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## Comparative Cognition

- ▶ A Salience Theory of Learning
- ▶ Learning in Invertebrates
- ▶ Linguistic and Cognitive Capacities of Apes

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## Comparative Music Education

- ▶ International Perspectives in Music Instruction and Learning

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## Comparative Psychology and Ethology

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### Definition

Comparative psychology and ethology are both sciences which study animal behavior, typically nonhuman behavior, though both have often studied humans. Comparative psychology is a subdiscipline of psychology and ethology of biology. Both can trace their roots to the late nineteenth century. Depending on which history one reads, the first comparative psychologist was Pierre Flourens, a protégé of Baron Cuvier, or George John

Romanes, a friend and student of Charles Darwin. Flourens' book title represented the first use of the term, comparative psychology (*Psychologie Comparée* 1864) and predated Romanes' *Animal Intelligence* (1882). Both proposed a science that would compare animal and human behavior, Romanes postulating the existence of a gradient of mental processes and intelligence from the simplest animals to man – the comparative approach much in use today. Romanes strengthened his proposal by a vast collection of anecdotal accounts of clever behavior in dozens of animal species. Though perhaps best known today for the fallacies of his anecdotal method and for his easy assignment of human mental faculties to animals – anthropomorphism – Romanes nevertheless succeeded in establishing his idea of a gradient of mental processes across the animal kingdom as a basic premise of early comparative psychology. Ethology too has a mixed parentage. Isidore Geoffroy-Saint-Hillaire first used the term in 1859, though Oskar Heinroth, a late nineteenth century German biologist, was one of the first to apply the methods of comparative morphology to animal behavior; he is thus considered to be one of the founders of ethology.

Both disciplines had many adherents in the early and middle parts of twentieth century: Comparative Psychology in the USA under the influence of the learning psychologists (e.g., Ivan Pavlov and Edward Thorndike), the behaviorists (e.g., Zing-Yang Kuo, John Watson, and B. F. Skinner), and the epigeneticists (e.g., T. C. Schneirla, Daniel Lehrman, Ethel Tobach, and Gilbert Gottlieb), while Ethology became firmly established after World War II in Europe under the influence of biologists such as William Thorpe, Nikko Tinbergen, and Konrad Lorenz. The latter two, in fact, were awarded the Nobel Prize in medicine (there is no separate prize for behavioral research) in 1972 for their animal behavior studies (they shared this prize with Karl von Frisch, an early twentieth century biologist).

### Theoretical Background

Given the biological roots of both comparative psychology and ethology, evolution was seen to play an important role in behavioral origins by both disciplines, though in different ways. Comparative psychology, strongly influenced by early twentieth century Functionalists (e.g., William James, John Dewey), believed behavior allowed organisms to adapt to their

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environments (i.e., Darwinism); behavior itself was not an evolved phenomenon, though the organism was. Thus, as organisms changed through evolution, new or different behavioral potentials arose. Ethologists, on the other hand, understood behavior itself to be an evolved process, the route being genes → instincts, or inherited behaviors. In later years, this one-way route, from genes to behavior, became to be known as the central dogma of molecular biology. Additionally, while comparative psychology tended to engage primarily in laboratory research, ethology emphasized the significance and importance of studying behavior outside the laboratory, in natural settings.

These two fundamentally different approaches to the study of behavior lead to a serious intellectual and theoretical “war” around the 1950s. Ethology advocated the position that behavior was a biological phenomenon, *determined*, and not merely *influenced* by the organism’s genotype; much animal behavior was thus believed to be instinctive. Indeed, Lorenz, whose mentor was Oskar Heniroth, and Tinbergen spelled out the full meaning of what instinctive behavior was. The clearest statement of this is found in Tinbergen’s book, *The Study of Instinct* (1951). Comparative psychologists, on the other hand, tended to take an epigenetic approach, stressing the importance of development, experience, and other psychological processes. The differences were summarized in an important paper by Daniel Lehrman (1953), which today still represents one of the best critiques of instinct theory. While healthy, the ensuing debates settled little. It was an important 1966 book by Robert Hinde (*Animal behaviour: A synthesis of ethology and comparative psychology*) that seemed to resolve the differences between these two opposing views. Indeed, a later 1981 book by the ethologist S. A. Barnett (*Modern ethology: The science of animal behavior*) was able to discuss the discipline without resorting to instinct explanations.

### Important Scientific Research and Open Questions

The two disciplines historically sparred over the nature–nurture issue: Was behavior a biological or a psychological phenomenon? Endless debates over this issue have yet to see it formally resolved. Contemporary reports of the discovery of a gene for a behavior are routinely retracted following failures to replicate such findings – but the search continues. This is as true in psychology as

it is in biology, though many in both camps understand behavior to be a biopsychosocial phenomenon. The significance of both psychological and biological development, long ignored, is now seen to be crucial to a full understanding of behavioral origins. While focusing primarily on issues of comparative psychology, the many open questions still confronting the study of animal behavior are reviewed in a recent textbook (Greenberg and Haraway 2002). For example, though studied now for well over 100 years, there are still new developments to be found in the area of learning.

### Current Status

While comparative psychology grew in America, ethology remained somewhat stagnant in Europe. Many still identified with the discipline, though it was clear that they had abandoned the hard-nosed biological determinism of the classical ethologists. Beginning in 1944 with the initiation of the American Psychological Association’s divisional structure, comparative psychology had a home in Division 6, Physiological Psychology and Comparative Psychology. In the 1990s, in an effort to attract new members, the division entered into discussion of a name change – the important point for the present discussion was the retention of “comparative psychology” in the new name adopted at the 1995 APA meeting, Behavioral Neuroscience and Comparative Psychology. While membership in Division 6 was falling, comparative psychology as a field of study remained healthy as illustrated by the appearance of several comparative psychology societies in the closing years of the twentieth century: The Southwestern Comparative Psychology Association (founded in 1983 by Michael Domjan, Del Thiessen, Steve Davis, and Gary Greenberg); the Comparative Cognition Society (founded in 1994 by Ron Weisman, Mark Bouton, Marcia Spetch, and Ed Wasserman); and the International Society for Comparative Psychology (founded in 1983 by Ethel Tobach and Gary Greenberg). An even earlier group, the International Society for Developmental Psychobiology, was founded in 1967 by George Collier, Norman Spear, Bryon Campbell, John Paul Scott, and others. The annual and biennial meetings of these societies attract animal behavior researchers from several disciplines across the globe; their membership is also international. There are, of course, several other such societies in countries around the world.

The picture was not so rosy for ethology which seemed to languish in the same period. This was likely because, "The simple truth is that ethology never did deliver as a science of comparative behavior..." (Plotkin 2004, p. 105). Indeed, in 1989 ethology was declared:

- ▶ dead, or at least senescent. That is, if you think of ethology in the narrow sense – the study of animal behavior as elaborated by Konrad Lorenz, Nikolas Tinbergen, and Karl von Frisch. It has been quiescent for some time. No exciting ideas were emerging, and data gathering on key issues had lost its direction. (Barlow 1989, p. 2)

However, the biological study of animal behavior has thrived well into the twenty-first century. Ethology was reborn in the early 1970s as a new science, that of sociobiology (Wilson 1975), the goal of which was to biologize the social sciences. But this blatant attempt at understanding animal and human behavior as a purely biological phenomenon was met with scathing criticism (Hull 1988; Lustig et al. 2004) from numerous quarters. The main point of contention centered around the continuing nature–nurture issue and the question of whether behavior, especially human behavior, was the result of genetic and biological determinism. To many opponents of sociobiology, psychology was not a biological science at all, but a uniquely psychological science (e.g., Greenberg 2007).

The intellectual sparks flew for years, well into the end of the twentieth century, which witnessed the appearance of a still new iteration of ethology, evolutionary psychology. This approach focuses primarily on human behavior and posited that we owe our universal nature to evolutionary adaptations faced by our Pleistocene ancestors that we have inherited in our genomes. A good source for reviewing the tenets and the research conducted in this field is *The Handbook of evolutionary psychology* (Buss 2005). With evolutionary psychology, instincts are once again in vogue. As with ethology and sociobiology, evolutionary psychology is not without its critics (e.g., Lickliter and Honeycutt 2003). It is not the application of evolution to behavior that is at question, but the manner in which it is understood to apply to behavioral origins. Evolutionary psychology, though seen by many to be seriously flawed, is a rather popular orientation in the contemporary behavioral sciences. After all, what serious

scientist in 2011 can object to the significance of evolution to psychology?

There has also been new life breathed into ethology and sociobiology. The sociobiological idea of the genetic basis of human altruism has recently been somewhat retracted by one of its earliest proponents, E. O. Wilson. While this is comforting news to many non-reductionistic comparative psychologists and other animal behaviorists, it does not sit well with all students of behavior (Marshall 2010), attesting to the staying power of the classical ideas of ethology. In a recent analysis, Salzen (2010) makes a case for interpreting the ideas of ethology in modern neuroscientific terms. There is in fact a discipline known as "neuroethology," which describes animal behavior in terms of how the nervous system works. As a comparative psychologist, I take comfort in the staying power of my discipline. Its history has been long, though not nearly as tumultuous as that of ethology.

## Cross-References

- ▶ Animal Culture
- ▶ Biological and Evolutionary Constraints of Learning
- ▶ Developmental Cognitive Neuroscience and Learning
- ▶ Evolution of Learning

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## Comparative Psychology of Learning

- Evolution of Learning

## Comparator Hypothesis of Associative Learning

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### Synonyms

Comparator theory; Performance-focused model; Response rules; Retrieval-focused model

### Definition

The central tenet of the Comparator Hypothesis is that responding to a cue requires that the cue signal a change in reinforcement. That is, given prior cue-outcome pairings, responding to the cue is not a direct function of the strength of the outcome representation activated by the cue. Instead, responding depends on the degree to which the cue predicts an increase (or decrease) in the likelihood of the outcome relative to the likelihood of the outcome in the training context (which might differ from the test context) in the absence of the cue.

### Theoretical Background

Both early theorizing and prevailing contemporary models of learning (e.g., Rescorla and Wagner 1972) posit that responding to a cue in a Pavlovian situation

reflects the degree to which a cue activates a neural representation of the outcome. However, there are a number of observations that challenge that simple assumption. Most notably, studies of contingency found that behavioral control by a cue depends not only on the probability of the cue being followed by the outcome ( $p[\text{outcome}|\text{cue}]$ ), but also on the probability of the outcome in the absence of the cue, that is the context ( $p[\text{outcome}|\text{context alone}]$ ). Thus, behavioral control by a cue seemingly reflected  $p(\text{outcome}|\text{cue}) - p(\text{outcome}|\text{context alone})$ . Initially, it was unclear whether the critical context was that of training or test, and whether the computation occurred after each training trial or at the beginning of each test trial. But subsequent research determined that the critical context was that of training and that this computation occurred at the time of each test trial.

Miller and Matzel (1988) used these two findings to formulate, in associative terminology (as opposed to conditional probabilities), the original Comparator Hypothesis, which went well beyond contingency theory by allowing nontarget cues that were present during target training (not only the training context) to serve as the basis of comparison (i.e., as comparator stimuli). This provided a new account of cue competition (e.g., overshadowing and blocking) as well as the contingency phenomena on which the model was based. Prior accounts of cue competition assumed that cue competition is caused by a failure to acquire the target cue-outcome association. When the pairings occurred in the presence of another cue, the most common account asserted that the two cues competed for a limited amount of available associative strength that could be supported by the outcome. The Comparator Hypothesis instead assumes that each cue acquires an association with the outcome independent of the presence of the other cue. The impaired behavioral control of the target cue after it is trained in compound with a nontarget [comparator] cue is a consequence of a comparison between the target cue-outcome and comparator stimulus-outcome associations; each serves as the context of learning for the other. However, as testing of the target can occur in the absence of the comparator stimulus, activation of the comparator-outcome association must be mediated by activation of the target cue-comparator stimulus association (see Fig. 1). Thus, the Comparator Hypothesis states that behavioral control by a target cue is a direct function of