Comparative Primate Psychology

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Glossary

Adaptation A genetically controlled trait that has evolved by natural selection.

Analogous traits Similar traits that evolved independently in different species in response to similar environmental pressures.

Comparative psychology The study of mind and behavior in nonhuman animals.

Convergent evolution The process by which natural selection produces similar adaptations in different species that live in similar environments.

Homologous traits Similar traits possessed by different species as a result of inheritance from a common ancestor.

Phylogeny The evolutionary development and history of a species or higher taxonomic grouping of organisms.

Primatology The discipline that studies nonhuman primates.

Trait A morphological, physiological, or behavioral characteristic of an organism.

Evolutionary Foundations of Comparative Primate Psychology

Psychology is the discipline that studies mind and behavior. Within psychology, there are many subfields including, among others, biological, clinical, cognitive, comparative, developmental, educational, evolutionary, industrial/organizational, personality and individual differences, and social psychology. Some of these subfields are often recognized as independent disciplines. Comparative psychology, which involves the study of mental processes and behavior in other animals, is also known as ethology or behavioral biology. Within comparative psychology, there are subfields specializing in the study of particular groups of animals. For example, the comparative psychology of nonhuman primates is sometimes called behavioral primatology, or simply primatology.

All of these multilevel disciplinary subdivisions have resulted from the growth of psychological research, its expansion in many different directions, and the increasing specialization of researchers addressing different types of questions about mind and behavior. Although specialization is both welcome and inevitable, the risk involved in these sub-fields turning into independent disciplines is that they may become conceptually disconnected from psychology and from each other. With regard to the study of mental and behavioral processes in nonhuman primates, it is important to discuss how this area of research is conceptually linked both to comparative psychology and to psychology in general.

A frequently used rationale for conducting comparative psychological research is the 'animal model' argument. This argument is that similarities in brain structure and function, or physiological processes, or learning abilities in animals and humans allow researchers to use animals as models for a specific aspect of human behavior, or cognitive process, or its underlying neurobiological or physiological regulation. For example, according to Gottlieb and Lickliter, the 'animal model' approach entails finding "nonhuman species with behavioral and psychological repertoires that are similar to humans so that the results of experiments with the model may throw light on seemingly related behavior in human beings" (pp. 311–312). Evolutionary arguments do not figure prominently in comparative research conducted with the animal model approach. Particular organisms are selected mainly on the basis of practical criteria, such as they are small and cheap to maintain in the laboratory, they reproduce frequently, and it is easier to conduct experimental studies that may require highly invasive procedures. The most common organisms that fit these criteria and are used in comparative psychological research include fruit flies, cockroaches, some frogs and reptiles, pigeons and some other birds, and of course, rats, mice, and other rodents. Although comparative research with these 'model organisms' can make some beneficial contributions to psychology, there are risks involved in selecting organisms based solely on practical criteria. One of these risks is that the extrapolation of findings or conclusions from animal to human research may be inappropriate.

Comparative psychologists who use the 'animal model' argument as rationale for their research not only recognize the limitations of this approach but, surprisingly, also minimize the contributions comparative research can make to psychology. This position is exemplified by Gottlieb and Lickliter, who argued that "the certainty that animal models are faithfully mimicking their presumed human counterparts in the arena of psychological, social, and behavioral function is always open to even greater question" (p. 312). As a result, they conclude that the main contribution of comparative research to psychology is to provide food for thought, that is, hypotheses but not data, general principles but not facts.

In a critique of Gottlieb & Lickliter's article, I argued that a logical corollary of their position is that the rationale for doing comparative animal research in general is very weak. Computer simulations can be a good source of testable hypotheses about human behavior. Studying human behavior can be an excellent source of testable hypotheses about human behavior. Why bother with animals? Given the economic costs, the logistic difficulties, and the ethical issues associated with animal research, such research would no longer be warranted if its contribution were only to provide hypotheses or food for thought. Even animal studies with highly invasive

experimental procedures that are impossible in humans would be difficult to justify if their main contribution were only to provide hypotheses. I argued instead that animal studies provide much more than food for thought, and discussed many cases in which animal data have clear cross-species validity and direct extrapolability to the human condition. To give just one example, in his 1969 formulation of attachment theory, British psychoanalyst John Bowlby did not use information from nonhuman primate research just to develop the hypothesis that there they might be an attachment system in humans or some general principles about its functioning. He showed that there were 'formal similarities' in the infant response to separation, the development of fear of strangers, and the use of the mother as a secure base in monkeys and in humans. Based on these and other similarities, he argued that the development, regulation, and adaptive function of the attachment system are very similar in humans and some other primates, and that this similarity is probably due to common descent, that is, humans and closely related primates inherited the infant attachment system from their common ancestors. Thus, Bowlby provided a clear example of how data from nonhuman animals, and not just hypotheses or general principles, can be directly extrapolated to humans and how one can develop a theory of behavior that has a strong evolutionary foundation and cross-species validity.

Evolutionary biologist Theodosius Dobzhansky once said "Nothing in biology makes sense except in light of evolution." Many evolutionary and comparative psychologists believe that the same should be said about psychology as well. Comparative psychological research can be strongly justified on evolutionary grounds, and evolutionary arguments can also help select the best study organisms and the research questions that can be best addressed from a comparative perspective. One evolutionary rationale for conducting comparative research is that similarities in behavior between animals and humans are the result of common phylogenetic history. In this view, certain traits are similar in animals and humans because they were inherited from a common ancestor, that is, they are 'homologous.' Studying these traits in animals helps one elucidate the phylogenetic history of human behavior. In general, the probability that two species have homologous traits is higher the closer the phylogenetic relationship between the species. Thus, human behavior is more likely to be homologous to the behavior of other primates than to the behavior of nonprimate animals. This provides a strong evolutionary rationale for using nonhuman primates, especially primates that are closely related to humans, in comparative psychological research.

Another evolutionary rationale for conducting comparative research is that similarities in behavior between animals and humans may be the result of convergent evolution. This means that similar traits in animals and humans evolved by natural selection in response to similar pressures from the environment, but independently in different species. These traits are considered 'analogous' and studying them can help one understand how the environment has shaped human behavior through the action of natural selection. Similar adaptations to the environment can occur in species that are distantly related and, therefore, in theory, to investigate the adaptive aspects of human behavior from a comparative perspective, honeybees can be as good as models as chimpanzees are. In reality, however, there are many constraints on the type of adaptations to the environment that organisms can evolve through natural selection. Therefore, similarities in genetic, anatomical, physiological, and cognitive constraints increase the probability that organisms will evolve similar adaptations to the environment. Thus, human behavior is generally more likely to be analogous to the behavior of other primates than to the behavior of nonprimate species. This provides another strong evolutionary rationale for using nonhuman primates in comparative psychological research.

Studying the mind and behavior of nonhuman primates that are closely related to man can potentially enhance the understanding of many human mental and behavioral processes for clear evolutionary reasons. Although primatology and psychology are sometimes considered different disciplines, there is no conceptual reason why this should be the case. In fact, the history of research on primate minds and behavior illustrates that, from the very beginning, studies of primate and human minds and behavior were closely interwoven.

History of Comparative Primate Psychology

The implications of primate behavior research for understanding human behavior were first explicitly recognized by Darwin, who in his 1872 book on '*The Expression of Emotions in Animals and Man*' drew several parallels between the facial expressions of nonhuman primates and those of human beings. However, it was psychologists rather than evolutionary biologists who began the systematic study of primate behavior and cognition at the beginning of the twentieth century.

One of the first psychologists to conduct systematic primate behavioral research was Wolfgang Köhler. As a Gestalt psychologist, Köhler was interested in cognitive processes other than learning and was curious to see if apes could use 'insight' to solve novel cognitive tasks. In a research station established at Tenerife on the Canary Islands, Köhler conducted many elegant experiments with chimpanzees during the period 1913–1917. Many of these experiments involved the manipulation of the environment to obtain food rewards and the use of previously familiar objects in novel and instrumental ways. Köhler's research questions and some of its procedures were very innovative and some of its findings are still highly cited in contemporary research. He can certainly be considered one of the founders of modern research on primate cognition.

In the United States, the systematic study of primate behavior was pioneered by Robert Yerkes, a Harvard-trained psychologist who established a primate research facility in Orange Park, Florida, with the goal of making primates available to many different kinds of scientific inquiry, most notably, psychological research. Yerkes felt that research on the behavior and cognitive abilities of primates, and in particular the great apes, would help answer some questions in psychology that had historically been very difficult to address. His contributions to primate behavior research were many and ranged from studies of spatial cognition and problem-solving to research on social and maternal behavior.

In addition to the pioneer efforts by Köhler and Yerkes, other early attempts to study primate behavior and cognition

were made in Russia, France, Cuba, and other parts of the world. The 1920s and 1930s also saw the beginning of attempts to teach language to chimpanzees. The first of such attempts was made in 1930 by Kellogg and Kellogg who raised a young chimpanzee named Gua along with their son Donald. The Kelloggs' experiment turned out to be a failure but it was followed by many others, using similar or different strategies.

Along with the growing recognition that primate behavior could be useful to understand human behavior, the years before World War II were characterized by increasing interest in studying primates in their natural habitat and understanding the basic principles regulating their social organization. With World War II, research on primate behavior was interrupted for almost a decade, but in the early 1950s and especially in the 1960s, there was renewed interest in studies of primate behavior all around the world. Japanese primatologists' intensive and long-term studies of social behavior led to the discovery of kinship systems and cultural traditions in macaque societies. Primate behavior research in Japan, however, was originally conducted within the tradition of anthropology, and it is only later that such research established a strong connection with psychological science. The 1950s also witnessed the resumption of research with rhesus macaques on the island of Cayo Santiago, in Puerto Rico, where an American zoologist, Clarence Ray Carpenter, had established a colony of these monkeys prior to the War. The availability of genealogical information on the animals and the long-term observations of their behavior contributed, along with the work of Japanese primatologists, to the identification of the matrilineal structure of macaque society and the mechanisms underlying the acquisition of dominance.

As more information on primate social behavior became available, Harvard anthropologist Sherwood Washburn developed the conviction that extant primate species could provide important information on human origins and social evolution. He and his graduate students pioneered field studies of primate behavior in Africa and Asia, placing particular emphasis on aggressive and maternal behavior. These two topics dominated much of primate behavior research through the 1960s and 1970s. Interest in anthropology and human origins also motivated paleontologist Robert Leakey to begin long-term studies of chimpanzees, gorillas, and orangutans, which were led by Jane Goodall, Diane Fossey, and Birute Galdikas, respectively.

Psychologists' interest in primate behavior rose dramatically with the resumption of research in captivity after World War II. Harry Harlow's research at the University of Wisconsin played a pivotal role in this process. After making important contributions to the study of primate learning, Harlow concentrated his efforts on elucidating the nature of infant attachment and social development in rhesus monkeys. Harlow's well-known experiments with surrogate mothers demonstrated that the mother's ability to provide contact comfort is a more important determinant of infant attachment than her ability to provide milk, thus providing a fatal blow to secondary-drive theories of attachment. Because Harlow's work touched upon many areas of research that were very important to psychologists at that time (e.g., learning and motivation, attachment, normal and abnormal social development, the social origin of affective disorders), and because Harlow's academic career took place within psychology, during the years in which most of his work was conducted and published, primate behavior research was very well known among psychologists.

Although Harlow was very effective in promoting the importance of primate behavior research in the scientific community and the general public, the person who made the most systematic effort to conceptually integrate primatology and psychology was probably the British ethologist Robert Hinde. Hinde's interest in primate research was sparked by John Bowlby, who encouraged him to set up a colony of rhesus monkeys in Cambridge and investigate mother–infant attachment processes. From the study of social influences on the mother–infant relationship, the scope of Hinde's research was gradually broadened and elaborated into a conceptual framework for the study of social processes, which distinguished three main levels of complexity: interactions, relationships, and social structure. Hinde made important conceptual contributions to the science of social relationships, and for decades was one of the most articulate proponents of the conceptual integration between biological and psychological approaches to the study of behavior.

Thanks to the efforts of talented and charismatic scientists such as Harlow and Hinde and the success of field studies of primate behavior begun in the 1960s, primatology reached a peak in popularity in the 1960s and early 1970s. In the mid- to late 1960s, in particular, behavioral research in the United States thrived at the newly established Regional Primate Research Centers, and most research proposals to study primate behavior were readily funded by federal and private agencies. In the 1960s and 1970s, a large number of articles and books on primate behavior were published, and primate behavior research was probably well represented in all branches of scientific psychology, including developmental, social, cognitive, and clinical. The heyday of primatology, however, did not last long. In the early 1970s, that is, only ten years after the establishment of the NIH-funded Regional Primate Research Centers, there were already significant cuts to research funding.

The realization that evolutionary theory could be effectively applied to the study of social behavior in the 1960s and 1970s gave a great boost to primate research in the field. Although anthropology and psychology had been the disciplines dominating primate behavior research up to the 1970s, ecology and evolutionary biology acquired a leading role in most subsequent research. The fact that behavioral ecologists were mostly interested in questions of adaptive function whereas psychologists were mostly interested in questions of proximate causation or development of behavior was one of the several factors that contributed to the growing separation between primate behavior research and psychological science that occurred in the 1980s and early 1990s. Another important factor was the rapid progress of biological disciplines such as genetics, molecular biology, and neuroscience and the growing popularity of scientific reductionism. In particular, the success of neuroscience led to the optimistic view that many important questions about behavior would eventually be answered by studies of brain anatomy and function, thus rendering behavioral research unnecessary. One corollary of this view was the belief that comparative research with primates may not be as useful as research with other species, given the difficulty of conducting molecular work with primates.

Despite the current weakness of primatological research, in the last decade, some favorable conditions have emerged for renewed cross-fertilization between primatology and psychology. The cognitive revolution that occurred in psychology in the middle of the century was followed, a few decades later, by a similar cognitive revolution in the field of animal behavior, and primate behavior in particular. Thanks to the efforts of pioneers such as Donald Griffin and Gordon Gallup, once it became scientifically acceptable to ask whether animals have a sense of self and understand other individuals as having a mental life of their own, the field of primate cognition boomed. It became apparent that many of the questions traditionally addressed by cognitive psychologists could also be addressed, with similar or new experimental procedures, in primates as well. Therefore, research on primate cognition shifted from the study of learned behavior to the study of mental representations of the self and of the physical and social environment. Today, cognition is the branch of scientific psychology in which primate behavior research is best known and represented. Interestingly, and in line with the notion that comparative psychological research should have strong evolutionary foundations, a further impetus for research on primate cognition has been provided by the framing of cognitive investigations within ecology and evolutionary biology, which has led to a new understanding of primate cognitive adaptations, their ecological significance, and evolutionary origins.

Comparative Primate Cognition

Primate cognitive adaptations can be conceptualized as complex "behavioral adaptations in which perceptual and behavioral processes are (1) organized flexibly, with the individual organism making decisions among possible courses of action based on an assessment of the current situation in relation to its current goal; and (2) involve some kind of mental representation that goes beyond the information given to direct perception." Cognitive adaptations, and their underlying neural substrates, evolve by natural selection in response to recurrent problems posed by the physical, ecological, or social environment. Within this framework, the question can be raised as to whether the primate order as a whole exhibits cognitive adaptations that are different from those of other animals, and whether primates that are phylogenetically closest to humans show evidence of cognitive specializations similar to those of the human species.

The study of primate cognitive adaptations has involved many aspects of physical and social cognition. Primate research in the domain of *physical cognition* has addressed how monkeys and apes acquire information about the physical space in which they live and the inanimate objects in it, how information is mentally represented and processed, and how it is retrieved and used to make decisions. Free-ranging primates form spatial maps that represent the environment in which they live and use them to make travel decisions as they search for food within their home range. In the laboratory, primates exhibit knowledge of movements of objects through space and understanding of object permanence, that is, the notion that objects continue to exist and maintain their features and properties if they have been moved or hidden from view. For example, primates search for hidden objects and can solve tasks that require mental rotation of object orientation. Though primates are proficient at these tasks, there is no evidence that primates have greater understanding of space and objects relative to other mammals, nor is there evidence of significant differences among primate species (e.g., between monkeys and apes).

Other research in the domain of physical cognition has involved object manipulation tasks, in which objects are used in relation to other objects, and which require an understanding of causality (e.g., the relation between the use of the tool and the goal to be accomplished with it). Many species of primates, and especially capuchin monkeys and the great apes, are proficient tool users and also show some evidence of understanding of causality. However, primates' tool using skills have been matched or even surpassed by those of some corvid birds. Discrimination learning studies have addressed whether primates learn to discriminate particular features of objects and assign these objects to categories on the basis of similarities and differences in these features. These studies have shown that primates can not only discriminate and categorize objects but also understand complex rules underlying categorization, for example, the notion that categories of objects can be formed on rules such as identity, oddity, sameness, or difference. Similar to birds and other mammals (e.g., laboratory rats), primates also possess the ability to make accurate estimates of small quantities of items as well as the ability to solve simple tasks involving quantity conservation or summation. The exact perceptual or conceptual mechanisms underlying these skills remain unclear.

Taken together, studies of primate physical cognition have shown that monkeys and apes possess the ability to form mental representations of their space and objects, including hidden ones, but show little evidence of greater learning skills or greater understanding of the physical world and its properties than other vertebrate animals do. The strongest evidence for a potentially unique primate cognitive specialization in the realm of physical cognition involves the use of tools and the understanding of relational properties of objects including causality. This is particularly strong in large-brained primate species that face strong ecological pressures for complex food processing such as capuchin monkeys, and for all species of great apes.

In the domain of *social cognition*, early studies of primates' ability to recognize themselves in a mirror were driven by the hypotheses that mirror self-recognition indicates self-awareness and that knowledge of the self forms the basis for theory of mind. On the mark test of self-recognition, primates as a whole perform better than other animals, and apes perform better than monkeys. However, the notion that learning how to use a mirror to inspect inaccessible aspects of one's body necessarily entails possessing a concept of self has been questioned. Experimental evidence for theory of mind skills including intentionality or attribution of knowledge or ignorance to others is scarce but stronger for chimpanzees and other apes than for monkeys. Theory of mind is clearly a unique primate cognitive specialization but could be limited to the human species, and possibly the great apes. Complex forms of social learning involving emulation, imitation, or teaching have also been documented mainly in great apes,

where they are believed to form the basis for the origin and spread of behavioral traditions that may approximate elementary forms of human culture. The question of whether or not culture can be considered a cognitive specialization unique to humans or shared by other primates rests on how culture is defined and what operational criteria are used for its identification across species.

While the question of whether nonhuman primates have the ability to think about other individuals' mental states remains unanswered, it is well recognized that they excel at the task of observing other individuals' behavior, remembering past interactions, and making predictions about the future. Primates form complex social relationships with others and have knowledge and memory not only of their own relationships, but also of relationships between other individuals. Studies investigating this aspect of social cognition have assessed primates' ability to recognize kinship, dominance rank relationships, or friendships between individuals that reside in their social group. Knowledge of social relationships is used in complex cooperative and competitive strategies involving exchange of favors, alliance formation, opportunistic exploitation of social situations, and manipulation of other individuals with deceitful tactics.

Complex social strategies in group-living monkeys and apes invariably entail the exchange of vocal or visual signals between individuals. *Communication* can therefore provide a window into the primate social mind. Specifically, many aspects of communication can provide insights into social cognition, including the role of social learning in the developmental acquisition of signal production, comprehension, and usage; the extent to which signals are under volitional control and can be used flexibly; the complexity in the structure of signals; the information content or meaning of signals; the extent to which signals are combined with other signals within the same modality or across different modalities to accomplish different functions; the extent to which combinations of signals exhibit properties of human languages such as grammar or syntax; and the extent to which the production of signals is modified in relation to the presence of particular individuals (audience effects), their attentional states or current behavior, and possibly also their mental states.

The search for cognitive complexity in primate communication has often focused on vocalizations, in part because of possible direct parallels between monkey vocalizations and human speech. For example, great emphasis has been placed on the finding that vervet monkeys and other primates possess different alarm calls for aerial and terrestrial predators, and are therefore capable of semantic communication. It is now recognized, however, that this ability is shared by a number of birds and other mammals. Food calls have also been given as examples of referential signals, as according to some researchers, they convey information about the type, quantity, and location of food to other conspecifics. It is unlikely, however, that primate vocalizations about predators or food require a higher degree of cognitive complexity than similar vocalizations used by other mammals, birds, and other animals. This is because the problems faced by most primates during foraging or escaping predators are simply no different in complexity from those faced by most other animal species. Therefore, it is difficult to argue that these activities posed a special pressure to evolve higher cognitive or communicative abilities in primates.

The agonistic screams of macaques appear to elicit different responses from other group members in relation to characteristics of opponents such as their dominance rank, and representational signaling in the context of recruitment of agonistic support is an ability that might have been strongly selected for in the social environment of group-living primates. Vocalizations that are emitted in order to coordinate the behavior of group members during travel or to facilitate affiliative and bonding interactions are an even more promising area of investigation because, unlike antipredator calls and recruitment screams, these signals are not obviously associated with states of high arousal. Contact vocalizations that facilitate coordination of group movements and close-range interactions are particularly well developed in arboreal species such as New World monkeys. The complexity of vocal structure and vocal sequences in New World monkeys, however, is likely to be the result of the pressures of arboreal life rather than those of social variables. Moreover, the referential nature of agonistic screams, grunts, or other short-range contact calls has been called into question even for the Old World monkeys and apes.

Regardless of how primate calls are interpreted, there is little or no evidence that primates as a whole show complex cognitive specializations in their vocal communication abilities relative to other animals. Moreover, there is no trend toward increasing complexity in the structure, function, and use of vocal signals from the prosimians to the New World monkeys, the Old World monkeys, and the great apes, suggesting that the evolutionary increase in brain size that occurred in the Cercopithecoids and the ape lineage was not associated with increasing complexity in vocal exchanges or their cognitive substrates. Such an evolutionary trend, however, is observable in the use of nonvocal signals. In the Old World monkeys and in the great apes, there is a clear increase in the role played by facial expressions (associated with the development of complex facial musculature) relative to vocalizations. Moreover, in the great apes, there is an involvement of the arms and hands in making social gestures to a degree that is not observed in other nonhuman primates or other animals.

Although there is no good evidence that manual gestures are socially learned from others, the flexibility with which great apes use gestures in different contexts likely requires considerable developmental learning and experience. If gestures develop through a process of ontogenetic ritualization, it would require many exposures to and opportunities to perform a particular action before it becomes a gesture. If the forms of gestures are largely innate, then a period of learning when different gestures are likely to be effective (e.g., visual only when visible) would be required. Thus, it is possible that primates, and especially great apes, have evolved cognitive specializations to attend to and learn to use social variables (such as identity, visual attention, and dominance) during communication, and particularly during gesture.

The importance of development in shaping primate communication has been investigated in only a limited number of studies, and almost all of them have focused on vocal communication. Additionally, little is known about the relationships between cognitive abilities such as understanding visual attention, gaze following, and individual recognition and the structure and use of communication systems in nonhuman primates. In humans, language develops alongside a whole

range of cognitive abilities – building upon some and providing the foundation for others. The relationship between the emergence of language and other cognitive abilities is well studied in humans: similar work is needed in nonhuman primates. Comparative developmental studies are needed to understand whether and how development of one ability (e.g., understanding social hierarchies) affects or is affected by the development of communicative behaviors (e.g., using different strategies when communicating with a dominant vs. a subordinate individual). Within this framework of research, developmental studies of gesture acquisition and experimental studies of gesture use have the potential to shed new light on the social-cognitive specializations of great apes and, more generally, provide a window into the nonhuman primate mind.

See also: Evolutionary Psychology; Primate Cognition.

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