Revista Mexicana de Análisis de la Conducta
Mexican Journal of Behavior Analysis
Vol 22, núm. 2, 1996, pp.139-151

AN ODYSSEY THROUGH LEARNING AND EVOLUTION

UNA ODISEA A TRAVÉS DEL APRENDIZAJE Y LA EVOLUCIÓN

MICHAEL D. ZEILER
Emory University

RESUMEN

El aprendizaje es una propiedad de los animales vivos y éste, como cualquier otro proceso biológico, es el producto de procesos evolutivos. Varias preguntas surgen cuando el aprendizaje es visto desde un contexto evolutivo. Una de estas preguntas es por qué los animales deben aprender en lo absoluto. Parafraseando en términos evolutivos, esta es la pregunta del significado adaptativo del aprendizaje. Una segunda pregunta está relacionada con las similitudes entre cómo la selección natural actúa al nivel de las especies y cómo el reforzamiento opera a nivel de los individuos durante su lapso de vida. ¿Son en realidad procesos idénticos operando a diferentes niveles? Una tercera pregunta es la generalidad de los principios del aprendizaje entre especies y situaciones. La cuarta pregunta es el grado en el que los procesos de aprendizaje descubiertos en el laboratorio son relevantes para la comprensión del aprendizaje mientras éste ocurre en el medio ambiente natural. Estas cuatro preguntas son el objetivo de este trabajo.

Palabras Clave: Evolución, aprendizaje.

ABSTRACT

Learning is a property of living animals, and so it, like other biological processes, is the product of evolutionary processes. Several questions arise when learning is viewed from an evolutionary context. One is why animals should learn at all. Phrased in evolutionary terms, this is the question of the adaptive significance of learning. A second relates to similarities in how natural selection works at the species level to how reinforcement operates at the level of individuals during their lifetime. Are they indeed identical processes operating at different levels? A third question is the generality of learning principles across species and situations. A fourth is the extent to which learning processes revealed in the laboratory are revelant to understanding learning as it occurs in the natural environment. These four questions are the focus of this paper.

Key words: Evolution, learning.

The purpose of this essay is to discuss selected issues in the evolution of learning. The particular issues certainly are not exhaustive, but they are the ones that have concerned me of late. They are the question of why animals are able to learn at all, problems in drawing analogies between natural selection and reinforcement, the puzzling question of the generality of learning processes, and the relevance of laboratory learning to real life.

WHY LEARN

Why should animals learn? It is no wonder that we think learning is all important. Humans have neither the strength, the speed, the size, nor any other physical ability that might enable them to compete especially well against other animals. What they are good at is in altering their world so that it becomes more congenial, in finding novel ways to cope, and in passing the knowledge they accrue on to others. These others then build on what they have learned to develop still further knowledge. The ability to learn and remember and then to teach is in a large measure responsible for why humans are the most powerful creatures on Earth despite their physical shortcomings. Cumulative knowledge is our forte.

Given the importance of learning for us, it is no wonder that we tend to think that it is all-important. But consider other animals. Well-known scientific observations of animal behavior show that learning may not be terribly important in their everyday life. Digger wasps do not even learn that the nests they are digging are being refilled by interlopers and so they should go elsewhere to build a home (Baerends, 1941). Seagulls show an amazing inability to learn and identify their own eggs (Baerends & Kruijt, 1973). The ethologists described a great deal of animal behavior without reference to any learning at all. Much of the everyday behavior of animals could be explained as essentially innate automatic patterns of behavior in response to certain patterns of stimuli. Learning seems not to be the main driving force of much animal life.

If animals manage so well without much learning, why have they evolved the ability to learn at all? The answer must be in unstable features of their world -- they have evolved what Ernst Mayr (1942) has called an open program. Konrad Lorenz (1981) described it as a mechanism that enables the animal not only to acquire information not contained in the genes, but to retain it for a long time, maybe even until death. For some reason animals must learn the identities of their parents and children. Some even have to learn what species they belong to so that they eventually pick mates suitable for reproductive success. Why aren't those kinds of knowledge innate? Picking a mate of the same species is absolutely essential for reproduction to occur; there is no margin for error. So why should that system ever be an open one? It is less difficult to understand why animals need to be able to learn what tree or field they live in, because that knowledge is so unpredictable as to make genetic coding impossible. The same probably is true of knowing the good and bad places to find food in a particular environment. There strong genetic coding for specific actions and discriminations would seem impossible to attain.

But there is little suggestion of cumulative knowledge in any but humans. No matter how much an animal learns in its lifetime, the next generations do pretty much what the species always has done before. Like Penelope's veil, what is done today is undone tomorrow. Apparently there has been very little selective pressure for cumulative knowledge, probably because doing it on your own worked well enough. Of course, that may all be changing as an increasing number of species go extinct. They might do a lot better if they could learn from each other and pass the information on to the next generation. It is the absence of cumulative knowledge that makes so much animal behavior seem almost reflexive and strongly genetically determined. Since animals do learn, why do they not pass this learning on? Humans seem unique. Why should this be?

SELECTION AND REINFORCEMET

Now consider the analogy between natural selection and reinforcement. Natural selection and reinforcement both are processes that explain either change or stability. Natural selection explains the evolution of species, while reinforcement explains the evolution of individuals. Natural selection has three essential components. Unless these all are present, a species remains in the state of equilibrium described by the Hardy-Weinberg law.

I paraphrase Mark Ridley (1993) in summarizing the principles. The first is that offspring tend to resemble their parents. Like tends to produce like. The second is variation. Members of a species must differ from each other to some degree. The third principle is that some individuals are more likely to reproduce than are others. This is what evolutionary biologists mean by differences in fitness. For us, increased reproductive ability can be a mixed blessing and could even be unwelcome. But birth control is peculiarly human. For evolution, mammoth numbers of children offer unmitigated good news. Fitness usually is based on being better able to cope with the problems of the world under existing conditions. If all of these conditions are met -- heritability, variation, higher fitness -- then natural selection automatically results and the outcome is improved adaptation to the environment, and the species evolves in the new direction. The new characteristics set the stage for still further changes.

Now consider reinforcement. For reinforcement to occur, that is for behavior to change based on its consequences, three processes must hold. First, the physiological mechanism recording past events must preserve the information so that the same behavior can occur again in the future. This is analogous to heredity at the natural selection level. Second, behavior must be sufficiently variable for it to provide a candidate for reinforcement. This mirrors variation in natural selection. Third, different variants must differ in their success for one form to be able to emerge as predominant. This mirrors fitness. If all of these conditions are met -- physiological mechanism, variation, increased success -- the results are improved adaptation for the individual and a new behavioral repertoire. This new repertoire in turn opens new vistas for further changes and opportunities. So, analogous processes are responsible for both species and individual adaptation.

But equivalence between natural selection and reinforcement is imperfect. Learning produced by reinforcement is reversible, but evolution produced by natural selection is not. Evolution in principle might reverse to recreate a once-extinct species, but as far as I know that has occurred only in *Jurassic Park*. Because natural selection works only on what now exists, each change makes it increasingly difficult to return to what was before. Sometimes once-learned never-forgotten (bicycle-riding, swimming), but plenty of data now show that reversibility is a real truth in learning. Even imprinting can be reversed, we now know. It is equally true that evolution never has reversed. Data show a big difference between natural selection and reinforcement in this regard.

Once natural selection produces a particular form, the absence of further selection does not disturb what was produced. In contrast, after reinforcement has generated some behavior, the absence of further reinforcement causes that behavior to go away. "Extinction" has different meaning in the two contexts. In evolution it refers to the loss of a species that may still be supported by natural selection. In conditioning, it means loss of behavior that no longer works.

Another problem lies in the all-important variation in the two processes. For natural selection, because we have so many parts and rates of mutation are so high, each of us is essentially unique. We range from geniuses to ordinary, from 7-foot basketball players to midgets, from beautiful to plain, but all are recognizably human. Really large variants invariably fail in evolution. R. A. Fisher (1930) taught us that the variations leading to successful evolution must be small to be effective. Big ones are freaks that usually are poorly adapted and cannot reproduce. But big variants are as likely to star in behavior as to fail. Witness Mozart, Einstein, and Akeem Olajuwon.

GENERAL PROCESS

The next unresolved issue is general process learning. The major change in psychology in the past 25 years has been the decline in general process learning theory. The 19th century endowed the science of learning with a once non-controversial assumption. Philosophers concerned with how knowledge develops rarely believed that each type of knowledge required its own principles. David Hume (1748) proposed three laws to explain all knowledge. These were contiguity (experiences that occur close together in time tend to be linked), resemblance (experiences that are similar cause one to recall the other), and succession (experiences that invariably follow each other cause us to consider the first as causing the second). That knowledge was independent of the form that it takes was a belief that continued into the experimental science of learning.

The progress in physical science since the Renaissance generated physics as the model of proper science. One implication was that principles are the same whatever form a particular exemplar may take. Molecules follow the same laws whether they occur in living or in inanimate bodies, on Earth or on Mars, in water or on land. The specific materials used by a scientist who wants to study gravity or osmosis or electromagnetic force is more a matter of convenience rather than one of principle. This aspect of classical physics fit the philosophical beliefs about general laws of knowledge.

The physical sciences and philosophy guided psychology. A prime example was the pioneering experimental work on memory conducted by Hermann Ebbinghaus (1885). Ebbinghaus wanted to study the factors influencing memory. We remember and forget a lot of different things. But studying memory requires only some way that is convenient in terms of being manipulable and controlled. Because he believed that everyday memories probably are influenced by previous experience, it was necessary to develop a procedure that was uncontaminated by previous learning. To do so, Ebbinghaus invented nonsense syllables. Such syllables did not occur in any language that he knew, and so he was certain that he had not known them before. He then studied the factors that influenced his ability to remember the syllables.

Now Ebbinghaus never cared about nonsense syllables for their own sake. They provided a convenient and rigorous experimental procedure to determine the general laws of memory and forgetting. Any concern for generality that he may have had appears to have been incidental and disposed of by a few additional observations about more common feats of memory that seemed to follow the same principles. He favored nonsense syllables as the way to find out about memory, because they maximized experimental control over the variables that influenced remembering and forgetting. He was looking for laws of pure memory, not laws of nonsense syllables.

Another important influence at the time that the study of learning became the core of psychology was Darwinian evolutionary theory. Charles Darwin (1859), like some of his predecessors, saw evolution as being a process of descent with modification. The basic assumptions were: (1) species followed one from the other (that is the principle of common descent); and (2) characteristics unique to each species developed as the consequence of certain processes (that is the modification).

Common descent means that species share a common ancestor. But species continuity does not mean species identity. Indeed, the descendants of the same ancestor must have obvious differences for them to be seen as different species. This is why the history is "descent with modification" and not simply "common descent". Similarities between species must exist for Darwin's essential thesis to be credible. It is the similarity between tigers, lions, and cats that suggest a common ancestor; it is the similarities between types of monkey and between non-human primates and people that do the same. The ability to generate very different looking pigeons through selective breeding supported the hypothesis that "descent with modification" is what evolution is all about.

Descent with modification provides no guidance in understanding which characteristics have changed and which have remained the same in the succession of species. A paw might stay a paw or might become a foot, or an eye might develop or lose color vision, or a heart might or might not increase or decrease its number of chambers, or a breathing apparatus might or might not develop the ability to operate out of the water. That can only be answered by collecting data on similarities and differences. But that is not what occurred.

Edward Thorndike's (1911) original interest was frankly comparative -- he wanted to study if and how various animals developed associations. He began with studies of chickens, and then moved on to cats, fishes, monkeys, and humans. The particular behavior that Thorndike chose to reveal learning necessarily differed with the species under investigation. All species reflected the joint operation of the laws of instinct, exercise, and effect. Thorndike said in 1911:

> Formally, the crab, fish, turtle, dog, cat, monkey and baby have very similar intellects and characters. All are systems of connections subject to change by the laws of exercise and effect...Nowhere more truly than in his mental capacities is man a part of nature. His instincts, that is, his inborn tendencies to feel and act in certain ways, show throughout marks of kinship with the lower animals, especially with our nearest relatives physically, the monkeys. His sense-powers show no new creation. His intellect we have seen to

> be a simple though extended variation from the general animal sort. ... Amongst the minds of animals that of man leads, not as a demigod from another planet, but as a king from the same race (pp. 280-294).
>
> Edward Tolman (1938):
>
> I believe that everything important in psychology (except perhaps such matters as the building up of a superego, that is everything save such matters as involve society and words) can be investigated in essence through the continued experimental and theoretical analysis of the determiners of rat behavior at a choice point in a maze. Herein I believe I agree with Professors Hull and Thorndike (p. 172).
>
> B. F Skinner (1938):
>
> In the broadest sense a science of behavior should be concerned with all kinds of organisms, but it is reasonable to limit oneself, at least in the beginning, to a single representative example ... The organism used here is the white rat (p. 47).

It is interesting that all of these influential theorists acknowledged differences among species in sensory capacity, the activities that the species were capable of performing, and in limitations in what could be learned. The prevailing assumption was that any differences were in *what* could be learned; the process of learning, or *how* learning occurred was believed to be common across species. "Continuity without change" rather than "descent with modification" was the rule. Any uniqueness rested in whatever new motor or sensory abilities had evolved or were lost (e.g. the ability to speak allowed humans to learn new social skills, but the lesser sensitivity of humans to smells than dogs made them unable to discriminate odors equally effectively).

To summarize, the psychology of learning operated under strong convictions about generality. Combine the philosophy physics beliefs with species continuity, and the result is that any learnable response in any species is equally appropriate for studying the general principles of how learning occurs. See what Skinner said in 1938.

> The general topography of operant behavior is not important, because most if not all specific operants are conditioned... There should be no incentive to 'botanize'. The present work is accordingly confined to a single reflex -- the behavior of pressing downward a horizontal bar or lever (pp. 45-46).

Continuity across species and across stimuli and responses together led to what became known as *general process learning theory*. The consequence was a heavy concentration of research on rats learning to run or to choose among alternatives in mazes or learning to press levers and later on pigeons learning to peck at round plastic disks mounted at eye level in small experimental chambers.

Not everyone agreed that the information gained in this way would apply to how all species learned everything, but even influential psychologists who did not were largely ignored. Ernest Hilgard, the author of the definitive reference on learning theory, doubted the applicability of learning in non-humans to how humans learn. Hilgard (1956) reacted to Clark Hull's assertion that all behavior of all species including man follows the same laws:

> It is strange that the opposite point of view is not more often made explicit -- that at the human level there have emerged capacities for retraining, reorganizing, and foreseeing experiences which are not approached by the lower animals, including the other primates ... There are probably a number of different kinds of learning which have emerged at different evolutionary periods, with the more highly evolved organisms using several of them. It is quite probable that these different kinds of learning follow different laws, and it is foolhardy to allow our desire for parsimony to cause us to overlook persisting differences (p. 461).

Frank Beach (1960) was so much against the belief that learning is learning and can be studied as well in one species as in another that he suggested restricting psychology to the study of human behavior. Yet both Hilgard and Beach had strong evolutionary orientations. In no way did they think that lack of generality challenged Darwinian theory. After all, descent *with modification* could apply just as well to learning as to any other characteristic. Nothing in evolutionary theory implies fixity or constancy in any biological characteristic. earning might change across species and new forms of learning also could emerge. This is not an issue to be answered via debate. It requires data.

Contemporary students of learning by animals are well aware of the research that shows that particular stimuli and responses and situations do matter. Rats are better able to learn to run than to press a lever to avoid shock, even though they learn either response readily to obtain food. Rats do not relate light or noise to bad food, but they immediately relate a distinctive taste to bad food. But they learn about lights and sounds as signals for painful shocks while being unable to learn that a taste signals a shock. Learning looks different in open and closed feeding economies.

Such data generated the revolution against general process that flew the banner of "biological constraints on learning", and the activists shouted that obviously learning processes were not general. The revolutionaries ignored that the data actually showed limitations in "what" can be learned rather than in "how" learning occurs. That animals might differ in what they can learn is not the same as saying that they differ in how they learn whenever they do learn. Even the most diehard general process theorist recognizes that animals differ in sensory capacities and this must lead to differences in what stimuli can be learned about. They differ in motor abilities, and this must lead to differences in what they can learn to do. These qualifications are trivial. More interesting is their ability to learn about certain stimuli and to make certain responses only under certain conditions. This clearly is not an issue of sensory capacity or motor ability. If the same animal learns readily to obtain food by operating a switch only when a light is green but cannot learn to do the same thing to avoid shock, blame cannot be placed on what it is able to see or to do. That they immediately learn that a particular taste signals bad food but cannot learn when it signals a painful shock means that ability to discriminate the particular taste is not the issue. Such observations, and there have been many in the last 20 years, mean that what an animal can learn depends on characteristics of particular species operating in particular environments. This is impressive evidence for the role of ecological factors in determining what is learned. But it does not mean that how learning occurs when it does occur necessarily is equally ecologically determined. This is the question of the processes of learning. I hope the distinction between content and process is clear.

Recently the idea has developed that how learning occurs must differ with what is being learned. This assertion emerges from a group known as evolutionary psychologists. Cosmides and Tooby (1987) distinguish between "domain general learning" and"domain specific learning". Domain general learning is equated with the assumption tnat learning is independent of its contents, which everyone now agrees is wrong. That's old news. But it also is taken to mean that learning is accomplished only through a few simple domain general mechanisms. That cannot be true, they say, because how learning occurs must depend on ecological context and on the specific problem that learning solves in a particular situation. How learning occurs must be as domain specific as is what is learned. Why? Because only domain specific learning could maximize inclusive fitness. Inclusive fitness refers to long-term reproductive success, where success refers not to number of children, grandchildren, great-grandchildren, or any number of generations descended directly from you, but to the frequency with which genes identical to yours are represented in future populations. Mechanisms of learning must be domain-specific, because no single learning strategy is best under all the situations that were likely to have been encountered in times past, much less in contemporary life.

Their argument is based on a view of evolution that never was universally accepted by evolutionary theorists in the first place and still is maintained only by the most simplistic sociobiologists. The essence of the view is that each important characteristic -- be it a pattern of behavior, an anatomical characteristic, a physiological mechanism, or anything else -- necessarily has evolved into the form that maximizes reproductive success (or at least did so under past conditions, which Cosmides and Tooby hypothesize were those of the Pleistocene era). An early criticism of this view was the now-classic "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme" paper of Stephen Jay Gould and Richard C. Lewontin, written in 1978.

Gould and Lewontin describe the central dome of St. Marks Cathedral in Venice. The dome is supported by arches. "Spandrel" is an architectural term that refers to the tapering triangular spaces that must occur when two rounded arches intersect at right angles. The spandrels of San Marco contain mosaics beautifully designed to fit the space. But to view gorgeous mosaics as the cause of arches is to make a serious mistake. The existence and shape of the spandrels are a necessary architectural constraint for the dome. Given their necessity, the mosaicists then decorated them magnificently. To say that spandrels exist because they are the perfect home for the mosaics is tantamount to Voltaire's Dr. Pangloss who said that things are as they are because that is how they turn out best. To say that all characteristics are determined because they maximize fitness is what Gould and Lewontin mean by the Panglossian paradigm in biology. Natural selection becomes not only important but a perfect designer operating on the basis of ideals. Each characteristic has been shaped by natural selection so as to now have achieved its optimal form. The whole organism is reduced to a collection of optimal parts. When this analysis is shown inadequate (which it invariably is), the theoretical out is that optimization of one feature may interfere with the optimization of another. The optimal solution, then, is the compromise that produces Dr. Pangloss' best of all possible worlds.

So, when Cosmides and Tooby say that domain-general learning is "no alternative at all" because "more general sets of decision procedures are less likely to provide correct guidance" then will domain-specific procedures and therefore that genes for general process could not possibly outcompete genes that code for specialized learning, they have adopted the Panglossian paradigm and evolutionary reductionism. Furthermore, they have no data on which to base their claims. Deductions based upon fitness are condemned to the role of story-telling, no matter how plausible they may seem. Neither Cosmides and Tooby nor anyone else can actually show that the less-than-optimal fitness resulting from general process learning really has had any effect on the processes currently responsible for learning.

There are some very basic general learning processes. Habituation appears to be virtually identical in all species. Reinforcers typically improve state of affairs and have been seen to work in all species under some conditions. Stimulus control also occurs in all species. There is wide generality for the principle that learning is strongly influenced by success and failure.

Perhaps the central question in learning is what conditions underlie learning. After years of believing that contiguity of stimuli or of stimuli and response and reinforcer was the foundation of learning (or at least of Pavlovian and operant learning), a less mechanical mechanism was proposed. This became known as contingency theory. The idea is that animals accumulate positive and negative instances and learn what really is going on during an extensive history. They are sophisticated integrators of information, not stupid contiguity machines driven by what has just happened to them. But now evidence has accumulated that they do not integrate and differentiate but simply follow contiguity rules (cf. Papini & Bitterman, 1990). Or at least that is true of the animals and situations studied to date, including humans. Well, is or is not contiguity learning a general process? Superstitious behavior in every species studied to date supports that hypothesis in that every species. Every species, at least for a while, produces the ritual that just happened to precede a reinforcer even though it did so purely by chance. Do even humans learn contingencies? My own data suggest that they also are not very good at integrating information, but they are exquisite contiguity machines.

I doubt very much that being driven by contiguous events is the best of all possible ways to enhance inclusive fitness. Surely, it would be far better to learn what really is responsible for an event. But contiguity does give animals an immediate rule of thumb. Far better to do what worked the first time than to judiciously wait and gather information about whether what you did really was what saved you from a predator. Natural selection operates only on what it has, not on what it would be nice to have. We would be better off if we could see around corners and behind us or if we could fly, but selection never had the appropriate structures to select. The same may be true of functioning like a computer. Arguments from what would maximize fitness just are sterile. We need good data, not debate.

OBSERVATIONAL LEARNING

Finally, I am concerned about the importance of the kinds of learning emphasized in our laboratories for the learned behavior of animals in their world. Learning about bad food quickly is an important ability for animals prone to eat anything they find, so here a well-studied laboratory phenomenon probably tells us a lot about learning in nature. Scores of birds learn and relearn every year not to snack on Monarch butterflies (Brower, 1985). But consider shaping, a wonderful procedure for teaching new responses. Has any parent of any species (other than those taught by us or by animal trainers) ever trained their young to do anything by the method of successive approximations? We do it because B. F. Skinner applied principles of contiguity and extinction to the problem of generating new behavior. I believe shaping is derived from the laboratory and the circus, not because it occurs in nature.

A lot of new learning involves directing already established or developing patterns to stimuli which previously didn't generate them. We do have some examples of apparently new learning in animals. Take the famous creamstealing blue tits in England (Hinde & Fisher, 1951) or the washing of food by Japanese monkeys (Kawamura, 1963). The blue tits broke the foil on milk bottles left on British doorsteps and stole the cream from the top; the monkeys washed the sand off potatoes. That surely sounds like new behavior. But in fact the pecking response for food is something that every bird normally does, and rubbing food is common in monkeys. They simply were doing old behavior under new conditions. The learning involved stimulus control, not new responses.

How about laboratory studies of avoidance learning? Animals probably do learn to avoid certain unpleasant events in the way they are required to do in the laboratory, but it certainly cannot be fully general. Surely this cannot be a way to learn about avoiding predators, since most animals would be dead after one trial involving the teeth or claws of the predator. Some lucky ones might escape, but this cannot explain why so many animals perform avoidance responses to their typical predators. It cannot be that they know all this innately, because predators differ with locale.

The little bit of data we have suggests that they learn not from trial-and error but from observing others. Mineka and Cook (1988) showed that young monkeys have no fear of snakes, until they see an older monkey scream hysterically and run away from a snake. After that the babies are terrified and run as well. This does not sound like either operant or Pavlovian learning, but rather like a strong predisposition to learn from others. It also explains how animals can learn to avoid a predator without ever having been bitten or attacked.

Do animals learn about good food through operant conditioning? Taste aversion explains avoiding bad food, but how does an omnivore like the rat develop dietary preferences when almost everything is edible. Do they eat at random and then get reinforced for that choice when it turns out to be a good one? Galef's (1990) work with rats shows that that is not the predominant strategy for rats. Instead they learn from each other. Given a choice of foods, rats pick the one that they have smelled on the breath of a friend or relative. They learn from each other, not by the consequences of their action. Potato washing and cream stealing spread through social learning as well.

After years of thinking that animals do not learn by imitation or observation, we now know that they do. What has changed? I think the big factor is that the earlier work tried to teach new response patterns by imitation, while the more recent and successful experiments involve transferring established responses to new situations.

Herbert Simon (1990) hypothesized that we evolve with a strong predisposition to learn from others. The data on traumatic avoidance learning and social learning about food support that hunch. Based on a highly creative and productive series of experiments Donald Baer and his colleagues suggested that humans must be trained to imitate (e.g., Baer & Sherman, 1964). I wonder if they really did have to learn to imitate or whether what they actually had to learn was the relevance of the particular model.

It probably is foolish to believe that animals never learn new response patterns. It is not easy to say "never" after one has dramatically increased the behavioral repertoire of previously inactive severely retarded people and used a combination of shaping and imitation to teach them to speak. More often in nature the role of reinforcement may be to organize sequences of existing response components rather than to create behavior.

The animal data on observational and social learning bring me full circle. Is this evidence that animals are like humans in having cumulative knowledge? Well, it surely is a step in that direction. But non-humans certainly have not built on it to change the status of rats and monkeys very significantly. I suspect that contemporary dogs are doing pretty much the same things and know just about as much as they did in Athens during the age of Pericles. In contrast, even a genius like Aristotle would find the modern advanced world and university science curriculum unfamiliar. Without doubt he could come to learn about it through education and other experiences. What genes do we have that animals lack to make us so prone to cumulate knowledge? Is language cause or effect or both? Maybe he could figure that out as well.

REFERENCES

Baer, D. M., & Sherman, J. A. (1964). Reinforcement control o f generalized imitation. *Journal of Experimental Child Psychology, 1*, 37-49.

Baerends, G. P. (1941). Fortpflanzungsverhalten und Orienterung der Grabwespe *Ammophilia campestris. Tijdschrift voor Entomologie, 84*, 68-275.

Baerends, G. P., & Kruijt, J. P. (1973). Stimulus selection. In R. A. Hinde & J. Stevenson-Hinde (Eds.), *Constraints on learning: Limitations and predispositions* (pp. 23-50). New York: Academic Press.

Beach, F. A. (1960). Experimental investigations of species-specific behavior. *American Psychologist, 15*, 1-18.

Brower, L. P. (1985). Foraging dynamics of bird predators on overwintering monarch butterflies in Mexico. *Evolution, 39*, 852-868.

Cosmides, L., & Tooby, J. (1987) From evolution to behavior: Evolutionary psychology as the missing link. In J. Dupre (Ed.), *The latest on the best: Essays on evolution and optimality* (pp. 277-304). Cambridge, MA: MIT Press.

Darwin, C. (1859). *On the origin of species*. London: Murray.

Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford: Oxford University Press.

Ebbinghaus, H. (1885). *Uber das Gedachtniss*. Leipzig: Drucker and Humblant Galef, B. G., Jr. (1990) . An adaptationist perspective on social learning, social feeding, and social foraging in Norway rats. In D. A. Dewsbury (Ed.), *Contemporary issues in comparative psychology* (pp. 55-79). Sunderland, MA: Sinauer.

Gould, S. J., & Lewontin, R. C. (1978). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society*

Hilgard, E. H. (1956). *Theories of learning* (2nd edition). New York: Appleton-Century-Crofts.

Hinde, R. A., & Fisher, J. (1951). Further observations on the opening of milk bottles by birds. *British Birds, 44*, 393-396.

Hume, D. (1748). *An enquiry concerning human understanding*.

Kawamura, S. (1963). The process of sub-culture propagation among Japanese macaques. In C. H. Southwick (Ed.), *Primate social behaviour* (pp. 82-90). New York: Van Nostrand.

Lorenz, K. (1981). *The foundations of ethology*. New York: Springer-Verlag.

Mayr, E. (1942). *Systematics and the origin of species*. New York: Columbia University Press.

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys. In T. Zentall & B. G. Galef, Jr. (Eds.), *Social learning* (pp. 51-73). Hillsdale, NJ: Erlbaum.

Papini, M. R., & Bitterman, M. E. (1990). The role of contingency in classical conditioning. *Psychological Review, 97*, 396-403.

Ridley, M. (1993). *Evolution*. Cambridge, MA: Blackwell.

Simon, H. A. (1990). A mechanism for social selection and successful altruism. *Science, 250*, 1665-1668.

Skinner, B. F. *The behavior of organisms*. New York: Appleton-Century-Crofts.

Skinner, B. F. *The behavior of organisms*. New York: Appleton-Century-Crofts.

Thorndike, E. L. (1911). *Animal intelligence*. New York: Macmillan.

Tolman, E. C. (1938). The determiners of behavior at a choice point. *Psychological Review, 45*, 1-41. Reprinted in E. C. Tolman (1958), *Behavior and psychological man* (pp. 144-178). Berkeley: University of California Press.