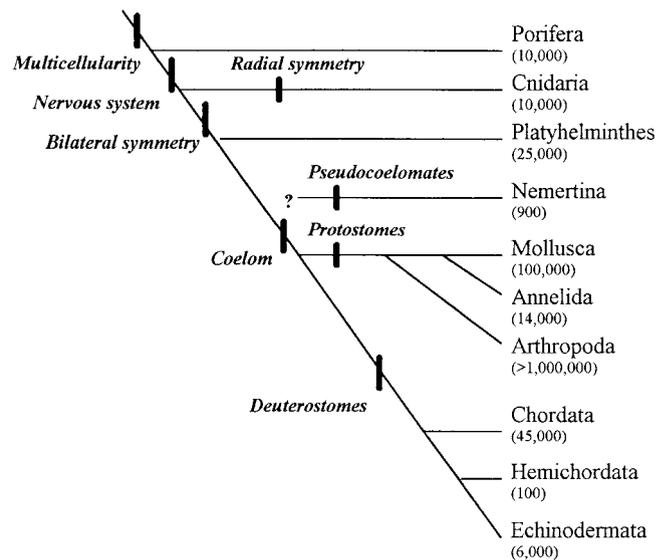


Figure 4. A cladogram of the most common animal phyla. The relationships and approximate number of extant described species are based on Nielsen's (1995) study with one exception: Nielsen classified the Urochordata, Cephalochordata, and Vertebrata at the phylum level, whereas the more traditional phylum Chordata is used here. Multicellularity refers to the presence of differentiated tissue within an organism. No true nervous tissue has been described in the Porifera. Bilateral symmetry refers to animals with a clear anterior–posterior axis and paired appendages and organs. Bilateral symmetry may be lost in the adults of some lineages, such as is the case with starfish (Echinodermata). Protostomes and deuterostomes are two major groups of phyla distinguished by features of their embryology (see text for further details). Comparative research on learning includes isolated studies with cnidarians, planarians, and annelids, an emerging literature with the nematode *Caenorhabditis elegans*, and a relatively extensive list of publications with protostome species, mainly arthropods (honeybees, fruit flies, etc.) and molluscs (*Aplysia*, *Hermisenda*, etc.). By far, the bulk of knowledge on animal learning comes from a selected group of chordates.

tials, miniature end plate potentials, action potentials, spatial and temporal summation, calcium-dependent release of neurotransmitter at chemical synapses, and electrical synapses (Spencer, 1989). Basic forms of nonassociative learning (e.g., habituation, pseudoconditioning, and sensitization) and associative learning (e.g., acquisition, extinction, and discrimination) under either Pavlovian (i.e., response-independent pairing of stimuli) or instrumental (i.e., response-dependent reinforcement) contingencies can be safely assumed to be general phenomena, common perhaps to all bilateral animals. Indeed, the list of similarities is impressive when the comparison involves honeybees (a protostome insect) and mammals (deuterostome chordates). Factors such as the amount of training, reinforcer magnitude, and reinforcer probability, and well-known learning phenomena such as overshadowing, blocking, and spatial learning, provide striking parallels between honeybees and mammals (Bitterman, 1988, 1996). These similarities suggest the possibility of extensive evolutionary convergence in learning phenomena between insects and mammals. The fact that the common ancestor of protostomes and deuterostomes was a bilateral animal probably resembling extant planaria (Willmer, 1990) seems consistent with a convergent argument. Alternatively, as Bitterman suggested, it is possible that at least some of these phenomena are based on highly conserved, homologous synaptic properties. Of course, as pointed out by Bitterman, it is still a long way from phenomena and principles to the details of mechanism, particularly at the molecular level, but these similarities cannot be easily dismissed, and, indeed, they should most profitably be embraced and their evolutionary basis (homology or homoplasy) sought.

It is this type of generality that appears to lack adaptive relevance because it applies to organisms that have evolved in vastly different ecological niches. The fact is, however, that evolutionary stasis of the type shown by learning phenomena is a common feature of other biological traits, as the following brief review shows. As already mentioned, the nearly universal genetic code used by cells to assemble amino acids into proteins is a striking example of the important physical and chemical constraints on the organization of molecules with self-replicating properties. Some specific proteins, and their associated genes, are so general that their structural analysis allows for comparisons among organisms that bear no obvious macroscopic resemblance to one another. For example, cytochrome *c*, a mitochondrial protein involved in the transport of oxygen, is present in all eukaryote organisms, from yeast to fungi, wheat, flies, and chimpanzees. In fact, traits like cytochrome *c* allowed for the first phylogenetic comparisons on the basis of molecular evidence during the 1960s (Fitch & Margoliash, 1967).

Also surprisingly general across animal phyla are regulatory gene clusters that control ontogenetic processes (Carroll, 1995). The Hox cluster is among the best known of these regulatory genes from the comparative point of view. It is striking in that genes within the cluster as well as across species from a variety of phyla share a sequence of 180 base pairs, called the *homeobox*. Protein products from these genes seem to bind preferentially to DNA, thus playing a regulatory role by influencing the transcription of other genes. Mutations of Hox genes result in changes in the identity of parts of the body where protein expression occurs. For example, homeobox mutations in the fruit fly (*Drosophila melanogaster*) may transform a segment that normally develops a pair

of halteres into one developing an extra pair of wings. This so-called “bithorax mutant” implies a radical change in body plan; the presence of two wings in the wild type is actually a diagnostic character for *D. melanogaster*'s taxon (i.e., Diptera, literally “two wings”). It is yet unclear whether Hox genes can be found in Porifera, but they have been identified in Cnidaria, primitive bilaterals such as flatworms, nematodes such as *Caenorhabditis elegans*, protostomes, and deuterostomes (Ruddle et al., 1994). The function of Hox genes is also stable across phyla: They encode information about the relative position of body parts independently of the actual structures that develop in those parts. Slack, Holland, and Graham (1993) referred to this spatial pattern of gene expression as the zootype and suggested that herein lies a definition of *animal*.

The distinction between protostomes and deuterostomes (see Figure 4) is also based on characters that are “stubbornly” general (Raff & Kaufman, 1983, p. 103). The main example involves the position of the mouth and anus relative to the blastopore—the site where cells invaginate during gastrulation to build the digestive tract. In protostome embryos, the mouth develops from cells located near the blastopore, whereas the other end of the tract becomes the anus. By contrast, the mouth of deuterostomes arises at a site anterior to the blastopore, whereas the opening near the blastopore becomes the anus. Thus, in relation to an anterior–posterior axis in the embryo, the mouth is posterior in protostomes but anterior in deuterostomes. The generality of these developmental features contrasts remarkably with the extreme differences in adult morphology exhibited by protostomes and deuterostomes.

There is also impressive functional stability across widely divergent taxa. Consider the immune system as an example. Only vertebrates possess the ability to generate immunoglobulins (i.e., circulating antibodies) by rearrangement of gene segments. Immunoglobulins produced in this manner are so specific in recognizing a foreign body that they can be said to show “memory” and to allow the system to respond in anticipation. No protostome species is known to possess rearranging immunoglobulins, although there are mechanisms allowing for the discrimination between self and nonself in virtually all animals (Marchalonis & Schluter, 1990). *Endothermic homeothermy*, or the ability to maintain a relatively constant internal temperature in the face of environmental variations, is common to mammals and birds. Although mammalian and avian endothermy evolved independently from poikilotherm ancestors, as shown by important differences in underlying mechanisms and structure (Ruben, 1995) and suggested by cladistic analysis of amniote evolution (Kemp, 1988), it is striking that the function is preserved in these two classes of vertebrates given the wide range of ecological adaptations exhibited by mammals and birds.

There is impressive morphological and functional conservatism in neural processes, as was mentioned previously in connection with cnidarian neurons. Recent progress in comparative neurology shows that the major divisions of pallium and subpallium are recognizable in terms of their connectivity and histochemistry in most vertebrate classes. Using mammalian terminology, such areas as the hippocampal formation, neocortex, septum, and corpus striatum, to name just a few, can clearly be traced in all gnathan vertebrates. This conclusion includes teleost fish, the most abundant extant taxon of fishes, which show a developmental profile characterized by the eversion of the dorsal part of the neural tube

rather than its inward folding as occurs in all other vertebrates. Eversion results in a peculiar topographical distribution of homologous areas (Northcutt, 1995; Striedter, 1997). Commonality of neurobiological features is paralleled by common functional roles in learning tasks, particularly among birds and mammals, for which there is a substantial body of behavioral evidence (Macphail, 2000). This is not to say that there are no macroscopic, or even fine-grain, neurological differences among vertebrates. For example, the six-layered neocortex and the interlocking dentate gyrus and CA fields of the hippocampal formation are unique to mammals. However, cell populations with similar embryological origin exist in other vertebrates, although organized in a different manner. It is presently unclear whether the architectural level is functionally important or just a neutral by-product of different developmental trajectories.

The foregoing review provides an appropriate framework in which to evaluate the generality of learning processes. In the context provided by these extremely stable traits, the possibility that at least some learning mechanisms could be homologous among widely divergent animal lineages, as postulated by the general-process view of learning, seems biologically plausible and meaningful. This is particularly obvious if the word *mechanism* refers to synaptic properties or molecular processes responsible for neural plasticity. Furthermore, the most meaningful comparisons for very stable characters (e.g., Hox genes, cytochrome c, endothermy, telencephalic morphology, etc.) are actually those involving distantly related species. A striking feature of the biological characters reviewed in this section is that they do not correlate with ecological conditions or even modes of life. Paraphrasing Cuvier and Darwin, it would appear that the “conditions of existence” must accommodate to these characters rather than vice versa, as a simple adaptationist viewpoint would appear to suggest. Obviously, conserved traits must also meet adaptive criteria, or natural selection would rapidly eliminate the genes responsible for the trait. But the adaptive significance of a particular trait need not be obvious at the taxonomic level of a species. This point was made clearly by Osorio, Bacon, and Whittington (1997) who, after reviewing arthropod neural development, arrived at the following conclusion:

The picture that emerges from comparative studies of lamina [a ganglion receiving visual input] in insects and crayfish is one of remarkable uniformity from animals whose life-styles and evolutionary lineages should set them far apart. Not only are they probably separated by over 500 million years of independent evolution, but insects also are fast moving aerial animals, whereas crayfish are comparatively sluggish, aquatic, and often nocturnal. Even so, we find the same set of neurons making up a lamina cartridge, with the same physiological responses. (p. 253)

Comparative Learning: Three Examples and Some Conclusions

Although I have emphasized stable aspects of evolution in the previous sections, evolution does involve a complex interaction of pattern and process, and it is possible, at least in principle, to assess the contribution of both aspects to the evolution of any biological trait, including learning. Such an assessment demands not only careful analysis of learning processes but also attention to underlying mechanisms, comparative neurological issues, and phyloge-

netic hypotheses. From the several currently active areas of comparative research, three were selected as examples: Phylogenetic analysis of cellular properties of learning in molluscs (illustrating evolutionary reversal), spatial learning and hippocampal size in food-storing birds (illustrating parallel evolution), and surprising nonreward in appetitive learning in vertebrates (illustrating divergent evolution). This selection is not intended as an exhaustive review of these areas but rather is meant to provide examples that demonstrate the extent of the integration of evolutionary concepts into the experimental study of learning.

Cellular Properties of Learning in Molluscs

This first example illustrates one way in which cladistic analysis can be integrated with research on learning mechanisms. Such an integration permits the development of evolutionary hypotheses concerning the divergence, homology, and homoplasy of learning mechanisms. The polarity of evolutionary change can also be established by cladistic analysis (i.e., which of two mechanisms evolved first in a particular lineage).

Molluscs have been prime models for the cellular analysis of simple forms of learning given some notable features of their neurobiology (Carew & Sahley, 1986; Kandel, 1976). Large, identifiable neurons, predictably located within the ganglia and easily accessible for stimulation and recording, are some of their main features. In addition, simple reflexes can be modified by experience to yield nonassociative and associative learning. In a typical conditioning experiment, stimulation of mechanosensory neurons from the slug's siphon is used as a conditioned stimulus (CS), a shock delivered to the tail as the unconditioned stimulus (US), and either the siphon's withdrawal or the excitatory postsynaptic potentials (EPSPs) registered from a siphon motoneuron serve as the conditioned response. CS-US pairings result in increased amplitude of EPSPs compared with unpaired controls. Further analysis of sensory neuron activity indicates that pairings lead to the broadening of action potentials and to an increase in sensory neuron excitability, both mediated by the neurotransmitter serotonin. Increased excitability and spike broadening occur in sensory neurons that have been activated in close contiguity with the US input. Moreover, both short- and long-term sensitization are based on similar functional changes occurring in mechanosensory neurons.

Wright and collaborators (Erixon, DeMartini, & Wright, 1999; Wright, 1998; Wright, Kirschman, Rozen, & Maynard, 1996) have carried this analysis a step further in a comparative context. They reasoned that “excitability” and “spike broadening” are part of the neuromodulatory phenotype of *Aplysia's* mechanosensory neurons. Would these mechanisms be present in homologous neurons from other molluscs? Could this information tell something about the evolution of excitability and spike broadening in molluscs? Their approach essentially involved four steps. First, seven species of opisthobranch molluscs were selected for analysis (Genera: *Bulla*, *Akera*, *Aplysia*, *Dolabella*, *Bursatella*, *Phyllaplysia*, and *Dolabrifera*). Second, their phylogenetic relationship was determined by standard cladistic analysis based on a matrix of morphological characters used in molluscan taxonomy. Third, they identified sensory neurons in each species that were homologous to the tail-sensory neurons of *Aplysia*. Neuronal homology was argued on the basis of such features as the neuron's location in the

ganglion, its size, and its resting physiology, among others. Although none of these features demonstrate that two neurons are homologous, taken together they build up a persuasive argument. Finally, the state of the two neuromodulatory characters (presence or absence of serotonin-induced excitability and spike broadening) was determined for each species in sensory-neuron homologues and mapped into the cladogram. The resulting distribution is shown in Figure 5.

Two main conclusions can be drawn from this phylogenetic analysis. The first conclusion is that increased excitability evolved before spike broadening in this particular population of sensory neurons. This conclusion is based on the presence of excitability and the absence of spike broadening in two out-groups, represented here by *Akera* and *Bulla*. An out-group is a lineage that clearly lies outside of the clade being studied but that is also closely related to it. If a particular character is present in the out-group (e.g., excitability), it is thus assumed to be primitive or plesiomorphic; if, however, the character is absent (e.g., spike broadening), it is considered to be derived or synapomorphic. One implication of this finding is that excitability and spike broadening have evolved independently because there are species that show the former but not the latter mechanism. The second conclusion is that both excitability and spike broadening have apparently been lost in the tail-sensory neurons of the ancestors of *Dolabrifera*. Consistent with this analysis, Wright (1998) has shown that training protocols inducing short- and long-term sensitization in *Aplysia* fail to induce similar behavioral changes in *Dolabrifera*. However, these two species exhibit comparable levels of habituation of the mantle-withdrawal response, suggesting that *Dolabrifera* is capable of some forms of learning.

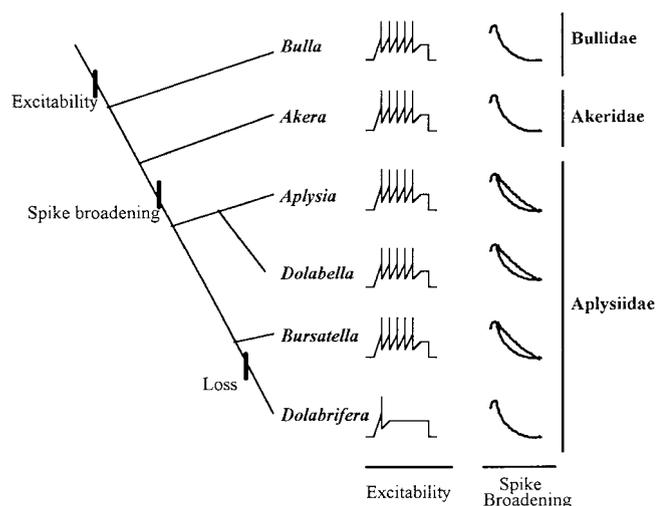


Figure 5. Cladogram representing the phylogenetic relationship among seven genera of opisthobranch molluscs. Neuromodulatory phenotypes (increased excitability and spike broadening) have been determined for one species in each genus and mapped into the cladogram. The cladogram is based on molecular data from Medina (1998). Modified from "Dissociation Between Sensitization and Learning-Related Neuromodulation in an Aplysiid Species," by N. Erixon, L. J. DeMartini, and W. G. Wright, 1999, *Journal of Comparative Neurology*, 408, Figure 4, p. 513. Copyright © 1999 John Wiley & Sons. Adapted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

Relevant to the present discussion is the ability of cladistic analysis to provide for an independent and objective source of phylogenetic information. The uncoupling of learning mechanisms (e.g., spike broadening, excitability) suggests they can evolve independently, and, therefore, the issue of the polarity of change is raised: Which of the two evolved first? Consider the absence of spike broadening in *Bulla* and *Dolabrifera*; the use of cladistic analysis opens the possibility for differential interpretations of what is essentially the same fact. In this case, the absence of spike broadening is interpreted as primitive or plesiomorphic in *Bulla* but as due to evolutionary reversal to the plesiomorphic condition in *Dolabrifera* (see Figure 3 for a representation of evolutionary reversal).

Spatial Learning and Hippocampal Size in Food-Storing Birds

Species within several avian orders, including raptors (hawks and owls), woodpeckers, and passerines, have evolved various degrees of food-storing behavior (Vander Wall, 1990). In food-storing species, consumption is deferred for periods ranging between minutes and months. Figure 6 shows the families of perching birds (order Passeriformes) in which at least one food-storing species has been described. The following discussion centers on studies involving marsh tits (*Parus palustris*; Paridae) and Clark's nutcrackers (*Nucifraga columbiana*; Corvidae) because the role of spatial learning in food-storing behavior has been studied in greatest detail in these species.

There are two related issues to be explored from an evolutionary point of view. First, did learning mechanisms in food-storing marsh tits and Clark's nutcrackers diverge from those of nonstoring species within their respective families? An answer to this question requires a comparison of storer with nonstorer species. Because food-storing behavior varies among species of parids and corvids, within-family comparisons are necessary to determine the presence of a divergence in spatial learning mechanisms that might explain the distribution of this trait. Such comparisons would also minimize the influence of contextual or nonlearning factors on performance (e.g., species differences in sensory-perceptual, motivational, or motor processes). To tease apart the contribution of learning and nonlearning factors to performance, comparative researchers vary training parameters and determine how these variables affect behavior in different species, a strategy known as *systematic variation* (Bitterman, 1960). Use of such research strategy has made it possible to determine that food recovery depends on spatial learning in both the marsh tit (Shettleworth & Krebs, 1982) and the nutcracker (Kamil & Balda, 1985). However, it is not yet completely clear whether storing behavior is based on divergent learning mechanisms relative to those of nonstorer species.

Studies comparing marsh tits with some nonstoring parid show nondifferential performance in tests involving retention intervals ranging between 1 min and 24 hr, in delayed matching to sample tests with retention intervals of 30 s, 5 min, and 15 min, and in analogs of the radial-maze task widely used with rodents (Healy & Krebs, 1992a, 1992b; Hilton & Krebs, 1990). Somewhat more positive results were reported in a comparison of marsh tits and nonstorer blue tits (*Parus caeruleus*) trained to find hidden food that could be eaten only partially. After a 30-min retention interval,

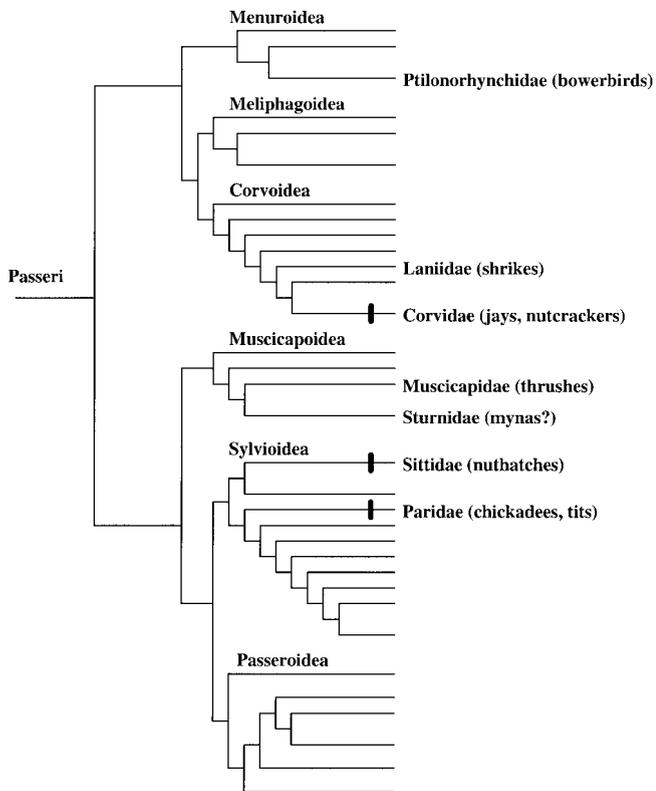


Figure 6. Cladogram of the Passeriformes based on DNA–DNA hybridization data from Sibley and Ahlquist (1990). Phylogenetic distance is not in scale. Each horizontal line represents a family; a single family may include dozens of species but species not necessary to the discussion here have been omitted for clarity. All the superfamilies (-idea ending) are listed in this cladogram, but only those families (-dae ending) with at least one known food-storing species (Vander Wall, 1990) are named (common names of storers are written in parentheses). Bars mark lineages (Corvidae, Sittidae, and Paridae) for which at least one species is known to have a relatively large hippocampal formation (see text for details).

birds were allowed a second opportunity to find the remaining food. Storers exhibited fewer errors than nonstorers in this task but still needed an average of about two visits to locate the food (vs. about three visits in the nonstorers). Some experiments comparing the storer black-capped chickadee (*Parus atricapillus*; Sylvioidea, Paridae) and the nonstorer dark-eyed junco (*Junco hyemalis*; Passeroidea, Fringillidae) suggest that the difference in behavior may be caused by the differential salience of spatial and visual cues (Brodbeck, 1994; Brodbeck & Shettleworth, 1995). Birds from both species learned equally easily to locate food on the basis of a spatial-color compound; however, when the elements were dissociated in test trials, chickadees responded first on the basis of spatial location rather than color, whereas juncos exhibited no bias. A perceptual bias (a nonlearning factor) could be a way of influencing food-storing behavior without necessarily involving new learning mechanisms.

As for Clark’s nutcrackers, they tolerate longer temporal delays in a nonmatching to sample task than pigeons (*Columba livia*), a remotely related nonstoring species. However, the long-term storer scrub jays (*Aphelocoma coerulescens*; Corvidae) perform at about

the same level as pigeons, exhibiting a similar degree of inter-individual variability (Olson, 1991). Moreover, comparison of four different storer corvids showed significant differences in radial-maze analogs and spatial nonmatching to sample tasks (Kamil, Balda, & Olson, 1994; Olson, Kamil, Balda, & Nims, 1995). It seems puzzling that there would be such differences in spatial learning among species that depend on food storing for survival during the winter, although, as pointed out by these authors, they may be differentially dependent on cache food in the wild. An experiment comparing nutcrackers with the food-storing pinyon jays (*Gymnorhinus cyanocephalus*; Corvidae) points to a potentially important source of species differences. Pinyon jays performed significantly better than nutcrackers in a seed-storing and recovering task, but the difference in accuracy could be traced to the jays’ tendency to store seeds in closer proximity in the test arena (Balda & Kamil, 1989). Although available information suggests the possibility of divergence in spatial-learning mechanisms between storers and nonstorers, the answer to the first question posed above is still tentative. Complex learned behavior must not be assumed to necessarily involve complex learning mechanisms; solutions to the problem of food storage may have involved the evolution of a perceptual bias (as in marsh tits) or of specific response strategies (as in pinyon jays) coupled with general-purpose learning mechanisms.

Second, is the similarity in food-storing behavior among marsh tits and Clark’s nutcrackers due to homology or homoplasy? This question could be answered by comparing the learning mechanisms underlying food-storing abilities among Paridae and Corvidae, but this strategy has rarely been used. Instead, comparisons can be made in terms of the relative size of the hippocampal formation, a brain structure associated with spatial learning in a variety of vertebrates (Macphail, 2000; Salas et al., 1996; Sherry, Jacobs, & Gaulin, 1992). In a study involving species from 13 families of Passeri, three storing species, the black-capped chickadee (*P. atricapillus*; Paridae), the blue jay (*Cyanocitta cristata*; Corvidae), and the red-breasted nuthatch (*Sitta canadensis*; Sittidae), exhibited a larger hippocampus relative to both body size and telencephalic size than did nonstoring passerines from 10 different families (Sherry, Vaccarino, Buckenham, & Herz, 1989). Among the Paridae, which show extensive species variation in food storing, degree of storing is directly correlated with hippocampal size but not with the size of the body or telencephalon (Healy & Krebs, 1996). Suggestive data from the Corvidae also point to the same pattern, although only a single non-storing corvid has been described so far (Basil, Kamil, Balda, & Fite, 1996).

This comparative information on relative hippocampal size can now be mapped onto a cladogram and interpreted according to phylogenetic rules. Figure 6 shows a cladogram of the suborder Passeri based on DNA–DNA hybridization data (Sibley & Ahlquist, 1990). For clarity, only families with at least one food-storing species are listed on the right (Vander Wall, 1990); common names correspond to food storers. However, it is important to keep in mind that each horizontal line represents a family, and each family includes many species. The bars mark families for which there is at least one species in which a relatively large hippocampal formation has been found. Similarities in relative hippocampal size among these species could in principle be accounted for by two evolutionary hypotheses. One possibility is that the large hippocampal size of the few species of corvids, sittids, and parids that

have been studied is homologous, that is, derived from a common ancestor that already had a large hippocampal size and was, by implication, a food storer. Common ancestry is usually a parsimonious interpretation unless, as in this case, it forces the assumption that the trait has been selectively lost in all the extant lineages that do not exhibit it (i.e., evolutionary reversal). A second more parsimonious hypothesis suggests that the large hippocampal size evolved independently in several lineages and is therefore homoplastic. The presence of many nonstoring species in each of the families in which storers have been identified suggests that food-storing behavior has evolved independently at least in each family and perhaps in more than one lineage within each family. Food-storing behavior, its underlying learning mechanisms, and their neurobiological substratum most likely constitute an example of parallel evolution driven by similar ecological pressures (see Figure 3 for a representation of parallel evolution).

Surprising Nonreward in Vertebrate Instrumental Learning

A broader taxonomic base is involved in this third example, although the evolutionary hypotheses would be essentially the same as those considered in the previous two examples (i.e., homology, homoplasy, and divergence of learning mechanisms). Mammals exposed to signals for an impending appetitive reinforcer that fails to occur or that occurs in a degraded fashion (degraded either in quantity or quality) exhibit a wide variety of behavioral and physiological responses that could collectively be referred to as aversive and emotional (Papini & Dudley, 1997). For example, rats (*Rattus norvegicus*) exposed to surprising nonreward exhibit increased levels of locomotor activity (Gallup & Altomari, 1969) and aggressive behavior if a conspecific is near (Gallup, 1965), and they rapidly acquire a response that removes them from the situation (Daly, 1974). Rats, goats, and pigs show increased glucocorticoid levels (Carbonaro, Friend, Dellmeier, & Nuti, 1992; Dantzer, Arnone, & Mormede, 1980; Davis, Memmott, MacFadden, & Levine, 1976), whereas human infants cry and fuss in extinction after training with a variety of appetitive reinforcers (Lewis, Alessandri, & Sullivan, 1990; Mast, Fagen, Rovee-Collier, & Sullivan, 1980). Invigoration of current behavior after surprising nonreward (the frustration effect) has been reported in children (Ryan & Watson, 1968), rats (Dudley & Papini, 1995, 1997), and opossums (*Lutreolina crassicaudata*; Papini & Ramallo, 1990), all of which also show consummatory negative contrast—that is, a suppression of drinking after an unexpected downshift in incentive value (Flaherty, Becker, & Pohorecky, 1985; Kobre & Lipsitt, 1972; Papini, Mustaca, & Bitterman, 1988). Such consummatory suppression can be attenuated by treatment with anxiolytic drugs such as chlordiazepoxide and diazepam (Flaherty, Grigson, & Rowan, 1986; Mustaca, Bentosela, & Papini, 2000).

Amsel's (1992) frustration theory provides a parsimonious explanation for the effects of manipulations involving surprising nonreward. These effects can be interpreted as resulting in part from primary frustration (R_F). R_F is an aversive, arousal-inducing internal response that results from surprising omissions or reductions in reward quantity or quality. R_F has the additional property that it can be anticipated on the basis of preceding cues. The resulting internal response, called *anticipatory frustration*, or r_F , is assumed to have similar properties except that, unlike R_F , it

suppresses appetitively motivated instrumental behavior. These two mechanisms appear to be subserved by different areas within the mammalian limbic system. For example, the behavioral consequences of R_F depend on an intact amygdala (Henke, 1973; Henke & Maxwell, 1973), although they do not seem to depend on an intact septohippocampal system (Henke, 1977; Swanson & Isaacson, 1969). By contrast, the behavioral consequences of r_F depend on an intact septohippocampal system (Feldon, Rawlins, & Gray, 1985; Franchina & Brown, 1971; Lobaugh, Bootin, & Amsel, 1985), but not on the amygdala (Henke, 1977). Because r_F depends, in turn, on R_F , lesions in the amygdala may disrupt some, but not all aspects of R_F , perhaps those related to arousal and response facilitation (Henke, 1977; Kapp, Whalen, Supple, & Pascoe, 1992).

A major phenomenon assessing the disruptive effects of r_F is that of successive negative contrast. Contrast occurs, for example, in rats trained to run for a preferred reward and then unexpectedly shifted to a less preferred reward. The behavior of the shifted animals deteriorates beyond the level of an unshifted control (e.g., Crespi, 1942; Elliott, 1928). These experiments have classically administered a single trial per day to avoid carryover stimuli across trials. Under these conditions, suppression of performance is widely assumed to result from r_F —that is, from anticipating the aversive state of frustration prior to making contact with the reinforcer. Contrast and other related phenomena have consistently failed to appear in widely spaced experiments with a variety of vertebrates (Bitterman, 1975; Papini, 1997; Papini, Muzio, & Segura, 1995). Systematic variation of several training variables known to affect learned performance suggests that these differences may reflect a divergence in learning mechanisms (see Figure 3 for a representation of divergence). Contrast may depend on the ability to reinstate previous outcomes (such as surprising nonreward) or the emotional reaction to these outcomes (Bitterman, 1975). A major alternative possibility is that the absence of spaced-trial contrast in nonmammalian vertebrates represents the effect of heretofore unidentified nonlearning variables (Macphail, 1982).

The same basic evolutionary hypotheses presented before are also applicable to the case of r_F and contrast. Figure 7 summarizes comparative research on spaced-trial contrast in vertebrates. The phylogeny depicted in this figure is based on information from a variety of sources; it assumes that the lineages leading to modern turtles, mammals, and other reptiles plus birds all diverged from early basal amniotes (Benton, 1990; Gauthier, Kluge, & Rowe, 1988; Kemp, 1988; Lee, 1993). Some guiding evolutionary hypotheses can be drawn from this evidence. An aspect common to the associative processes of all studied vertebrates is that response tendencies are strengthened (S) by positive reinforcement and weakened (W) by nonreinforcement (Macphail, 1982). This basic S–W learning mechanism has been assumed by most theories of learning, from Thorndike's initial stimulus–response theory to the more contemporary models (Domjan, 1998), including those of a neural network variety (Schmajuk, 1997). The S–W mechanism can thus be considered a primitive, or plesiomorphic, character in the vertebrates (see Figure 7, Number 1).

The absence of contrast in pigeons should be taken with caution. Although downshifts in reward magnitude do not lead to contrast performance in pigeons (Papini, 1997; Papini & Thomas, 1997), there is evidence of other frustration-related phenomena. For ex-

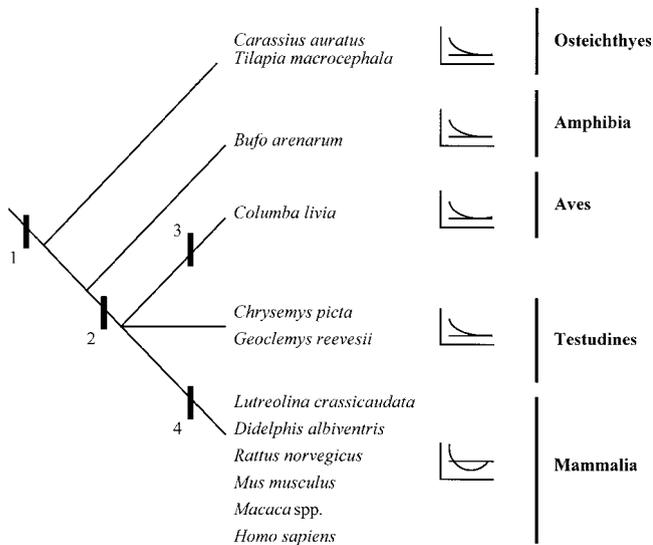


Figure 7. Phylogenetic tree of selected vertebrate lineages showing species that have been studied in the successive negative contrast paradigm. This learning phenomenon has typically been obtained with mammals but not with nonmammalian vertebrates. The graphs show idealized versions of the contrast phenomenon (note undershooting of performance in the condition shifted from large to small reward magnitude) and its absence (note gradual adjustment of postshift performance). These two types of behavioral adjustments to a surprising reduction in reward quantity or quality are mediated by different mechanisms. The numbers refer to evolutionary hypotheses about the origin of such learning mechanisms (see text for details).

ample, pigeons attack conspecifics when shifted from reinforced training to un signaled extinction (Azrin, Hutchinson, & Hake, 1966). Extinction-induced aggression can be interpreted as arising from an aversive state of frustration, and it has been observed in mammals (see Papini & Dudley, 1997). Second, pigeons learn to peck at a key to terminate a cue signaling nonreinforcement (Rilling, Askew, Ahlskog, & Kramer, 1969; Terrace, 1971); this indicates the aversive nature of the internal state induced by nonreinforcement. Finally, pigeons show greater resistance to extinction after partial reinforcement training than after continuous reinforcement training in spaced-training conditions and in key-pecking and runway situations (Roberts, Bullock, & Bitterman, 1963; Thomas, 2001). It is possible, therefore, that pigeons would eventually yield evidence of contrast, which would raise interesting evolutionary possibilities (Papini, 1997). For example, given the evolutionary relationship between major amniote lineages, a single-origin hypothesis (see Figure 7, Number 2) would predict contrast in all living reptiles, or, in cases in which contrast does not occur (as in turtles, e.g.), this hypothesis would require an assumption of evolutionary reversal. However, an independent-origin hypothesis (see Figure 7, Numbers 3 and 4) would suggest that behavioral similarities in the adjustment of birds and mammals to situations involving surprising nonreward are merely convergent and based on different underlying mechanisms. Frustration-like performance, not attributable to invigoration caused by surprising nonreward, was found in pigeons (Papini & Hollingsworth, 1998). Birds and mammals have evolved from different reptilian lineages (saurischian dinosaurs and cynodonts, respectively; Benton, 1990)

but exhibit many evolutionary convergences (Kemp, 1988). Features common to birds and mammals but not found in extant reptiles include a relatively large brain size, similar activity levels, cycles of sleep–wakefulness, endothermy, and complex reproductive behavior, among others. Convergent evolution in learning was suggested for movement mimicry among psittacine birds and primates (Moore, 1992). It is plausible that convergent evolution has led to similar behavioral adjustments to surprising nonreward in birds and mammals on the basis of different mechanisms (convergence is represented in Figure 3).

Comparative Learning: Some Conclusions From These Examples

These examples demonstrate how a combination of behavioral, physiological, molecular, and cladistic methods can be used to understand the evolutionary basis of learning processes. They make it clear that the dichotomy between the ecological and general-process views is not so enlightening. Whether the comparisons involve a relatively low-level taxon (as in the food-storing example involving species from the suborder Passeri) or a high-level taxon (as in the surprising nonreward example involving species from the subphylum Vertebrata), the basic research strategy is essentially the same. Systematic variation of theoretically relevant variables is used to separate the contribution to behavior of learning and nonlearning factors, and neurobiological analysis provides an independent source of evidence. The three examples covered in this section are probably representative of other areas of research in terms of showing that no learning phenomenon seems to be strictly analogous to beak size and shape in the Hawaiian honeycreepers (see Figure 2); that is, no learning phenomenon appears to be so unique that it is literally species specific (some aspects of human language acquisition may be the exception; Macphail, 1982). Learning processes tend to be of a more general kind. However, it is perhaps also true that novel learning processes have evolved in some animal lineages. At least in some cases, such novelties appear restricted to higher taxonomic units (e.g., frustrative nonreward mechanisms of higher vertebrates or, perhaps, just mammals). In other cases, however, novelties can be detected at lower taxonomic levels (e.g., tail-sensory neurons of opisthobranch molluscs).

It is also possible that part of the generality on which the general-process view is based rests on a failure to organize research demonstrations around the central concepts of homology and homoplasy. As shown in the examples described in the preceding sections, cladistic analysis based on the species distribution of learning phenotypes suggests hypotheses concerning the evolutionary history of the phenotypes and the polarity of the change (i.e., which variation is plesiomorphic and which synapomorphic), but these hypotheses need to be explored at a more fundamental level. It is not enough to show that similar learning phenomena are observed in distantly related species, such as pigeons and rats; comparative analysis must proceed to the level of underlying mechanisms. Clearly, simply stating that a learning phenomenon is similar in two different species is an oversimplification because it obviates the homology–homoplasy distinction. What is required is a definition of *mechanism* that captures the various levels of analysis that are possible in the study of learning.

Learning mechanisms are processes hypothesized to be responsible for the empirical findings observed in learning experiments, and they are typically phrased in terms of psychological, neurobiological, neurochemical, or molecular factors. For example, Pavlovian conditioning involving CS–US pairings and leading to some change in a response may be said to occur because of (a) the development of stimulus–stimulus associations (a psychological mechanism), (b) the confluence of neural input from the CS and US pathways on a particular brain nucleus (a neurobiological mechanism), (c) synaptic plasticity (a neurochemical mechanism), or (d) the engagement of a cellular process that results in synaptic plasticity (a cell–molecular mechanism). A distinction of mechanistic levels allows, in principle, for the development of criteria for distinguishing homologous from homoplastic learning phenomena. A criterion for homology could require that a given learning phenomenon be dependent on the same mechanisms at all levels of analysis across different species. For example, benzodiazepine drugs eliminate consummatory negative contrast in both rats and mice (Mustaca et al., 2000), a result consistent with the homology hypothesis. Further similarities need to be documented at various mechanistic levels to strengthen this homology hypothesis. Establishing homologies is also important whenever research on some learning phenomenon is used as a model of human behavioral disorders (e.g., successive negative contrast has been suggested as an animal model of anxiety; Flaherty, 1991). By contrast, the presence of different processes at any level of analysis would be consistent with homoplasmy. For example, Moore (1992) argued that movement imitation in parrots contrasts with that typically observed in apes in its slow development, its long incubation time (i.e., the time since acquisition to expression of the movement), and its relation to social displays rather than to tool making. Moore suggested that although parrots imitate movements in a manner similar to apes, imitation abilities appear to have evolved independently (i.e., homoplasmy).

Adaptation, Modularity, and Co-Option

Quite apart from the study of learning, the biological reality of adaptation cannot be easily questioned. Adaptive divergence produced by natural selection has been amply documented in natural populations, in populations introduced for experimental purposes in natural environments, and in the laboratory through the use of artificial selection techniques (Grant, 1986; Losey, Ives, Harmon, Ballantyne, & Brown, 1997; Reznick, Shaw, Rodd, & Shaw, 1997; Stoltenberg, Hirsch, & Berlocher, 1995). In the field of learning, adaptive specializations generally have been studied indirectly, with researchers assuming that natural selection has shaped underlying mechanisms in some special way (see Domjan, 1998). More recently, the connection between learning and reproductive success has been examined more directly in the blue gourami (*Trichogaster trichopterus*; Hollis, Pharr, Dumas, Britton, & Field, 1997) and Japanese quail (*Coturnix japonica*; Domjan, Blesbois, & Williams, 1998; Gutierrez & Domjan, 1996). For example, male blue gouramis, territorial fish, engage in early courtship when exposed to a Pavlovian signal predicting the impending appearance of a receptive female in the territory. Pavlovian males produce more offspring than males for which females are unsignaled; unsignaled females tend to elicit significant numbers of aggressive attacks that would normally be directed toward other males and

that reduce the female's receptivity to courtship. Although in these experiments variation occurs in the organism's environment rather than in a trait, they strongly suggest a connection between learning and adaptation. If there were genetic variation in learning mechanisms so that animals with a learning phenotype (analogous to Pavlovian animals) would learn more efficiently than animals with an alternative phenotype (analogous to unpaired controls), then the learning phenotype would enjoy a reproductive advantage over the alternative.

But how likely is it that learning mechanisms evolving in this manner would be entirely novel? Several lines of research suggest that, at least in vertebrates, learning mechanisms could be rather conservative, as is the case with other biological processes. The examples reviewed previously suggest that novel associative processes have arisen only rarely in the history of vertebrates and that natural selection has acted most commonly on nonlearning processes, such as sensory, motivational, and motor mechanisms, to allow for the evolution of new behavioral capacities. In this context, it is striking that selective breeding for both efficient and poor learned performance in mammals has generally produced its effects by influencing processes other than learning mechanisms. From the classic work by Tryon (1934) with maze-bright and maze-dull rats, which were not generally bright or dull (e.g., Searle, 1949), to more contemporary work on avoidance learning that led to strain differences in emotionality (e.g., Brush, 1985), selective breeding seems to have affected learned behavior by means of nonlearning factors rather than by influencing learning mechanisms directly.

One way to conceptualize such evolutionary stasis is to think of learning mechanisms as self-contained modules. A similar approach was suggested by Hollis, ten Cate, and Bateson (1991) in their attempt to reconcile the phenomenon of filial imprinting, found in precocial birds, with the more general processes underlying conditioning. Each of the mechanistic levels distinguished in the previous section could be thought of as acting in a modular manner. For example, it is possible to think about such modules at the cell-molecular level (e.g., specific cellular changes that result in synaptic plasticity) or at the neurobiological level (e.g., specific wiring architectures that allow for certain behavioral properties). Modules evolved to deal with one particular ecological problem, such as learning about the food signals, could be co-opted to mediate learning in novel situations, such as sexual conditioning. The genetic information underlying the module would remain stable, although its co-option to a novel function would require changes in regulatory processes that activate gene expression in brain areas responsible for the new function, as is thought to occur with other biological characters (Raff, 1996). An example from a different area illustrates this point. Circadian rhythms in a wide range of organisms depend on so-called clock genes (e.g., *period*, *frequency*), which can be shown to regulate rhythms in both diurnal and nocturnal species (Dunlap, 1996). Obviously, these genes and their products can be coupled in different arrangements to produce peak activity levels at the ecologically appropriate time of day, depending on whether the species is diurnal or nocturnal. A very similar evolutionary process could be responsible for stasis in learning mechanisms used to solve very different environmental problems, such as obtaining food and sexual partners or avoiding predators.

Evidence consistent with a view that emphasizes general-purpose modules may be found in studies on the genetic basis of learning in selected invertebrates. Mutants showing relatively specific learning deficits have been isolated in the nematode *Caenorhabditis elegans* (Wen et al., 1997) and in the fruit fly *D. melanogaster* (Dubnau & Tully, 1998). Genetic analysis of mutants exhibiting deficits in the acquisition or retention of some forms of learning is well underway in the case of the fruit fly, and the products of such gene complexes can be determined. Some of these mutations associated with learning impairments (e.g., the so-called *dunce* and *rutabaga*) affect genes encoding for proteins involved in the cyclic adenosine monophosphate (cAMP) pathway. The cAMP pathway is activated in neurons undergoing rapid stimulation, such as occurs during behavioral training. One consequence of increased cytoplasmic levels of cAMP is to induce cAMP-dependent enzymes to enter the cell nucleus. Once in the nucleus, these enzymes bind to proteins referred to as *cAMP-responsive element binding* transcription factors that induce the transcription of specific genes. It is thought that the resulting products may change synaptic efficacy on a long-term basis (Nestler & Greengard, 1994). Interestingly enough, cAMP is also a critical component of learning in distantly related species, including the mollusc *Aplysia californica* and rodents (Cedar, Kandel, & Schwartz, 1972; Huang & Kandel, 1994). Note that these species do not share brain structures (e.g., there is nothing in *Drosophila* or *Aplysia* homologous to, say, the amygdala of vertebrates), yet they may share a homology at the cell-molecular level. Kandel and Abel (1995) pointed out that cAMP is present in bacteria and may be among the most ancient second-messenger systems. cAMP's co-option into playing a role in associative learning may have occurred early in animal phylogeny, which would account for its ubiquity. Ultimately, research on these molecular modules may provide a biological basis for the notion of general learning processes, itself derived entirely from the comparative analysis of learning phenomena.

Conclusions

Over a century ago, Thorndike (1898) published the results of a series of experiments on the comparative analysis of learning and opened the field to scientific inquiry. Working within a Darwinian framework, Thorndike was not surprised to find impressive generalities across species; he was ready to interpret them in terms of mental continuity. Evolutionary biology has made substantial progress since Thorndike's time, and now it seems possible to develop a metatheoretical basis for the comparative study of learning that more closely relates to concepts and methods developed in allied disciplines, such as comparative neurology, molecular genetics, and cladistics, among others.

All the conceptual elements and research strategies seem to be available to attempt the development of evolutionary hypotheses about the divergence, homology, and homoplasy of learning mechanisms through comparative research. It might seem premature to postulate evolutionary hypotheses given the meager comparative database available in the animal learning literature, but it is the postulation of specific evolutionary hypotheses that provides the impetus for comparative research of any kind. Rather than shying away from evolutionary theorizing until more information is available, I argue that more information will become available when

comparative psychologists can use their talents to test specific evolutionary hypotheses.

A full integration of "learning thinking" and "evolutionary thinking" will demand more than loose adaptationist speculation. Not only hard data on the relationship between learning and reproductive success should be welcome, but also hypotheses about the evolutionary divergence, homology, and homoplasy of learning mechanisms should be made explicit and tested using criteria similar to those developed in other fields of evolutionary science.

References

- Aboitiz, F. (1996). Does bigger mean better? Evolutionary determinants of brain size and structure. *Brain, Behavior and Evolution*, *47*, 225–245.
- Amsel, A. (1992). *Frustration theory*. Cambridge, England: Cambridge University Press.
- Azrin, N. H., Hutchinson, R. R., & Hake, D. F. (1966). Extinction-induced aggression. *Journal of the Experimental Analysis of Behavior*, *9*, 191–204.
- Balda, R. P., & Kamil, A. C. (1989). A comparative study of cache recovery by three corvid species. *Animal Behaviour*, *38*, 486–495.
- Basil, J. A., Kamil, A. C., Balda, R. P., & Fite, K. V. (1996). Differences in hippocampal volume among food storing corvids. *Brain, Behavior and Evolution*, *47*, 156–164.
- Benton, M. J. (1990). Phylogeny of the major tetrapod groups: Morphological data and divergence dates. *Journal of Molecular Evolution*, *30*, 409–424.
- Benton, M. J. (1995, April 7). Diversification and extinction in the history of life. *Science*, *268*, 52–58.
- Bitterman, M. E. (1960). Toward a comparative psychology of learning. *American Psychologist*, *15*, 704–712.
- Bitterman, M. E. (1975, May 16). The comparative analysis of learning. *Science*, *188*, 699–709.
- Bitterman, M. E. (1984). Migration and learning in fishes. In M. D. McCleave, G. P. Arnold, J. J. Dodson, & W. H. Neill (Eds.), *Mechanisms of migration in fishes* (pp. 397–420). New York: Plenum.
- Bitterman, M. E. (1988). Vertebrate–invertebrate comparisons. In H. J. Jerison & I. Jerison (Eds.), *Intelligence and evolutionary biology* (pp. 251–275). Berlin, Germany: Springer-Verlag.
- Bitterman, M. E. (1996). Comparative analysis of learning in honeybees. *Animal Learning and Behavior*, *24*, 123–141.
- Briggs, D. E. G., Erwin, D. H., & Collier, F. J. (1994). *The fossils of the Burgess Shale*. Washington, DC: Smithsonian Institution Press.
- Brodbeck, D. R. (1994). Memory for spatial and local cues: A comparison of a storing and a nonstoring species. *Animal Learning and Behavior*, *22*, 119–133.
- Brodbeck, D. R., & Shettleworth, S. J. (1995). Matching location and color of a compound stimulus: Comparison of a food-storing and a nonstoring bird species. *Journal of Experimental Psychology: Animal Behavior Processes*, *21*, 64–77.
- Brusca, R. C., & Brusca, G. J. (1990). *Invertebrates*. Sunderland, MA: Sinauer.
- Brush, F. R. (1985). Genetic determinants of avoidance learning: Mediation by emotionality? In F. R. Brush & J. B. Overmier (Eds.), *Affect, conditioning, and cognition: Essays on the determinants of behavior* (pp. 27–42). Hillsdale, NJ: Erlbaum.
- Carbonaro, D. A., Friend, T. H., Dellmeier, G. R., & Nuti, L. C. (1992). Behavioral and physiological responses of dairy goats to food thwarting. *Physiology and Behavior*, *51*, 303–308.
- Carew, T. J., & Sahley, C. L. (1986). Invertebrate learning and memory: From behavior to molecules. *Annual Review of Neuroscience*, *9*, 435–487.

- Carroll, S. B. (1995, August 10). Homeotic genes and the evolution of arthropods and chordates. *Nature*, 376, 479–485.
- Cedar, H., Kandel, E. R., & Schwartz, J. H. (1972). Cyclic adenosine monophosphate in the nervous system of *Aplysia californica*: I. Increased synthesis in response to synaptic stimulation. *Journal of General Physiology*, 60, 558–569.
- Coddington, J. A. (1988). Cladistic tests of adaptational hypotheses. *Cladistics*, 4, 3–22.
- Crespi, L. P. (1942). Quantitative variation of incentive and performance in the white rat. *American Journal of Psychology*, 55, 467–517.
- Daly, H. B. (1974). Reinforcing properties of escape from frustration aroused in various learning situations. *Psychology of Learning and Motivation*, 8, 187–231.
- Dantzer, R., Arnone, M., & Mormede, P. (1980). Effects of frustration on behaviour and plasma corticosteroid levels in pigs. *Physiology and Behavior*, 24, 1–4.
- Darwin, C. (1993). *The origin of species*. New York: Random House. (Original work published 1859)
- Davis, H., Memmott, J., MacFadden, L., & Levine, S. (1976). Pituitary-adrenal activity under different appetitive extinction procedures. *Physiology and Behavior*, 17, 687–690.
- Dickinson, A. (1980). *Contemporary animal learning theory*. Cambridge, England: Cambridge University Press.
- Domjan, M. (1998). *The principles of learning and behavior* (4th ed.). New York: Brooks/Cole.
- Domjan, M., Blesbois, E., & Williams, J. (1998). The adaptive significance of sexual conditioning: Pavlovian control of sperm release. *Psychological Science*, 5, 411–415.
- Doolittle, R. F., Feng, D. F., Tsang, S., Cho, G., & Little, E. (1996, January 26). Determining divergence times of the major kingdoms of living organisms with a protein clock. *Science*, 271, 470–477.
- Dubnau, J., & Tully, T. (1998). Gene discovery in *Drosophila*: New insights for learning and memory. *Annual Review of Neuroscience*, 21, 407–444.
- Dudley, R. T., & Papini, M. R. (1995). Pavlovian performance of rats following unexpected reward omissions. *Learning and Motivation*, 26, 63–82.
- Dudley, R. T., & Papini, M. R. (1997). Amsel's frustration effect: A Pavlovian replication with control for frequency and distribution of rewards. *Physiology and Behavior*, 61, 627–629.
- Dunlap, J. C. (1996). Genetic and molecular analysis of circadian rhythms. *Annual Review of Genetics*, 30, 579–601.
- Elliott, M. H. (1928). The effect of change of reward on the maze performance of rats. *University of California Publications in Psychology*, 4, 19–30.
- Erixon, N., DeMartini, L. J., & Wright, W. G. (1999). Dissociation between sensitization and learning-related neuromodulation in an aplysiid species. *Journal of Comparative Neurology*, 408, 506–514.
- Feldon, J., Rawlins, J. N. P., & Gray, J. A. (1985). Fornix-fimbria section and the partial reinforcement extinction effect. *Experimental Brain Research*, 58, 435–439.
- Fitch, W. M., & Margoliash, E. (1967, January 20). Construction of phylogenetic trees. *Science*, 155, 279–284.
- Flaherty, C. F. (1991). Incentive contrast and selected animal models of anxiety. In L. Dachowski & C. F. Flaherty (Eds.), *Current topics in animal learning: Brain, emotion, and cognition* (pp. 207–243). Hillsdale, NJ: Erlbaum.
- Flaherty, C. F., Becker, H. C., & Pohorecky, L. (1985). Correlation of corticosterone elevation and negative contrast varies as a function of postshift day. *Animal Learning and Behavior*, 13, 309–314.
- Flaherty, C. F., Grigson, P. S., & Rowan, G. A. (1986). Chlordiazepoxide and the determinants of contrast. *Animal Learning and Behavior*, 14, 315–321.
- Franchina, J. J., & Brown, T. S. (1971). Reward magnitude shift effects in rats with hippocampal lesions. *Journal of Comparative and Physiological Psychology*, 76, 365–370.
- Futuyma, D. J. (1979). *Evolutionary biology*. Sunderland, MA: Sinauer.
- Gallup, G. G., Jr. (1965). Aggression in rats as a function of frustrative nonreward in a straight alley. *Psychonomic Science*, 3, 99–100.
- Gallup, G. G., Jr., & Altomari, T. S. (1969). Activity as a postsituation measure of frustrative nonreward. *Journal of Comparative and Physiological Psychology*, 68, 382–384.
- Gauthier, J., Kluge, A. G., & Rowe, T. (1988). Amniote phylogeny and the importance of fossils. *Cladistics*, 4, 105–209.
- Gibbs, H. L., & Grant, P. R. (1987, June 11). Oscillating selection on Darwin's finches. *Nature*, 327, 511–513.
- Gould, S. J., & Eldredge, N. (1977). Punctuated equilibria: The tempo and mode of evolution reconsidered. *Paleobiology*, 3, 115–151.
- Grant, P. R. (1986). *Ecology and evolution of Darwin's finches*. Princeton, NJ: Princeton University Press.
- Gutierrez, G., & Domjan, M. (1996). Learning and male-male sexual competition in Japanese quail. *Journal of Comparative Psychology*, 110, 170–175.
- Hall, B. K. (1992). *Evolutionary developmental biology*. London: Chapman & Hall.
- Hall, B. K. (Ed.). (1994). *Homology: The hierarchical basis of comparative biology*. San Diego, CA: Academic Press.
- Haralson, S. J., & Haralson, J. B. (1988). Habituation in the sea anemone (*Anthopleura elegantissima*): Spatial discrimination. *International Journal of Comparative Psychology*, 1, 245–253.
- Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford, England: Oxford University Press.
- Healy, S. D., & Krebs, J. R. (1992a). Comparing spatial memory in two species of tit: Recalling a single positive location. *Animal Learning and Behavior*, 20, 121–126.
- Healy, S. D., & Krebs, J. R. (1992b). Delayed-matching-to-sample by marsh tits and great tits. *Quarterly Journal of Experimental Psychology*, 45B, 33–47.
- Healy, S. D., & Krebs, J. R. (1996). Food storing and the hippocampus in Paridae. *Brain, Behavior and Evolution*, 47, 195–199.
- Henke, P. G. (1973). Effects of reinforcement omission on rats with lesions in the amygdala. *Journal of Comparative and Physiological Psychology*, 84, 187–193.
- Henke, P. G. (1977). Dissociation of the frustration effect and the partial reinforcement extinction effect after limbic lesions in rats. *Journal of Comparative and Physiological Psychology*, 91, 1032–1038.
- Henke, P. G., & Maxwell, D. (1973). Lesions in the amygdala and the frustration effect. *Physiology and Behavior*, 10, 647–650.
- Hilton, S. C., & Krebs, J. R. (1990). Spatial memory of four species of *Parus*: Performance in an open-field analogue of a radial maze. *Quarterly Journal of Experimental Psychology*, 42B, 345–368.
- Hodos, W., & Campbell, C. B. G. (1969). *Scala naturae*: Why there is no theory in comparative psychology. *Psychological Review*, 76, 337–350.
- Hollis, K. L., Pharr, V. L., Dumas, M. J., Britton, G. B., & Field, J. (1997). Classical conditioning provides paternity advantage for territorial male blue gouramis (*Trichogaster trichopterus*). *Journal of Comparative Psychology*, 111, 219–225.
- Hollis, K. L., ten Cate, C., & Bateson, P. (1991). Stimulus representation: A subprocess of imprinting and conditioning. *Journal of Comparative Psychology*, 105, 307–317.
- Huang, Y. Y., & Kandel, E. R. (1994). Recruitment of long-lasting and protein kinase A-dependent long-term potentiation in the CA1 region of hippocampus requires repeated tetanization. *Learning and Memory*, 1, 74–82.
- Johnson, M. C., & Wuensch, K. L. (1994). An investigation of habituation in the jellyfish *Aurelia aurita*. *Behavioral and Neural Biology*, 61, 54–59.
- 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*, 95–111.
- Kamil, A. C., Balda, R. P., & Olson, D. J. (1994). Performance of four seed-caching corvid species in the radial-arm maze analog. *Journal of Comparative Psychology*, *108*, 385–393.
- Kamil, A. C., & Clements, K. C. (1990). Learning, memory, and foraging behavior. In D. A. Dewsbury (Ed.), *Contemporary issues in comparative psychology* (pp. 7–30). Sunderland, MA: Sinauer.
- Kandel, E. R. (1976). *Cellular basis of behavior*. San Francisco, CA: Freeman.
- Kandel, E. R., & Abel, T. (1995, May 12). Neuropeptides, adenylyl cyclase, and memory storage. *Science*, *268*, 825–826.
- Kapp, B. S., Whalen, P. J., Supple, W. F., & Pascoe, J. P. (1992). Amygdaloid contributions to conditioned arousal and sensory information processing. In J. P. Aggleton (Ed.), *The amygdala* (pp. 229–254). New York: Wiley-Liss.
- Kemp, T. S. (1988). Haemothermia or Archosauria? The interrelationships of mammals, birds, and crocodiles. *Zoological Journal of the Linnean Society*, *92*, 67–104.
- Kobre, K. R., & Lipsitt, L. P. (1972). A negative contrast effect in newborns. *Journal of Experimental Child Psychology*, *14*, 81–91.
- Lee, M. S. Y. (1993, September 24). The origin of the turtle body plan: Bridging a famous morphological gap. *Science*, *261*, 1716–1720.
- Lewis, M., Alessandri, S. M., & Sullivan, M. W. (1990). Violation of expectancy, loss of control, and anger expressions in young infants. *Developmental Psychology*, *26*, 745–751.
- Lobaugh, N. J., Bootin, M., & Amsel, A. (1985). Sparing of patterned alternation but not partial reinforcement effect after infant and adult hippocampal lesions in the rat. *Behavioral Neuroscience*, *99*, 46–59.
- Losey, J. E., Ives, A. R., Harmon, J., Ballantyne, F., & Brown, C. (1997, July 17). A polymorphism maintained by opposite patterns of parasitism and predation. *Nature*, *388*, 269–272.
- Macphail, E. M. (1982). *Brain and intelligence in vertebrates*. Oxford, England: Clarendon Press.
- Macphail, E. M. (2000). Conservation of brain organisation and cognition in vertebrates. In G. Roth & M. F. Wulliman (Eds.), *Evolution of brain and cognition* (pp. 401–430). Heidelberg, Germany: Spektrum/Wiley.
- Marchalonis, J. J., & Schluter, S. F. (1990). Origins of immunoglobulins and immune recognition molecules. *BioScience*, *40*, 758–768.
- Mast, V. K., Fagen, J. W., Rovee-Collier, C. K., & Sullivan, M. W. (1980). Immediate and long-term memory for reinforcement context: The development of learned expectancies in early infancy. *Child Development*, *51*, 700–707.
- Medina, M. (1998). *Molecular systematics and population genetics of sea hares (Gastropoda: Opisthobranchia: Anaspidea)*. Unpublished doctoral dissertation, University of Miami, Florida.
- Moore, R. B. (1992). Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning. *Behaviour*, *122*, 231–263.
- Mustaca, A. E., Bentosela, M., & Papini, M. R. (2000). Consummatory successive negative contrast in mice. *Learning and Motivation*, *31*, 272–282.
- Nestler, E. J., & Greengard, P. (1994). Protein phosphorylation and the regulation of neuronal function. In G. J. Siegel, B. W. Agranoff, R. W. Albers, & P. B. Molinoff (Eds.), *Basic neurochemistry* (5th ed., pp. 449–474). New York: Raven Press.
- Nielsen, C. (1995). *Animal evolution: Interrelationships of the living phyla*. Oxford, England: Oxford University Press.
- Northcutt, R. G. (1995). The forebrain of gnathostomes: In search of a morphotype. *Brain, Behavior and Evolution*, *46*, 275–318.
- Olson, D. J. (1991). Species differences in spatial memory among Clark's nutcrackers, scrub jays, and pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *17*, 363–376.
- Olson, D. J., Kamil, A. C., Balda, R. P., & Nims, P. J. (1995). Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory. *Journal of Comparative Psychology*, *109*, 173–181.
- Osorio, D., Bacon, J. P., & Whittington, P. M. (1997). The evolution of arthropod nervous systems. *American Scientist*, *85*, 244–253.
- Papini, M. R. (1997). Role of reinforcement in spaced-trial operant learning in pigeons (*Columba livia*). *Journal of Comparative Psychology*, *111*, 275–285.
- Papini, M. R., & Dudley, R. T. (1997). Consequences of surprising reward omissions. *Review of General Psychology*, *1*, 175–197.
- Papini, M. R., & Hollingsworth, P. R. (1998). Role of nonreinforcement in the fixed-interval performance of pigeons. *Psychonomic Bulletin & Review*, *5*, 84–90.
- Papini, M. R., Mustaca, A. E., & Bitterman, M. B. (1988). Successive negative contrast in the consummatory responding of didelphid marsupials. *Animal Learning and Behavior*, *16*, 53–57.
- Papini, M. R., Muzio, R. N., & Segura, E. T. (1995). Instrumental learning in toads (*Bufo arenarum*): Reinforcer magnitude and the medial pallium. *Brain, Behavior and Evolution*, *46*, 61–71.
- Papini, M. R., & Ramallo, P. (1990). Primary frustration in the red opossum, *Lutreolina crassicaudata*. *International Journal of Comparative Psychology*, *3*, 235–242.
- Papini, M. R., & Thomas, B. (1997). Spaced-trial learning with purely instrumental contingencies in pigeons (*Columba livia*). *International Journal of Comparative Psychology*, *10*, 128–136.
- Raff, R. A. (1996). *The shape of life*. Chicago, IL: University of Chicago Press.
- Raff, R. A., & Kaufman, T. C. (1983). *Embryos, genes, and evolution*. Bloomington: Indiana University Press.
- Reznick, D. N., Shaw, F. H., Rodd, F. H., & Shaw, R. G. (1997, March 28). Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science*, *275*, 1934–1937.
- Rilling, M., Askew, H. R., Ahlsgog, J. E., & Kramer, T. J. (1969). Aversive properties of the negative stimulus in a successive discrimination. *Journal of the Experimental Analysis of Behavior*, *12*, 917–932.
- Roberts, W. A., Bullock, D. H., & Bitterman, M. E. (1963). Resistance to extinction in the pigeon after partially reinforced instrumental training under discrete-trials conditions. *American Journal of Psychology*, *76*, 353–365.
- Ruben, J. (1995). The evolution of endothermy in mammals and birds: From physiology to fossils. *Annual Review of Physiology*, *57*, 69–95.
- Ruddle, F. H., Bartels, J. L., Bentley, K. L., Kappen, C., Murtha, M. R., & Pendleton, J. W. (1994). Evolution of Hox genes. *Annual Review of Genetics*, *28*, 423–442.
- Ryan, T. J., & Watson, P. (1968). Frustrative nonreward theory applied to children's behavior. *Psychological Bulletin*, *69*, 111–125.
- Salas, C., Broglio, C., Rodríguez, F., López, J. C., Portavella, M., & Torres, B. (1996). Telencephalic ablation in goldfish impairs performance in a spatial constancy problem but not in a cued one. *Behavioural Brain Research*, *79*, 193–200.
- Sanderson, M. J., & Hufford, L. (Eds.). (1996). *Homoplasy: The recurrence of similarity in evolution*. San Diego, CA: Academic Press.
- Schmajuk, N. (1997). *Animal learning and cognition*. Cambridge, England: Cambridge University Press.
- Searle, L. V. (1949). The organization of hereditary maze-brightness and maze-dullness. *Genetic Psychology Monographs*, *39*, 279–325.
- Sherry, D. F., Jacobs, L. F., & Gaulin, S. J. C. (1992). Spatial memory and adaptive specialization of the hippocampus. *Trends in Neuroscience*, *15*, 298–303.
- Sherry, D. F., & Schacter, D. L. (1987). The evolution of multiple memory systems. *Psychological Review*, *94*, 439–454.
- Sherry, D. F., Vaccarino, A. L., Buckenham, K., & Herz, R. S. (1989). The hippocampal complex of food-storing birds. *Brain, Behavior and Evolution*, *34*, 308–317.

- Shettleworth, S. J. (1998). *Cognition, evolution, and behavior*. New York: Oxford University Press.
- Shettleworth, S. J., & Krebs, J. R. (1982). How marsh tits find their hoards: The roles of site preference and spatial memory. *Journal of Experimental Psychology: Animal Behavior Processes*, 8, 354–375.
- Sibley, C. G., & Ahlquist, J. E. (1990). *Phylogeny and classification of birds: A study in molecular evolution*. New Haven, CT: Yale University Press.
- Slack, J. M. W., Holland, P. W. H., & Graham, C. F. (1993, February 11). The zootype and the phylotypic stage. *Nature*, 361, 490–492.
- Spencer, A. N. (1989). Chemical and electrical synaptic transmission in the Cnidaria. In P. A. V. Anderson (Ed.), *Evolution of the first nervous systems* (pp. 33–53). New York: Plenum.
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford, England: Oxford University Press.
- Stoltenberg, S. F., Hirsch, J., & Berlocher, S. H. (1995). Analyzing correlations of three types in selected lines of *Drosophila melanogaster* that have evolved stable extreme geotactic performance. *Journal of Comparative Psychology*, 109, 85–94.
- Striedter, G. F. (1997). The telencephalon of tetrapods in evolution. *Brain, Behavior and Evolution*, 49, 179–213.
- Swanson, A. M., & Isaacson, R. L. (1969). Hippocampal lesions and the frustration effect in rats. *Journal of Comparative and Physiological Psychology*, 68, 562–567.
- Terrace, H. S. (1971). Escape from S-. *Learning and Motivation*, 2, 148–163.
- Thomas, B. L. (2001). *Determinants of spaced-trial paradoxical learning effects in pigeons*. Unpublished doctoral dissertation, Texas Christian University.
- Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *Psychological Review*, 2, 1–109.
- Tryon, R. C. (1934). Individual differences. In F. A. Moss (Ed.), *Comparative psychology* (pp. 409–445). Englewood Cliffs, NJ: Prentice-Hall.
- Valentine, J. W. (1995). Late Precambrian bilaterians: Grades and clades. In W. M. Fitch & F. J. Ayala (Eds.), *Tempo and mode in evolution* (pp. 87–107). Washington, DC: National Academy Press.
- Vander Wall, S. B. (1990). *Food hoarding in animals*. Chicago, IL: University of Chicago Press.
- Walters, E. T. (1994). Injury-related behavior and neuronal plasticity: An evolutionary perspective on sensitization, hyperalgesia, and analgesia. *International Review of Neurobiology*, 36, 325–427.
- Wen, J. Y. M., Kumar, N., Morrison, G., Rambaldini, G., Runciman, S., Rousseau, J., & van der Kooy, D. (1997). Mutations that prevent associative learning in *C. elegans*. *Behavioral Neuroscience*, 111, 354–368.
- Willmer, P. (1990). *Invertebrate relationships: Patterns in animal evolution*. Cambridge, England: Cambridge University Press.
- Wray, G. A., Levinton, J. S., & Shapiro, L. H. (1996, October 25). Molecular evidence for deep Precambrian divergences among metazoan phyla. *Science*, 274, 568–573.
- Wright, W. G. (1998). Evolution of nonassociative learning: Behavioral analysis of a phylogenetic lesion. *Neurobiology of Learning and Memory*, 69, 326–337.
- Wright, W. G., Kirschman, D., Rozen, D., & Maynard, B. (1996). Phylogenetic analysis of learning-related neuromodulation in molluscan mechanosensory neurons. *Evolution*, 50, 2248–2263.

Received July 30, 1998

Revision received September 22, 2000

Accepted June 12, 2001 ■