

# Comparative Analyses of Learning

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At the heart of most human cultures lie stories and anecdotes comparing the mental abilities of different animals, especially the relative intelligence of human and nonhuman animals. A frequent point of these stories is to impress the listener that nonhuman animals are as clever as, and possibly wiser than, most humans. A second point is that nonhuman animals can equal or surpass humans in silly, greedy, unpleasant, and simple-minded behavior. Finally, in yet other stories, animals closely emulate average humans, so much so that they can be treated as informative and often humorous models. Although Western culture has its own versions of such comparisons, the latter half of the 19th century marked an important watershed in why and how scientists compare learning in different animals.

Darwin's (1859) theory of evolution provided an important conceptual justification for comparing variation in the mental abilities of animals, namely, to test the hypothesis that all species, including humans, derived from earlier forms through incremental changes brought about by the process of natural selection. As Darwin (1871) succinctly put it, "[T]he difference in mind between man and the higher animals . . . is one of degree and not of kind." Thus, if a dog could be shown to reason, or act ashamed, it provided evidence that these abilities were not unique to humans but had precursors in other animals. To establish such precursors, first Darwin and then Romanes collected large quantities of anecdotes. Romanes (1884) classified these stories by phyla and species to establish a continuum from single-cell organisms to humans that showed the precise phyletic point at which each new mental ability emerged.

Interest in a phyletic scale of mental ability rapidly dominated the study of learning. So complete was the domination that we would do well to look for reasons beyond the fluctuating influence of Darwin. In fact, Greek philosophers, Catholic scholastics, Lamarck, and Herbert Spencer (1855) had similar ordered rankings of organisms in which the mental abilities of the smartest humans was assumed to represent the pinnacle (at least on earth). The capacities of the remaining creatures were ordered with respect to how well they represented this ideal, and, in most conceptions, individuals were assumed to strive upward toward it (Hodos & Campbell, 1969).

As the 20th century opened, careful experimental research gradually replaced anecdotes in the comparison of learning in different species. As the experimental movement took over, the importance of an all-encompassing continuum of mental life began to wane in favor of concern with the general mechanisms and laws of learning that applied across all phyla (Galef, 1988; Glickman, 1985). These two concerns were combined in the assumption that although species are likely to show quantitative differences in learning, the underlying principles were the same (Macphail, 1982; Skinner, 1966; Thorndike, 1911). This view came to dominate the majority of the research in this century (Beach, 1950; Maier & Schneirla, 1935; Warden, Jenkins, & Warner, 1934), and is still reflected in current work on learning mechanisms and animal models.

Finally, the latter third of the 20th century has seen a slow shift from the dominance of artificial laboratory tests toward a concern with problems encountered in natural environments (e.g., song learning, imprinting, and foraging; see

Shettleworth, 1994). Even learning in laboratory tests like maze running and Pavlovian conditioning has been interpreted as related to ecological variables, first in the literature on constraints on learning (Hinde & Stevenson-Hinde, 1973) and then in the adaptive-evolutionary approach (Kamil, 1988; Rozin & Schull, 1988) and the framework of behavior systems (Fanselow & Lester, 1988; Timberlake & Lucas, 1989).

In the remainder of this essay the variety of comparative analyses of learning are briefly considered. To clarify their relation to phylogenetic and ecological variables, we have divided the comparative analyses into four overlapping categories: protoevolutionary, phylogenetic, ecological, and microevolutionary (Timberlake, 1993). Protoevolutionary comparisons are concerned primarily with common principles and progressive trends in learning across groups of animals as measured by performance on standardized tests. Phylogenetic comparisons examine similarities and differences in learning across a more restricted range of species of known phylogeny. Ecological comparisons study the convergence of learning abilities among disparate species that share similar selection pressures and the divergence of learning in related species subjected to different selection pressures. Microevolutionary comparisons consider both phylogenetic and ecological variables in exploring how learning abilities evolved.

### Protoevolutionary Comparisons

The point of protoevolutionary comparisons has been to arrange species in a progressive order that is assumed to be broadly related to evolution, while still affirming the commonality of learning principles and mechanisms across all phyla. There is little concern about specific phylogenetic relations among species or about the selection pressures that may have produced them.

### Experiment-Based Orders

Early attempts to order the learning abilities of unrelated species reflected the combination of Romanes's scale with the developing experimental methodology for studying learning (e.g., Small, 1899; Thorndike, 1898). Experimenters initially tested many species on the same task. Thus, the speed of learning in a simple choice maze was recorded by investigators like Yerkes for animals ranging from earthworms through

fish, frogs, snakes, raccoons, pigs, and human (see Maier & Schneirla, 1935). The results were often surprising. For example, raccoons failed the maze test because they spent their time marking the wooden walls; in complex multiple-choice mazes, rats had the temerity to be better than humans. Critics of this work pointed to methodological difficulties in ensuring similar motivation levels in different species and in creating tasks that were unaffected by differences in sensory and motor capabilities.

Subsequent efforts used more complex tasks that were less easily affected by motivational and sensory-motor differences. For example, Bitterman (1965) used two types of choice behavior as indicators of intelligence: (1) the ability to improve performance on successive reversals of the correct arm of a choice maze and (2) the ability to choose exclusively the most likely of two probabilistically rewarded responses (thereby maximizing the total reward over a series of choices). These tasks were less open to criticism because one measured improvement in a type of problem the animal could already perform, and the other measured the ability to integrate the total reward over a series of choices. Based on these tasks, Bitterman ordered a variety of vertebrate animals in terms of their resemblance to a goldfish (no improvement with successive choice reversals and no maximizing) or a rat (improvement with successive reversals and maximizing).

Many researchers focused on "higher" mammals by using learning set problems, a variant of the "improvement" approach mentioned before. Experimenters first taught animals a discrimination (thereby providing baseline evidence of learning) and then measured improvements in performance with further exposures to the same type of problem (learning-to-learn). Thus, Warren (1973) ordered a variety of mammalian species in terms of their ability to improve on successive problems. A major objection to this approach was that the results depended on the modality of the discriminative cue (Pearce, 1987). For example, bottle-nosed dolphins rapidly form learning sets in auditory discrimination problems but not in visual (shape) discrimination problems (Herman & Arbeit, 1973).

### Levels and Trends

Beginning with Wallace (1870) some writers interested in protoevolutionary comparisons

focused on more qualitative differences in the progressive increase of mental abilities. Thus, Morgan (1930) divided mental abilities into percipience, perception, and reflection (see later work on levels by Greenberg, 1984; Schneirla, 1949). Most researchers referenced levels of abilities to specific laboratory tests. For example, Razran (1971) divided learning into fixed types and then ordered different phyla and subgroups of animals in terms of how many types they could learn.

Gallup (1983) has used mirror recognition as a measure of the self-concept, a measure that places chimpanzees and orangutans a cut above other nonhuman mammals (but see Heyes, 1994; Swartz this volume). Researchers such as Gagnon and Dore (1992) and Parker (1977) have tested animal species on their ability to pass the stages of Piaget's object permanence tests. Still others have dealt with animals' ability to count (Davis & Perusse, 1988) and estimate numerosity (Pepperberg, 1990). Recent cognitive ethologists have argued for the widespread existence of human traits (e.g., deception in nonhuman animals—Cheney & Seyfarth, 1990; Gyger & Marler, 1988; Ristau, 1991; but see Moffatt & Hogan, 1992). A few researchers have compared nonhuman animals with humans to the latter's detriment, for example, in their ability to perform spatial feats of dead reckoning and path integration (Gallistel, 1990).

#### **Correlation-Based Scales**

A rather different method of protoevolutionary comparison explores species and group differences in the ratio of brain size to body weight (Jerison, 1973). This method is untroubled by issues of motivation or task equivalence and can be applied relatively easily to both living and fossil species. The rationale for this ratio resembles Hebb's (1949) argument for using the ratio of brain size to the size of the spinal cord as an estimate of intelligence. Speaking loosely, the larger the brain in relation to the "house-keeping" required to maintain the sensory-motor functioning of the body, the proportionally greater amount is available for the processing related to complex learning.

The results of comparing ratios of brain size to body weight are consistent in showing progressive differences between large groupings of species; for example, mammalian species have higher ratios than reptiles, and later rep-

tiles average higher ratios than earlier reptiles. More recent investigators have related body size to other measures such as neural complexity and learning ability (see Gittleman, 1989). A difficulty with this approach is that it is not clear how learning is related to a gross measure of excess brain material. In addition there are problematic findings such as those of Angermeier (1984), in which the speed of learning a simple operant task in a variety of vertebrates and one invertebrate appears, if anything, negatively correlated with the ratio of brain size to body weight.

#### **Model Systems, Animal Models, and Model Animals**

Interest in a common model of learning lies at the heart of much protoevolutionary research. Model systems, animal models, and model animals are examples of this type of interest. A model system involves the selection of a species for its tractability as a representative of a larger group of animals. Thus, the neurophysiology of learning is often studied in *aplysia* because the nervous system is relatively constrained and readily accessible, attributes that facilitate the neuronal analysis of learning (Hawkins & Kandel, 1984). An animal model is a model system that is studied for its specific relation to other species, usually humans. So rats are studied as models of addiction, and pigs are kept as models of obesity.

A model animal is the emulation of an "animal" in software, hardware, or both, to test the effects of the experimenter's rules and assumptions on behavior. Software "animals" are used to simulate the performance of a model to see how closely the results mimic the data of real animals. Hardware "animats" (animal robots) are designed with varying degrees of memory and goal orientation to move about real environments and accomplish particular tasks (e.g., McFarland & Bossert, 1993).

Underlying these approaches is the implicit idea that the laws and even the mechanisms of learning and purposive behavior should apply to large groups of animals (Macphail, 1982, 1985; Skinner, 1953; Thorndike, 1911). A possible reason for such generality is that the mechanisms of learning are phylogenetically conserved. For example, the calcium channels identified in the neuronal firing of marine mollusks are present to a degree in mammals as well. Similarly, once the experience-based pro-

cesses of addiction are identified and controlled in rats, they can be dealt with in humans as well. In a related sense, the rules imposed on model animals are presumably candidates for mechanisms instantiated in the flesh of real animals.

### Phylogenetic Comparisons

Phylogenetic comparisons differ from proto-evolutionary work in that they primarily focus on more restricted groups of related species. Lorenz (1950) provided an example of how behavior can be related to phylogeny in his study of displays in a number of duck species (but see Hailman, 1982). Displays shared by most species were assumed to be the most primitive, while those patterns shared by the fewest were seen to indicate the most recent path of evolution. Subsequent research using multidimensional clustering techniques (Gittleman & Decker, 1994) has supported his conclusions. Though learning is more difficult to compare than stereotyped displays, there is a suggestion that a simplified version of this approach might be useful. For example, MacLean (1990) and Masterton, Heffner, and Ravizza (1969) related learning to the phylogeny of mammals by focusing on changes in brain circuitry and development. Kroodsmma (1988) and Kroodsmma and Konishi (1991) compared the characteristics of song learning between song birds and their subsong relatives. If sufficient data could be collected, it might prove worthwhile to apply clustering techniques to examples of learning in different species.

### Mental Life in Primates

The majority of phylogenetically relevant studies of learning have focused on comparing primates, particularly chimpanzees, with humans. Early work focused on the ability of primates to solve problems by insight or imitation (e.g., Köhler, 1925; Whiten & Ham, 1992). More recent researchers have used the manipulative abilities of chimpanzees to study how closely they resemble humans in characteristics ranging from visual processing to complex mental abilities. For example, chimpanzees filter visual stimuli in the same way as humans: outer contour elements first, straight-line elements with more difficulty (Tomonaga & Matsuzawa, 1992). They also appear to "filter" more complex stimuli in similar ways. Premack and his co-workers have demonstrated that com-

munication-trained chimpanzees readily learn analogical relations and can identify causal sequences of behavior (Premack, 1983, 1988).

A great deal of recent work on mental life has focused on social cognition in primates, particularly the possibility that primates infer mental states in others (Byrne & Whiten, 1988; Cheney & Seyfarth, 1990; Heyes, 1994). For example, Whiten and Byrne (1991) reviewed the use of "tactical deception" in primates, and Byrne (1994) related it to Dunbar's (1992) allometric index of neocortical enlargement, a measure of the amount of "extra" cortical circuitry available in apes and monkeys. Povinelli, Parks, and Novak (1992) and Povinelli, Nelson, and Boysen (1992) showed that chimpanzees, but not rhesus monkeys, apparently can infer the state of an observer. Though unquestionable advances have been made over Darwin's time, Heyes's (1994) review indicates some continuing uncertainty about how to define and measure mental life.

### Human Language

Perhaps the unique human characteristic (aside from a strange hairlessness for a species living in harsh weather) is language. A longtime goal of the comparative study of learning has been to explore precursors to human language, usually in chimpanzees. Hayes and Hayes's (1951) definitive repetition of previous attempts to raise a chimpanzee like a child and teach it to speak replicated previous findings in producing a spoken vocabulary of just four words. Much greater success has been achieved by eliminating a vocal production requirement through the use of sign language (Gardner, Gardner & Van Cantfort, 1989; Terrace, 1979) or manipulable symbols (Premack, 1976; Rumbaugh & Savage-Rumbaugh, 1994).

The study of possible predecessors to human language has been extended to other apes (orangutans and gorillas—Patterson, 1990) and a variety of nonprimate species (e.g., parrots—Pepperberg, 1990; starlings—West, Stroud & King, 1983; and dolphins—Herman, Richards & Wolz, 1984). Vocal production is simple for some birds, but inducing or generalizing (as opposed to copying examples of) syntax rules may be easier for mammals. Early learning in a language environment appears to be an important contributor to vocabulary, syntactic organization, and the meaning of sentences, particularly for the pygmy chimpan-

zee (Rumbaugh & Savage-Rumbaugh, 1994). Despite interesting work, though, the evolutionary roots of human language are still not fixed.

## Ecological Comparisons

Ecological concerns influenced the initial phases of the experimental study of learning (Timberlake, 1983), but beginning with Thorndike the emphasis shifted to arbitrary tasks designed to isolate the study of learning from the influence of instinctive behavior. However, over the last 25 years ecological variables have re-entered the study of learning. We will look at the comparisons based on convergence (the effects of common selection pressures on unrelated species) and on divergence (the effect of diverging selection pressures on related species).

### Convergence

A number of authors have provided data showing that specific characteristics of the ecological niche are correlated with the ability to learn and with the form learning takes. For example, Logue (1988) provided evidence for a convergence of strategies among vertebrates to avoid poisonous foods, while Vander Wall (1990) outlined ecological similarities among phylogenetically diverse food hoarders. Sherry, Vaccarino, Buckenham, and Herz (1989) found that families of food-storing passerines show a larger hippocampus relative to the size of their telencephalon and body weight than do non-food-storing families.

Some ecological effects appear to hold across widely disparate groups of animals. In testing the exploratory behavior of vertebrate zoo animals, Glickman and Scroggs (1966) found that the level of curiosity shown by a species related better to ecological factors such as the variety of food in the diet, predator pressure, and the importance of social communication than to the phylogenetic group to which it belonged. Bitterman and Couvillon (1991) summarized data showing a high degree of similarity between rats and bees on a variety of learning tasks, a similarity they attributed to common ecological requirements. Finally, researchers such as Staddon (1988) and Dickinson (1980) have argued that the causal structure of the world selects for similar mechanisms of causal inference across all phyla.

### Divergence

The most compelling evidence for divergent learning ability would require the demonstration of learning differences and divergent selection pressures in species that are closely related phylogenetically. However, most examples depend on the face validity of inferred selection pressure. Beecher (1990) predicted and confirmed that bank swallows that nest in packed colonies learn readily to identify the calls of their offspring whereas a solitary nesting species did not. Dukas and Real (1991) showed that social bumblebees showed faster learning about rewards than did a solitary carpenter bee. In the laboratory, Timberlake and Washburne (1989) showed that the ease with which rodent species learned to contact an artificial moving stimulus to obtain food was directly correlated with the observed tendency of that species to kill and eat moving prey.

Kamil and Balda (1990), working with corvids, and Shettleworth (1990) and Krebs (1990), working with parids, have shown that differences in food storing within each taxonomic group are highly correlated with differences in the ability to remember spatial locations. This ability can be measured in standard laboratory tests of memory (e.g., Olson, 1991) as well as in field simulations. Similarly, Daly, Rauschenberger, and Behrends (1982) predicted and found differences among specialist and generalist kangaroo rats in laboratory taste-aversion learning based on the degree of dietary specialization. Some caution is necessary in such comparisons because, depending on the tests, two species may show large differences in the wild but no difference in the laboratory, or the reverse. An adequate laboratory test of divergence requires considerable understanding of how the test relates to the selection pressures and mechanisms involved.

## Microevolutionary Comparisons

Microevolutionary learning comparisons focus on how ecological selection pressures interact with phylogenetic variables. The line between ecological and microevolutionary comparisons becomes increasingly blurred as ecological comparisons include more evidence about the mechanisms involved.

### Differences within Species

There is at least a 60-year history of attempts to

breed for differences in learning ability in non-human species, especially rats. The most famous example was the successful establishment of maze-bright and maze-dull strains by Tryon (1940); these were based on selective breeding for high and low errors in a multichoice maze. The difficulties with this approach include a lack of understanding of what is being selected, as well as how the changes in learning contribute to phylogenetic change. More recent studies of the genetics of learning have been clearer about the mechanism altered (Hoffman, 1994), but the ties to ecology remain largely under-realized.

An example of a comparison of learning abilities that has ties to both local evolution and ecology is the discovery that the males of many rodent species are more adept than females at spatial learning in both natural and laboratory environments (Gaulin, FitzGerald & Wartell, 1990; Gaulin & Wartell, 1990). This sex difference appears directly related to the size of the hippocampus, and occurs primarily in species with polygynous and promiscuous mating systems. In such mating systems males have larger home ranges than females. Sherry and Schacter (1987) also appealed to differences in within-species ecological requirements to argue for the adaptive specialization of memories. They pointed out that the requirements of an optimal memory for different tasks could easily conflict with each other, which leads to a selection pressure for a specialized type of memory for each task.

#### **Development, Niche Variation, and Culture**

Because the relation of development and evolution historically rested on the concept of Lamarckian inheritance, the rise of gene theory gave this relation a large black eye. Only recently have researchers again ventured to view development as critical to the understanding of evolution. For example, consider Gould's (1977) speculation that humans are neotonized chimpanzees, developmentally slowed by the change of a few timing genes. It could be argued that this single change holds the key to our long and flexible learning period, with its great dependency on adults and culture for survival and instruction. To clarify the evolutionary ramifications of such a developmental change, it would be necessary to represent the structure and learning processes of the child, relate them to changes in the rearing niche, and see how

both interact with culture. Though we have not managed to do this for our own species, an increasing number of investigators are developing the concepts and tools that are important to such an endeavor.

In terms of representation of the developing organism, Berridge (1994) and Hogan (1994) have shown the advantages of characterizing learning in development as changes in the structure of a behavior system. In terms of the rearing niche Alberts and Cramer (1988) and Moore (1990) have called attention to the complex selection pressures and co-dependencies present in the uterine and nursing environment of the rat, while Plomin (1994) has emphasized the differences in individual environments that exist in the same human family. Plotkin (1994) has explored the evolutionary basis of a capacity to learn, and beginning with Boyd and Richerson (1985), researchers have argued for a special role for social learning in evolution.

Researchers have been moving toward a view that animals, especially social animals, construct a niche that has important consequences for development and evolution. King and West (1990) have argued for an ontogenetic inheritance of niche features, which alters selection and behavior. Odling-Smee (1994) has shown how behavior (including learning) can contribute to the construction of the physical and cultural niche of a species. Because the niche determines the selection pressures operating on an individual, any change in phenotype as a function of niche construction may change the selection pressures operating on a population. The complexity of such interactions suggests the need for computer modeling to develop these ideas further.

#### **Computer Analysis and Modeling**

The ready availability of more powerful computers has provided easy access to more complex multivariate analyses and modeling. As mentioned earlier, biologists have developed many techniques for scaling body size against variables such as brain weight. What we didn't mention was the movement toward interpreting deviations from the overall group relation on the basis of ecological variables (Gittleman, 1989). Similar multivariate techniques can be used to separate phylogenetic and ecological influences in large groups of animals (Harvey & Pagel, 1991). It would seem interesting, but difficult, to apply these techniques to the study of learning.

Mathematical techniques provided by game theory, optimality theory, and dynamic programming can help answer, for a given set of attributes, whether a particular form of learning is a stable and adaptive outcome (e.g., Mangel & Clark, 1988; McNamara & Houston, 1985; Smith, 1982) or if learning is an interim stage in evolution and acts as an important contributor to subsequent selection pressures (Odling-Smee, 1994). Other work simulating evolution with genetic algorithms has been directed at discovering the conditions under which learning might evolve. For example, Todd and Miller (1991) showed that under "environmental" conditions in which food and poison occurred in separate large clusters, their artificial species evolved time-delay feedback connections in their neural nets and that these connections tracked the results of ingestion, so that these species learned the location of food versus poison (see also Todd & Miller, 1993). We expect the greater use of such imaginary worlds in unraveling the relation of evolution and learning.

## Conclusions

Most research in comparative psychology has used rigorous experimental procedures to establish a progressive psychological continuum relating nonhuman and human animals while supporting the species' generality of learning mechanisms (Hodos & Campbell, 1990). Evolution was assumed to have occurred, but progress, general mechanisms, and potential human applications were the primary focus of the research. In contrast, more recent forms of comparative analysis have emphasized specific forms of learning (such as taste-aversion or imprinting) that are presumed to be relatively specific adaptations to environmental selection pressures. Researchers have been increasingly interested in how these instances of learning evolved, in the same sense that teeth, claws, and backbones evolved. From this perspective, both similarities and differences in learning among species are expected. In fact, characteristics of learning within a single species may well differ depending on the circumstances.

Though it seems reasonable that learning should change with the complexity of the organism and its niche and thereby produce some trends over evolutionary time, it seems inappropriate to maintain that these changes must all fit a progressive pattern that continues through-

out all phyla and culminates in humans. The checkered nature of our own intelligence, the patterns of both great facility and poor ability to process information, appear less related to an ideal mind than to our primate heritage and the selection pressures of our evolution. At the least, consider the progressive order of species we might invoke if we were songbirds rather than primates. One would expect to find an emphasis on the ability to migrate via stars, to imitate complex auditory input rapidly, and to recognize landmarks from great distances rather than our present concern with complex pattern matching and flexible planning.

There is no single correct way to perform comparative analyses of learning. The proper focus of attention depends on the point of the comparison. Nonevolutionary or protoevolutionary comparisons can produce conclusions concerning differences in the types and mechanisms of learning among different species. However, our strong intuition is that as the comparative study of learning slowly establishes itself within a biological framework, comparative analyses of learning that are not well grounded in evolution are likely to be superseded by those that are (Shettleworth, 1994).

Two recent developments in the evolutionary study of learning appear worth emphasizing. The first places learning within the framework of an evolved system of behavior (e.g., Hogan, 1994; Timberlake & Lucas, 1989). This calls attention to the specific sensory and motor structure of learning as well as its overall function, and thereby provides a potentially clearer fit to the processes of selection and evolution. The second focuses attention on development and learning as a means of changing the organism's ecological niche (especially its culturally mediated niche) and, therefore, the selection pressures on individuals and populations. In this way learning and development can modify selection and become a significant factor in evolution.

In sum, there were important historical advantages to the initial focus on protoevolutionary comparisons—specific tests of learning that ordered the common learning abilities of different species. This approach rescued the comparative analysis of learning from the thrall of anecdotes and easy opinion. What is difficult to reconcile with evolution is the assumption that there exists a coherent continuum of learning stretching across phyla and culminating in an ideal type, the learning of humans. Other types of comparison

relate better to evolution as they consider the importance of phylogeny, ecology, and their combination. As the comparative study of learning continues to unfold, it should have implications for theories of both evolution and learning, for how researchers do experiments and interpret results, and for a better understanding of the evidence used to support the scales and trends that so dominated the thinking of comparative psychologists over the first 100 years.

#### References

- Alberts, J. R. & Cramer, C. P. (1988). Ecology and experience: Sources of means and meaning of developmental change. In E. M. Blass (Ed.), *Handbook of behavioral neurobiology* (Vol. 9, pp. 1-39). New York: Plenum.
- Angermeier, W. F. (1984). *The evolution of operant learning and memory: A comparative etho-psychology approach*. New York: Karger.
- Beach, F. A. (1950). The snark was a boojum. *American Psychologist*, 5, 115-124.
- Beecher, M. D. (1990). The evolution of parent-offspring recognition in swallows. In D. A. Dewsbury (Ed.), *Contemporary issues in comparative psychology* (pp. 360-380). Sunderland, MA: Sinauer Associates.
- Berridge, K. C. (1994). The development of action patterns. In J. A. Hogan & J. J. Bolhuis (Eds.), *Causal mechanisms of behavioural development* (pp. 147-180). Cambridge: Cambridge University Press.
- Bitterman, M. E. (1965). The evolution of intelligence. *Scientific American*, 212, 92-101.
- Bitterman, M. E. & Couvillon, P. A. (1991). Failures to find adaptive specialization in the learning of honey bees. In L. J. Goodman & R. C. Fisher (Eds.), *The behavior and physiology of bees* (pp. 288-305). Wallingford, U.K.: CAB International.
- Boyd, R. & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Byrne, R. W. (1994). The evolution of intelligence. In P. J. B. Slater & T. R. Halliday (Eds.), *Behaviour and evolution* (pp. 223-265). Cambridge: Cambridge University Press.
- Byrne, R. W. & Whiten, A. (Eds.). (1988). *Machiavellian intelligence: Social expertise and the evolution of the intellect in monkeys, apes, and humans*. Oxford: Clarendon Press.
- Cheney, D. L. & Seyfarth, R. M. (1990). *How monkeys see the world*. Chicago: University of Chicago Press.
- Daly, M., Rauschenberger, J. & Behrends, P. (1982). Food aversion learning in kangaroo rats: A specialist-generalist comparison. *Animal Learning and Behavior*, 10, 314-320.
- Darwin, C. (1859). *On the origin of species by means of natural selection*. London: Murray.
- . (1871). *The descent of man, and selection in relation to sex*. London: Murray.
- Davis, H. & Perusse, R. (1988). Numerical competence in animals: Definitional issues, current evidence, and a new research agenda. *Behavioral and Brain Sciences*, 11, 561-615.
- Dickinson, A. (1980). *Contemporary animal learning theory*. Cambridge: Cambridge University Press.
- Dukas, R. & Real, L. A. (1991). Learning foraging tasks by bees: A comparison between social and solitary species. *Animal Behaviour*, 42, 269-276.
- Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, 20, 469-493.
- Fanselow, M. S. & Lester, L. S. (1988). A functional behavioristic approach to aversively motivated behavior: Predator imminence as a determinant of the topography of defensive behavior. In R. C. Bolles & M. D. Beecher (Eds.), *Evolution and learning* (pp. 185-212). Hillsdale, NJ: Lawrence Erlbaum.
- Gagnon, S. & Dore, F. Y. (1992). Search behavior in various breeds of adult dogs (*Canis familiaris*): Object permanence and olfactory cues. *Journal of Comparative Psychology*, 106, 58-68.
- Galef, B. G. (1988). Evolution and learning before Thorndike: A forgotten epoch in the history of behavioral research. In R. C. Bolles & M. D. Beecher (Eds.), *Evolution and learning* (pp. 39-58). Hillsdale, NJ: Lawrence Erlbaum.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.
- Gallup, G. G. (1983). Toward a comparative psychology of mind. In R. E. Mellgren



- (Ed.), *Animal cognition and behavior* (pp. 473-510). Amsterdam: North-Holland.
- Gardner, R. A., Gardner, B. T. & Van Cantfort, T. E. (1989). *Teaching sign language to chimpanzees*. Albany, NY: SUNY Press.
- Gaulin, S. J., FitzGerald, R. W. & Wartell, M. S. (1990). Sex differences in spatial ability and activity in two vole species (*Microtus ochrogaster* and *M. pennsylvanicus*). *Journal of Comparative Psychology*, 104, 88-93.
- Gaulin, S. J. & Wartell, M. S. (1990). Effects of experience and motivation on symmetrical-maze performance in the prairie vole (*Microtus ochrogaster*). *Journal of Comparative Psychology*, 104, 183-189.
- Gittleman, J. L. (1989). The comparative approach in ethology: Aims and limitations. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in ethology* (pp. 55-83). New York: Plenum.
- Gittleman, J. L. & Decker, D. M. (1994). The phylogeny of behavior. In P. J. B. Slater & T. R. Halliday (Eds.), *Behaviour and evolution* (pp. 80-105). Cambridge: Cambridge University Press.
- Glickman, S. E. (1985). Some thoughts on the evolution of comparative psychology. In S. Koch & D. E. Leary (Eds.), *A century of psychology as science* (pp. 738-782). New York: McGraw-Hill.
- Glickman, S. E. & Scroggs, R. W. (1966). Curiosity in zoo animals. *Behaviour*, 26, 151-188.
- Gould, S. J. (1977). *Ontogeny and phylogeny*. Cambridge, MA: Belknap Press of Harvard University.
- Greenberg, G. (1984). T. C. Schneirla's impact on comparative psychology. In G. Greenberg & E. Tobach (Eds.), *Behavioral evolution and integrative levels: The T. C. Schneirla conference series* (pp. 49-81). Hillsdale, NJ: Lawrence Erlbaum.
- Gyger, M. & Marler, P. (1988). Food calling in the domestic fowl, *Gallus gallus*: The role of external referents and deception. *Animal Behavior*, 36, 358-365.
- Hailman, J. P. (1982). Evolution and behavior: An iconoclastic view. In H. C. Plotkin (Ed.), *Learning, development, and culture* (pp. 205-254). West Sussex, U.K.: Chichester.
- Harvey, P. H. & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Hawkins, R. D. & Kandel, E. R. (1984). Is there a cell-biological alphabet for simple forms of learning? *Psychological Review*, 91, 376-391.
- Hayes, K. J. & Hayes, C. (1951). The intellectual development of a home-raised chimpanzee. *Proceedings of the American Philosophical Society*, 95, 105-109.
- Hebb, D. O. (1949). *The organization of behavior*. New York: John Wiley.
- Herman, L. M. & Arbeit, W. R. (1973). Stimulus control and auditory discrimination learning sets in the bottlenose dolphin. *Journal of the Experimental Analysis of Behavior*, 19, 379-394.
- Herman, L. M., Richards, D. G. & Wolz, J. P. (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition*, 16, 1-90.
- Heyes, C. M. (1994). Social cognition in primates. In N. J. Mackintosh (Ed.), *Animal learning and cognition* (pp. 281-306). Cambridge: Cambridge University Press.
- Hinde, R. A. & Stevenson-Hinde, J. (Eds.). (1973). *Constraints on learning: Limitations and predispositions*. New York: Academic Press.
- Hodos, W. & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review*, 76, 337-350.
- . (1990). Evolutionary scales and comparative studies of animal cognition. In R. P. Kesner & D. S. Olton (Eds.), *Neurobiology of comparative cognition* (pp. 1-20). Hillsdale, NJ: Lawrence Erlbaum.
- Hoffman, A. A. (1994). Behavior genetics and evolution. In P. J. B. Slater & T. R. Halliday (Eds.), *Behaviour and evolution* (pp. 7-42). Cambridge: Cambridge University Press.
- Hogan, J. A. (1994). The development of behavior systems. In J. A. Hogan & J. J. Bolhuis (Eds.), *Causal mechanisms of behavioural development* (pp. 242-264). Cambridge: Cambridge University Press.
- Jerison, H. J. (1973). *Evolution of the brain and intelligence*. New York: Academic Press.
- Kamil, A. C. (1988). A synthetic approach to the study of animal intelligence. In D. W. Leger (Ed.), *Comparative perspectives in*

- modern psychology (Nebraska Symposium on Motivation, Vol. 35, pp. 257-308). Lincoln: University of Nebraska Press.
- Kamil, A. C. & Balda, R. P. (1990). Spatial memory in seed-caching corvids. In G. H. Bower (Ed.), *The Psychology of learning and motivation*, (Vol. 26, pp. 1-25). San Diego: Academic Press.
- King, A. P. & West, M. J. (1990). Variation in species typical behavior: A contemporary issue for comparative psychology. In D. A. Dewsbury (Ed.), *Contemporary issues in comparative psychology* (pp. 321-339). Sunderland, MA: Sinauer Associates.
- Köhler, W. (1925). *The mentality of apes*. New York: Harcourt, Brace & World.
- Krebs, J. R. (1990). Food storing birds: Adaptive specialization in brain and behaviour? *Philosophical Transactions of the Royal Society B*, 329, 55-62.
- Kroodsmma, D. E. (1988). Contrasting styles of song development and their consequences among passerine birds. In R. C. Bolles & M. D. Beecher (Eds.), *Evolution and learning* (pp. 157-184). Hillsdale, NJ: Lawrence Erlbaum.
- Kroodsmma, D. E. & Konishi, M. (1991). A suboscine bird (eastern phoebe, Sayornis phoebe) develops normal song without auditory feedback. *Animal Behavior*, 42, 477-487.
- Logue, A. W. (1988). A comparison of taste aversion learning in humans and other vertebrates: Evolutionary pressures in common. In R. C. Bolles & M. D. Beecher (Eds.), *Evolution and learning* (pp. 97-116). Hillsdale, NJ: Lawrence Erlbaum.
- Lorenz, K. (1950). The comparative method in studying innate behaviour patterns. In *Symposia of the Society of Experimental Biology*, 4, 221-268.
- MacLean, P. D. (1990). *The triune brain in evolution: Role in paleocerebral functions*. New York: Plenum.
- Macphail, E. M. (1982). *Brain and intelligence in vertebrates*. Oxford: Oxford University Press.
- . (1985). Vertebrate intelligence: The null hypothesis. In L. Weiskrantz (Ed.), *Animal intelligence* (pp. 37-51). Oxford: Clarendon Press.
- Maier, N. R. F. & Schneirla, T. C. (1935). *Principles of animal psychology*. New York: McGraw-Hill.
- Mangel, M. & Clark, C. W. (1988). *Dynamic modeling in behavioral ecology*. Princeton, NJ: Princeton University Press.
- Masterton, R. B., Heffner, H. & Ravizza, R. (1969). Evolution of human hearing. *Journal of the Acoustical Society of America*, 45, 966-985.
- McFarland, D. & Bossert, T. (1993). *Intelligent behavior in animals and robots*. London: MIT Press.
- McNamara, J. M. & Houston, A. T. (1985). Optimal foraging and learning. *Journal of Theoretical Biology*, 117, 231-249.
- Moffatt, C. A. & Hogan, J. A. (1992). Ontogeny of chick responses to maternal food calls in the Burmese red junglefowl (*Gallus gallus spadiceus*). *Journal of Comparative Psychology*, 106, 92-96.
- Moore, C. L. (1990). Comparative development of vertebrate sexual behavior: Levels, cascades, and webs. In D. A. Dewsbury (Ed.), *Contemporary issues in comparative psychology* (pp. 278-299). Sunderland, MA: Sinauer Associates.
- Morgan, C. L. (1930). *The animal mind*. London: Edward Arnold & Co.
- Odling-Smee, F. J. (1994). Niche construction, evolution and culture. In T. Ingold (Ed.), *Companion encyclopedia of anthropology*. London: Routledge.
- 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.
- Parker, S. T. (1977). Piaget's sensorimotor series in an infant macaque: A model for comparing unstereotyped behavior and intelligence in human and nonhuman primates. In S. Chevalier-Skolnikoff & F. Poirier (Eds.), *Primate bio-social development* (pp. 43-112). New York: Garland Press.
- Patterson, F. L. (1990). Language acquisition by a lowland gorilla: Koko's first ten years of vocabulary development. *Word*, 41, 97-143.
- Pearce, J. M. (1987). *An introduction to animal cognition*. Hillsdale, NJ: Lawrence Erlbaum.
- Pepperberg, I. M. (1990). Some cognitive capacities of an African Grey parrot (*Psittacus erithacus*). *Advances in the*

- Study of Behaviour*, 19, 357-409.
- Plomin, R. (1994). *Genetics and experience: The interplay between nature and nurture*. Newbury Park, CA: Sage Publications.
- Plotkin, H. (1994). *The nature of knowledge: Concerning adaptations, instinct and the evolution of intelligence*. London: Penguin Press.
- Povinelli, D. J., Nelson, K. E. & Boysen, S. T. (1992). Comprehension of role reversal in chimpanzees: Evidence of empathy? *Animal Behaviour*, 43, 633-640.
- Povinelli, D. J., Parks, K. A. & Novak, M. A. (1992). Role reversal by rhesus monkeys but no evidence of empathy. *Animal Behaviour*, 43, 269-281.
- Premack, D. (1976). *Intelligence in ape and man*. Hillsdale, NJ: Lawrence Erlbaum.
- . (1983) The codes of man and beasts. *Behavioral and Brain Sciences*, 6, 125-167.
- . (1988). "Does the chimpanzee have a theory of mind" revisited. In R. W. Byrne & A. Whiten (Eds.), *Machiavellian intelligence: Social expertise and the evolution of the intellect in monkeys, apes, and humans* (pp. 160-179). Oxford: Clarendon Press.
- Razran, G. (1971). *Mind in evolution*. New York: Houghton-Mifflin.
- Ristau, C. A. (Ed.). (1991). *Cognitive ethology: The mind of other animals*. Hillsdale, NJ: Lawrence Erlbaum.
- Romanes, G. J. (1884). *Mental evolution in animals*. New York: Appleton.
- Rozin, P. & Schull, J. (1988). The adaptive-evolutionary point of view in experimental psychology. In R. C. Atkinson, R. J. Herrnstein, G. Lindzey & R. D. Luce (Eds.), *Stevens' handbook of experimental psychology*, Vol. 2: *Learning and cognition* (2nd ed., pp. 503-546). New York: John Wiley.
- Rumbaugh, D. M. & Savage-Rumbaugh, S. E. (1994). Language in comparative perspective. In N. J. Mackintosh (Ed.), *Animal learning and cognition* (pp. 307-334). Cambridge: Cambridge University Press.
- Schneirla, T. C. (1949). Levels in the psychological capacities of animals. In R. W. Sellers, V. J. McGill & M. Farber (Eds.), *Philosophy for the future*. New York: MacMillan.
- 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 and Behavioral Evolution*, 34, 308-317.
- Shettleworth, S. J. (1990). Spatial memory in food-storing birds. *Philosophical Transactions of the Royal Society B*, 329, 143-151.
- . (1994). Biological approach to the study of learning. In N. J. Mackintosh (Ed.), *Animal learning and cognition* (pp. 185-220). Cambridge: Cambridge University Press.
- Skinner, B. F. (1953). *Science and human behavior*. New York: MacMillan.
- . (1966). The phylogeny and ontogeny of behavior. *Science*, 153, 1205-1213.
- Small, W. S. (1899). An experimental study of the mental processes of the rat. *American Journal of Psychology*, 11, 131-165.
- Smith, J. M. (1982). *Evolution and the theory of games*. Cambridge: Cambridge University Press.
- Spencer, H. (1855). *Principles of psychology*. 2 Vols. New York: Appleton.
- Staddon, J. E. R. (1988). Learning as inference. In R. C. Bolles & M. D. Beecher (Eds.), *Evolution and learning*. Hillsdale, NJ: Lawrence Erlbaum.
- Terrace, H. S. (1979). *Nim*. New York: Alfred Knopf.
- Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes of animals. *Psychological Review Monographs*, 2(8), 109.
- . (1911). *Animal intelligence*. New York: MacMillan.
- Timberlake, W. (1983). The functional organization of appetitive behavior: Behavior systems and learning. In M. D. Zeiler & P. Harzem (Eds.), *Biological factors in learning* (pp. 177-222). New York: John Wiley.
- . (1993). Animal behavior: A continuing synthesis. In *Annual Review of Psychology* (pp. 675-708). Palo Alto, CA: Annual Reviews, Inc.
- Timberlake, W. & Lucas, G. A. (1989). Behavior systems and learning: From misbehavior to general principles. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories: Instrumental*

- learning theory and the impact of biological constraints on learning* (pp. 237-275). Hillsdale, NJ: Lawrence Erlbaum.
- Timberlake, W. & Washburne, D. L. (1989). Feeding ecology and laboratory predatory behavior toward live and artificial moving prey in seven rodent species. *Animal Learning & Behavior*, 17, 2-11.
- Todd, P. M. & Miller, G. F. (1991). Exploring adaptive agency, II: Simulating the evolution of associative learning. In J. A. Meyer & S. W. Wilson (Eds.), *From animals to animats*. Cambridge, MA: MIT Press.
- . (1993). Parental guidance suggested: How parental imprinting evolves through sexual selection as an adaptive learning mechanism. *Adaptive Behavior*, 2, 5-47.
- Tomonaga, M. & Matsuzawa, T. (1992). Perception of complex geometric figures in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*): Analyses of visual similarity on the basis of choice reaction time. *Journal of Comparative Psychology*, 106, 43-54.
- Tryon, R. C. (1940). Genetic differences in maze learning ability in rats. *Yearbook of the National Society for the Study of Education*, 39, 111-119.
- Vander Wall, S. T. (1990). *Food hoarding in animals*. Chicago: University of Chicago Press.
- Wallace, A. R. (1870). *Contributions to the theory of natural selection*. New York: AMS Press.
- Warden, C. J., Jenkins, T. N. & Warner, L. H. (1934). *Comparative psychology: A comprehensive treatise*. New York: Ronald.
- Warren, J. M. (1973). Learning in vertebrates. In D. A. Dewsbury & D. A. Rethlingshafer (Eds.), *Comparative psychology: A modern survey* (pp. 471-509). New York: McGraw-Hill.
- West, M. J., Stroud, A. N. & King, A. P. (1983). Mimicry of the human voice by European starlings: The role of social interaction. *Wilson Bulletin*, 95, 635-640.
- Whiten, A. & Byrne, R. W. (1991). Tactical deception in primates. *Behavioral and Brain Sciences*, 11, 233-273.
- Whiten, A. & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In P. J. B. Slater, J. S. Rosenblatt, C. Beer & M. Milinski (Eds.), *Advances in the study of behavior* (Vol. 21, pp. 239-283). San Diego: Academic Press.