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 Romani collected large quantities of anecdotes. Romani (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.
focused on more qualitative differences in the progressive increase of mental abilities. Thus, birds (class Aves) have abilities into the domain to better understand 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 to resolve the complex tasks that were less easily affected by motivational and sensory-motor differences. For example, Bitterman (1963) 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 vertebrates 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 exposure 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 (Herren & Arbet, 1973).

Model Systems, Animal Models, and Model Animals
Interest in a common model of learning lies at the heart of 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 conserved and readily accessible, attributes that facilitate the neuronal analysis of learning (Hawkins & Kandel, 1984). An animal model is a 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 simulated performance resembles the data of real animals. Hardware "animals" (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 in a degree of mammals as well. Similarly, once the experience-based pro-

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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 protoreversionary 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 (1980) and Masterton, Heffner, and Ravizza (1969) related learning to the phylogeny of mammals by focusing on changes in brain circuitry and development. Kroodsma (1988) and Kroodsma 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.

**Human Language**

Perhaps the unique human characteristic (aside from a strange hallucination for creatures 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—Paterson, 1990) and a variety of nonprimate species (e.g., parrots—Pepperberg, 1990; sailors—West, Stroud & King, 1983; and dolphins—Herman, Richards & Wold, 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 chimpanzee (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 Thornhill 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 reentered 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, Vaccaro, Buczenk, 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 Scores (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 extant differences depend on the face validity of inferred selection pressure. Becher (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 Baldi (1990), working with corvids, and Stentlese (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, Rauschenber, 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
bred for differences in learning ability in nonhuman 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 maze-choice 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 unexplored.

An example of a comparison between the evolutionary ability of species to learn 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, 1996; 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 to the requirement of an optimal memory for different tasks could equally 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 a neotenic chimpanzee, developmentally slowed by the change of a few timing genes. It could be argued that this singe change holds the key to our long and flexible learning periods 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 relate 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 at the developing organism, Berrie (1994) and Hogan (1994) have shown the advantages of characterizing learning in terms of 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. Plomin (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 evolution of 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.

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 cages, the 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 program of study externalizing the continuum of human and animal differences. This work is 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 is 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 tested the comparative analysis of learning from the thrill of anecdotal and easy opinion. What is distinctive 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

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relate better to evolution as they consider the import-
ance of phylogeny, ecology, and their com-
bination. 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-
tions, and for a better understanding of the evi-
dence used to support the scales and trends that
so dominated the thinking of comparative psycholo-
gists over the first 100 years.

References
y and experience: Sources of means and
meaning of developmental change
In E. M. Blass (Ed.), Handbook of be-
havioral neurobiology (Vol. 9, pp. 1-33).
New York: Plenum.
operant learning and memory: A com-
parative etho-psychology approach.
New York: Karger.
Beach, F. A. (1950). The snark was a boojum.
Americans Psychologist, 5, 115-124.
Beecher, M. D. (1990). The evolution of pair-
ent recognition in birds: A review of
D. A. Doewsby (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. Dehaene (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.
Failure to find adaptive specialization is
the learning of honey bees. In J. L. Good-
man & R. C. Fisher (Eds.), The behavior
and physiology of bees (pp. 288-305).
and the evolutionary process. Chicago:
University of Chicago Press.
Byrne, R. W. (1994). The evolution of intelli-
gen. In P. J. B. Slater & T. R. Halliday
(Eds.), Behaviour and evolution (pp. 223-265). Cambridge: Cambridge Univer-
sity Press.
Macauvillian intelligence: Social exper-
tise and the evolution of the intellect in
monkeys, apes, and humans. Oxford:
Clarendon Press.
How monkeys see the world. Chicago:
University of Chicago Press.
Daly, M., Rauschenberger, J. & Behrends, P.
(1982). Food aversion learning in canga-
roo rats: A specialist-generalist compari-
son. Animal Learning and Behavior, 10,
314-320.
by means of natural selection. London:
Murray.
—— (1871). The descent of man, and selec-
tion in relation to sex. London:
Murray.
competence in animals: Definitional is-
stances, current evidence, and a new re-
search agenda. Behavioral and Brain
Sciences, 11, 561-615.
learning theory. Cambridge: Cambridge
University Press.
foraging tactics by 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. Jour-
nal of Human Evolution, 20, 469-93.
functional-analytic approach to aver-
sively motivated behavior: Predator
immunence as a determinant of the
topography of defensive behavior. In R. C.
Bolles & M. D. Beecher (Eds.), Evolution
and learning (pp. 185-212).
Halliday, NJ: Lawrence Erlbaum.
behavior in various breeds of adult dogs
(Canis familiaris): Object permanence and
olfactory cues. Journal of Compara-
tive Psychology, 106, 58-68.
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
psychology of mind. In R. E. Meglin
(Ed.), Animal cognition and behavior
(pp. 473-510). Amsterdam: North-Hol-
land.
Gardner, R. A., Gardner, B. T. & Van
language to chimpanzees. Albany, NY:
State University of New York Press.
Gaulin, S. J., Feist-Gerald, R. W. & Wattell,
M. S. (1990). Sex differences in spatial abili-
ty and activity in two vole species (Mi-
crotus ochrogaster and M. pennsylvanicus).
Journal of Comparative Psychology, 104, 183-189.
of experience and motivation on sym-
metrical-maze performance in the prairie
vole (Microtus ochrogaster). Journal of
Comparative Psychology, 104, 88-93.
Gittleman, J. L. (1989). The comparative ap-
proach in ethology: Aims and limita-
tions. In P. G. Bateson & P. H. Klopf-
er (Eds.), Perspectives in ethology (pp. 55-
phylogeny of behavior. In P. J. B. Slater
& T. R. Halliday (Eds.), Behaviour and
evolution (pp. 80-100). 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).
Curiosity in zoo animals. Behaviour, 26,
151-188.
Gould, S. J. (1977). Ontogeny and phylog-
eny. Cambridge, MA: Belknap Press of
Harvard University.
pact on comparative psychology. In G.
Greenberg & E. Tobach (Eds.), Behav-
ioral evolution and integrative levels: The
T. C. Schneirla conference series (pp.
49-81). Hillsdale, NJ: Lawrence
Erlbaum.
in the domestic fowl, Gallus gallus: The
role of external referents and deception.
Animal Behavior, 36, 338-165.
Hallman, J. P. (1982). Evolution and behav-
ior: An iconic analog view. In H. C.
Plomin (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 bi-
there a cell biological alphabet for simple
forms of learning? Psychological Review,
91, 376-391.
Hayes, K. J. & Hayes, C. (1951). The intel-
lectual development of a home-raised
chimpanzee. Proceedings of the Ameri-
can Philosophical Society, 95, 105-109.
Hebb, D. O. (1949). The organization of
Stimulus control and auditory discrimina-
tion learning sets in the bottlenose
dolphin. Journal of the Experimental
Analysis of Behavior, 19, 379-394.
Herman, L. M., Richards, D. G. & Wolz, J.
bottlenose dolphins. Cognition, 16, 1-
90.
Hayes, C. M. (1994). Social cognition in pri-
mates. 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: Limita-
tions and predispositions. New York:
Academic Press.
Scala naturae: Why there is no theory in
comparative psychology. Psychological
—— (1990). Evolutionary scales and com-
parative studies of animal cognition. In R.
P. Kesner & D. S. Otton (Eds.), Neuro-
obiology of comparative cognition (pp.
and evolution. In P. J. B. Slater & T. R.
Halliday (Eds.), Behaviour and evolution
(pp. 7-42). Cambridge: Cambridge Univer-
sity Press.
Hogan, J. A. (1994). The development of be-
havior systems. In J. A. Hogan & J. J.
Bolhus (Eds.), Causal mechanisms of
behavioural development (pp. 242-264).
Cambridge: Cambridge University Press.
and intelligence. New York: Academic
Press.
Kamil, A. C. (1988). A synthetic approach to
the study of animal intelligence. In D. W.
Leer (Ed.), Comparative perspectives in
Conditioned Preferences

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In omnivores such as the rat and man, most food preferences are learned. Preferences can be formed for any of the many elements of food, including taste, odor, texture, temperature, and appearance. We focus here on conditioned preferences for two of the most important elements, taste and odor, which together are referred to as flavor.

There are four basic tastes: sweet, sour, salt, and bitter. Preferences for these tastes appear to be genetically mediated in both rats and humans. Newborn infants will accept sweet tastes and reject sour and bitter tastes (Lipsitt & Behl, 1990). The newborn is indifferent to salt, but this appears to be because the receptors for the salt taste are not completely developed at birth. Once complete receptivity to salt is established, human infants prefer salt (Beauchamp, 1987). In contrast, there appear to be no genetically mediated preferences or aversions for odors. All affective reaction to odor is apparently learned.

Our wide range of adult likes and dislikes for foods is built on a base of preferences for salt and sweet, as well as dislikes of sour and bitter. I will discuss here three ways we know to produce changes in the affective reaction to a food: exposure, flavor-flavor learning, and flavor-nutrient learning. Animals can also learn to dislike foods through aversion conditioning, a topic covered elsewhere in this volume (Garcia & Riley).

Exposure

More exposure has been shown to increase the preference for all stimuli, not just foods (Zajoc, 1968). The process is particularly important with regard to food because we are all exposed to food. Thus our preferences are constantly being changed by our food experiences, whether we intend to change these preferences or not.

In eating, familiarity breeds liking. So one way to learn to like a food is to consume it. This appears to be a biologically built-in process that ensures the consumption of safe foods. Exposure to the smells of foods the mother eats, which are thereby presumably safe, produces a preference in the infant. This exposure effect begins prenatally. Beauchamp (Mennella & Beauchamp, 1993) has shown that the fetus is exposed to the odors of foods consumed by the mother in amniotic fluid. This process continues in breast-fed babies. Mothers’ milk tastes and smells differently depending on the foods consumed by the lactating mother. A preference for odors in breast milk will lead the infant again to prefer foods consumed by the mother. In rats, the mother’s odor differs depending on the food ingested. This produces a preference for those smells in the child (Galet, 1996). All of the experience leads the young animal to prefer and to eat foods eaten by the mother.

Leann Birch has shown that prior to the age of two, infants will consume almost anything. At about age two neophobia (fear of the new) develops. She showed that the food preferences of three-year-old children could be completely accounted for by sweetness and familiarity. This does not mean these preferences are unchangeable, and one way to change preferences is to use the exposure method. Birch and Marlin (1982) gave three-year-old children novel cheeses or fruits. Initially the children rejected the novel foods, but the experimenter persisted. After about 10 exposures, the chil-


