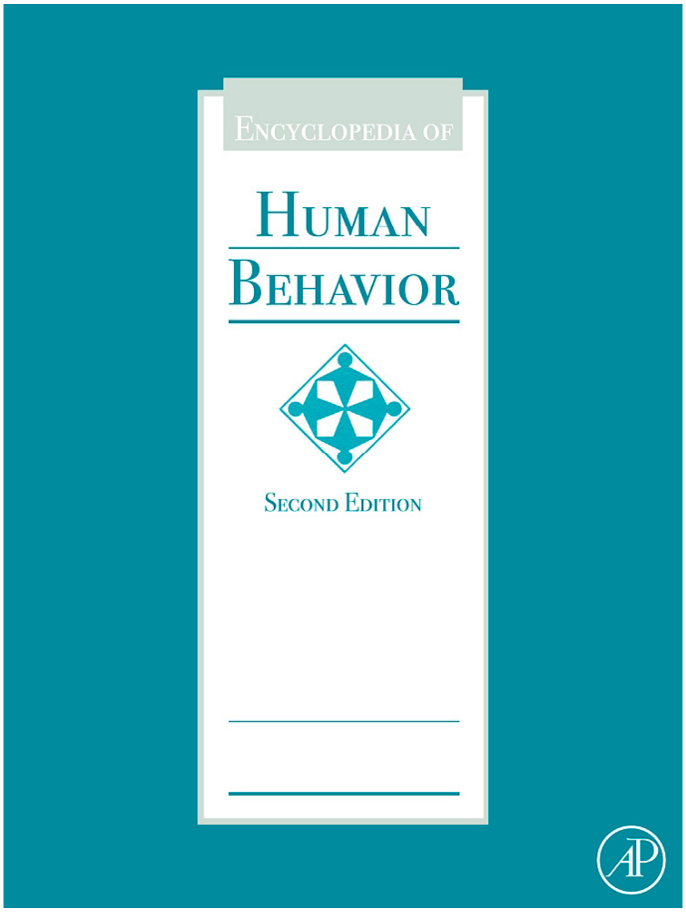

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Primate Cognition

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Glossary

Encephalization quotient The ratio of an individual's or species' brain to its body weight; humans have the largest EQ among the primates, followed by other apes and then the monkeys. Capuchin monkeys are unusual among monkeys in also possessing a large EQ.

Hominoids The phylogenetic term for the great ape species, including humans, chimpanzees, bonobos, gorillas, and orangutans. The great apes show a marked increase in the encephalization quotient as compared to other primates, except the capuchin monkey.

New World monkeys Five families of primates from Central and South America, including, Callitrichidae (marmosets and tamarins), Cebidae (capuchins and squirrel monkeys), Aotidae (owl monkeys), Pitheciidae (titis, sakis, and uakaris), and Atelidae (spider monkeys). These monkeys are typically arboreal and of smaller body size than the Old World monkeys. The New World monkeys and Hominoids shared a common ancestor ~40–50 Ma.

Nonhuman primates Any primate except humans, including prosimians, New World monkeys, Old World monkeys, and apes.

Old World monkeys Two subfamilies of primates from Asia and Africa, including Cercopithecinae (mainly African) and Colobinae (mostly Asian). These monkeys are very diverse; some are arboreal while some are solely terrestrial and range in body size from medium to large. The Old World monkeys and Hominoids shared a common ancestor ~20–25 Ma.

Physical cognition The cognitive skills used to survive in one's physical environment, including foraging skills, defense mechanisms, learning, and problem solving.

Social cognition The cognitive skills used for interacting with others, both opponents and collaborators. These skills include such things as defending one's group, navigating the dominance hierarchy, cooperating, and finding a mate.

Introduction

Cognition is the process by which a species learns, remembers, and solves problems with flexible behavior that may change depending on the situation, motivation level, and environmental pressures. Cognition in nonhuman primates is adaptive because it increases efficiency. Behavioral responses can go beyond trial-and-error learning and use problem solving and reasoning based on input from the environment, past experiences, and knowledge of the social environment. Nonhuman primate (hereafter primate) cognition is important to the understanding of the evolution of human minds, as well as a better understanding of the underlying cognitive mechanisms of primate behavior.

Humans are a primate and a member of the great apes, with chimpanzees and bonobos (to whom we are the most closely related), gorillas, and orangutans. We are next most closely related to the Old World monkeys (common ancestor ~25 Ma), followed by the New World monkeys (common ancestor ~40 Ma) and the prosimians (lorises, lemurs, and tarsiers; common ancestor ~80 Ma). While all primate species are interesting in their own right, those phylogenetically closest to humans are often studied based on the assumption that they are a better comparison to human behavior and cognition.

Cognition is commonly divided into physical and social cognition, both of which are important to individuals' success. Physical cognition addresses the skills used by primates to survive in their physical environment, including foraging skills, defense mechanisms, learning, memory, and problem solving. Social cognition is equally important to survival, as most primates are highly social, interacting with many other individuals on a regular basis. Social cognition provides skills for interacting with others, both opponents and collaborators, in situations ranging from defending one's group to finding a mate. We first focus on physical cognition, including object manipulation and tool use, features and categorization, numerosity, delay of gratification, memory, and metacognition. Next, we turn to social cognition, including social intelligence, cooperation, decision-making, social learning, communication, deception, and theory of mind.

Physical Cognition

Physical cognition is how an organism understands and manipulates its physical world. Much of this takes place in the context of foraging. The ability to locate, obtain, and manipulate food is at the forefront of survival for all species. Primates also attend to other nonfood objects they encounter in their environment.

Object Manipulation and Tool Use

Object manipulation skills likely evolved in the context of foraging, in particular, extracting and processing food. Tool use opens up further adaptive possibilities by allowing the animal to change their environmental niche. Some tool using species, including (but not limited to) primates, seem to understand the interaction of the tool with the environment; they use tools flexibly, modify tools, and even manufacture tools in novel situations.

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Ecological constraints strongly influence the degree of object manipulation. For instance, species showing more interest in object manipulation tend to consume a wider diet and use more flexible foraging techniques. Among primates, prosimians are the least exploratory of objects, possibly due to their restricted diet in comparison with the other primate orders. Monkeys show a more pronounced tendency to manipulate objects in their environments, including such behaviors as seriation, or arranging objects in a series or order. Great apes also excel at object manipulation and can even do fairly precise manipulations such as stacking objects. Human children are the most exploratory and manipulative primate species. In a study comparing juvenile bonobos and human children, the children engaged in more bimanual manipulation and tertiary relating and combining of objects, and could switch attention between objects more quickly and efficiently. In all of these cases, object manipulation and tool use clearly interact.

Tool use incorporates the use of objects in relation to each other and moves beyond simple object exploration. The use of tools demonstrates the ability to recognize the affordances of objects, rather than just their physical features. Tool use requires flexibility and complexity as well as mental representations. Flexibility and complexity are shown by using two or more tools in a sequence, such as when chimpanzees use one tool to open a beehive and another tool to extract honey. 'Metatools,' or using a tool to make another tool, are another form of flexibility and complexity. This may include chimpanzees using a support stone to level an anvil before nut cracking with a hammer stone. Mental representations are shown when a specific tool is chosen for a certain situation without overt trial-and-error and when an individual can adapt a normal pattern of tool use readily in a new circumstance. Both of these cases of mental representation show the use of insight or foresight.

Only some species appear to use tools habitually, including some monkeys (e.g., capuchins) and great apes. These species can make and use tools flexibly and may be relying on some form of mental representations. In captivity, some monkeys use tools even if they are not known to do so in the wild. This could be due to lack of data from the field or ecological constraints, in which they only develop tool use if it is necessary for their habitat. Primates are not the only tool using species. Many corvids spontaneously make or modify tools, rivaling primates in their skill. There is also some evidence of elephants and dolphins using tools.

Tools also provide information about how individuals understand causal relations. The classic observation was made by Kohler in 1925 after working with the chimpanzee Sarah. She showed insight learning in several contexts by fashioning a tool with no previous experience or exposure (e.g., fitting two sticks together to make one long stick or piling up boxes to climb to acquire a banana). Monkeys too appear to be able to understand simple causal relations, particularly in the context of the structure of social interactions (e.g., using vocalizations to interpret events outside their immediate visual field). However, monkeys have repeatedly failed more complex causal tasks, such as the trap tube task, which apes can solve, indicating that apes may understand causal relations better than monkeys.

Features and Categorization

Identifying objects and categorizing types of objects allows individuals to organize and simplify their worlds. These abilities are often tested with discrimination learning experiments, such as learning sets and delayed response tasks. Primates have demonstrated the ability to remember stimuli, categorize objects and phenomena, and learn general rules to use in novel situations. In a classic experiment by Harlow, monkeys learned to choose a correct (rewarded) choice in fewer trials as they gained experience. He argued that this transfer of learning across problems suggested some kind of conceptual mediation, thus speeding the process of learning in subsequent trials. Categorization also extends to social stimuli. In their natural environment, primates classify food items or other things, such as individuals as opponents, kin, or potential mates.

Primates are also able to conceptualize. For instance, primates can place objects into categories based on shared physical features, that is, identifying all triangles as similar, which has been described as the ability to conceptualize based on characteristics in common. In another example, match-to-sample tasks indicate that individuals can match two items utilizing a relational concept more advanced than stimulus-response learning. Several species of primates are able to generalize their knowledge of relational sameness and difference to novel stimuli. In addition, chimpanzees appear capable of using relations-between-relations to solve analogy problems. Although abstract discrimination skills are present in many species, primates typically generalize more rapidly and more widely than other species, indicating a selective premium on this type of conceptual learning, despite a similar predisposition to attend perceptually to physical features of the environment.

Finally, primates may also classify items based on an understanding of natural concepts that are more ecologically relevant. Classification has been extensively studied in a laboratory setting; a typical paradigm requires individuals to sort objects into groups based on shared characteristics. These classifications are not based on any shared physical features, but rather on the things that objects afford. Object sorting is a more difficult form of categorization because it requires both the comparison of objects and the manipulation of the objects according to previously made judgments. Chimpanzees show this ability to classify objects based on their functionality rather than physical similarities when they sort objects into superordinate categories, such as foods and tools, using symbols. Several primate species have been found to be capable of sorting objects based on various qualities, including color and kind, and most do so with little to no training. In fact, language-trained apes are able to sort objects more efficiently than 1- and 2-year-old human children and equivalently to 3- and 4-year olds.

Numerosity

Primates are very adept at quantity discriminations. They make use of these to complete everyday tasks such as foraging (e.g., estimating the quantity of food items available) and social interactions (e.g., estimating the number of potential mates or opponents). Such abilities do not necessarily require a concept of numerosity; they could be based purely on perceptual mechanisms. However, a purely perceptive mechanism cannot explain experimental results in which quantitative assessments are made when sets are spatially segregated or presented sequentially. For instance, primates can discriminate quantities when they are presented item-by-item, or when they see the items as they accumulate. Apes can also discriminate when food presentation differs spatially or temporally. These types of judgments seem to require an analogical system, rather than a perceptual estimation mechanism.

In experimental studies, primates are very proficient at choosing a group with more items from among several options (cardinality). Apes also appear to use ordinality, which refers to understanding the sequence of these labels or numbers. One chimpanzee, Ai, trained in numerical computer tasks showed evidence of using planning, executing, and monitoring phases when ordering numerals, much like humans.

Primates may also use transitivity, or the ability to recognize a sequentially ordered relationship. The ability to make transitive inferences may be crucial for animals living socially because it allows them to make judgments based on social ranking without having to learn each possible dyadic relationship individually. Humans, monkeys, and pigeons all perform well on serial-order tasks. However, humans and monkeys form mental representations that are well-organized into an associative chain while pigeons rely on discrimination cues. Nonetheless, sociality is clearly critical; in a study comparing highly social pinyon jays and relatively nonsocial western scrub-jays, pinyon jays learned to follow and assess relationships more quickly and accurately than western scrub-jays, indicating that there is more at work than phylogenetic distance from the primates. These studies support the social complexity hypothesis, which states that animals living in highly social groups should display more advanced cognitive skills in the domain of group living.

Delay of Gratification and Planning

Delay of gratification is the ability to wait for a better outcome, and is important in planning and foresight of goal-directed behavior. Such self-control may be particularly useful in primate foraging decisions, as individuals who understand the benefit of postponing a behavior instead of acting on it immediately may reap better rewards in the future. Although delay of gratification exists in nonprimate species such as dolphins, primates appear to be better at inhibition, possibly because of their higher encephalization quotient.

Two typical methods of assessment are the smaller-sooner/larger-later paradigm and the accumulation paradigm. The smaller-sooner/larger-later paradigm assesses an individual's ability to inhibit the impulse to take a smaller but sooner reward and instead wait for the larger but later pay off. The accumulation paradigm examines the individual's ability to inhibit reaching for rewards in order to allow them to accumulate. Studies employing these methods find a relationship among self-control, ecology, and life history. For instance, primates who live in fission–fusion groups show greater inhibitory skills than those in more cohesive primate social groups. This is possibly because social complexity seen in the fission–fusion societies supports higher cognitive abilities, such as inhibition, which is beneficial in a fluid social environment. Feeding ecology also plays a role. Among callitrichids, gum eating marmosets delay longer for food rewards than insectivorous tamarins. This differential ability likely evolved because marmosets must wait a period of time for the gum to exudate from trees, while tamarins must act quickly and impulsively to catch their insect prey.

The ability to delay gratification may function to increase planning. Apes engage in spontaneous planning behaviors, such as caching, or even manufacturing, tools for use at a later date. This indicates mental foresight of upcoming events. Primates may also use planning in their social interactions with conspecifics. For instance, chimpanzees gather stones to throw at human observers, and other chimpanzees have been described as planning an attack on another individual at night while the caretakers were gone. Finally, while the mechanisms for delaying gratification are largely unknown, primates use many techniques that humans do to increase their ability to wait. For instance, chimpanzees practice self-distraction with objects available in the environment, which allows them to wait for longer periods of time.

Memory

The ability to remember certain elements of the environment and information from one's social group is an important part of a primate's world. We will further discuss memory among social groups later (see section 'Social Cognition'); for now we focus on how memory serves primates in their physical environment.

Primates, like many other animals, must remember the locations of what they are seeking (e.g., the location of ripe food, water, or sleeping sites) and understand where they are in relation to other sites. Primate social groups may cover an extensive range throughout their day and must remember their environment in order to efficiently move throughout their territory and utilize its resources. Some primates travel up to 10 km a day and make use of cognitive mapping skills, or the ability to create and remember a mental representation of the spatial environment, in order to successfully manipulate their environment. Optimal foraging theory suggests animals make use of least effortful routes when foraging, minimizing effort while maximizing gains. Apes, Old World monkeys, and New World monkeys have been shown to use cognitive mapping while foraging both in experimental lab studies and in the wild.

Primates also show the ability to remember different entities within the laboratory. Chimpanzees can recall Arabic numbers in a memory task with an equal or greater success rate than novice undergraduate students. Monkeys can remember serial lists across various sensory domains, including photographs and auditory lists, and when items vary. Monkeys also appear to be able to access their memories to judge their own knowledge. In laboratory studies, monkeys avoid memory tests when their knowledge is lacking and they act spontaneously when they have the knowledge that is needed.

The goal-directed behavior seen in primate spatial movement is not only suggestive of cognitive mapping, but also episodic memory. Episodic memory is the ability to recall specific events in an individual's lifetime. It has been suggested that episodic memory is a uniquely human trait and nonhuman animals do not possess the capability of traveling back in time to a specific event. Experimentally, it is not possible to assess whether primates experience feelings of 'pastness' as is described in human accounts of episodic memory; so instead, nonhuman animal studies investigate 'episodic-like' memory, or the individual's ability to recall what, where, and when information. There is evidence for these episodic-like memories in apes and monkeys, but also in mice and scrub jays, indicating a fairly widespread ability. However, other species' episodic memory may differ from our own; for instance, in some tasks the time frame is relatively short (10 s).

Metacognition

Metacognition is the ability to monitor and adaptively control one's cognitive processing or thinking about thinking. Self-awareness of one's memory serves the function of allowing individuals to avoid situations where they lack knowledge which is needed. Although research in this area in nonhuman species is relatively new, it is clear that species beyond humans are also aware of what they do and do not know.

In a typical metacognition task, subjects are given a series of increasingly difficult discriminations but can indicate that they do not know. Old World monkeys reliably perform very well, choosing the uncertain response more often when the discriminations are more difficult. All great ape species demonstrate metacognition in a task in which they tried to collect necessary information that was missing before solving a task, such as seeking out the location of food in a tube by looking into the tube before making a decision.

New World monkeys have not performed well in most metacognition tasks. However, some capuchin monkeys recently demonstrate the capacity to opt out of a memory test based on past performance suggesting they are also able to make judgments on their knowledge. Nonetheless, the monkeys do not appear to be able to monitor the detailed contents of their short-term memory as well as Old World monkeys and apes. Although additional research is needed both within the primates and in other taxonomic groups, it appears that there are taxonomic differences which are consistent with other cognitive differences between the primates.

Social Cognition

Primates are good psychologists in their own right. Because most species are highly social, they must be able to interpret and predict others' behavior to maximize their own fitness. They must be able to recognize individuals and their relationships to oneself, recognize others' relationships, make judgments based on their knowledge, and use past experiences to predict the future. In order to do this, they appear to use mental representation of social knowledge and the properties of social relationships beyond simple associations.

There are several hypotheses for the evolution of advanced social cognition. First, it may be that the social pressures themselves drove the evolution of social cognition. The Social Intelligence hypothesis suggests the evolution of intelligence in primate species is a direct result of group living; intelligence has evolved in response to social living and the complexities that arise with it. The related Machiavellian Intelligence hypothesis argues that the brainpower needed to outmaneuver one's group mates motivated the advanced cognition seen in primates. In this case, cognition is argued to have arisen through individuals' need to cooperate, deceive, and manipulate. Ecological pressures may also have shaped primate intelligence, in tandem with social pressures. Most apes, including humans and some monkeys, live in dispersed social groups or fission–fusion societies (e.g., spider monkeys, baboons, and chimpanzees); this system is socially demanding and is argued to have selected for even more advanced cognition in these species.

Cooperation

Many species cooperate on a regular basis, including with unrelated individuals, or even with individuals of other species. There is clearly adaptive value to cooperation, although the reasons for the evolution of this behavior, and its attendant proximate mechanisms, are still the topic of much debate. In general, cooperation is believed to evolve in the context of indirect fitness (e.g., kin selection), mutual encounters in which there is no risk of defection (e.g., it is in each individuals' benefit to cooperate in each interaction), and in reciprocal interactions. Although all of these situations increase fitness, this latter is the most difficult to explain as there are incentives for individuals to not cooperate, or defect. Cooperation is widely present in ape and monkey species, occurring in foraging contexts (e.g., cooperative hunting) and social contexts, such as the coalitions and alliances used for group defense, dominance, and mating. Several factors seem to play a role in whether or not cooperation occurs. These include whether the cooperative opportunity is intuitive, the level of social tolerance among the interactors, and the structure of the payoffs.

Although it has been argued that reciprocal altruism rarely, if ever, occurs in nonhuman animals because it would require too many cognitive mechanisms, such as individual recognition and memory, many primates meet these criteria. Moreover, reciprocity and interchange (the exchange of different commodities) have been demonstrated in numerous situations in several species of primates. This is true in apes and monkeys, although there is variation between different species. In the field and in observational studies, reciprocity is common in grooming and food sharing, as well as interchanges among grooming, support, food, and mating. Most interactions occur over fairly long-time scales, making this behavior somewhat difficult to study experimentally. This issue of time scales as well as the fact that partner choice (the ability to choose one's partner) appears to be a critical component of reciprocity, may explain why contingent reciprocity has been so difficult to elicit in the lab.

Finally, not all instances of reciprocity need be cognitively complex. Although reciprocity may involve tit-for-tat and calculation, Brosnan and de Waal propose three types of reciprocity which vary on the requirement for calculation. At its simplest, cooperation may be symmetry-based, with reciprocity emerging based on individuals' relationships. At the next level, attitudinal reciprocity, behavior is contingent but not based on explicit calculation; instead individuals who receive favors feel a positive effect, which leads them to return the favor (or reciprocate). Finally, calculated reciprocity is both contingent and, as the name implies, calculated. Although much cooperation research, particularly among the primates, focuses on the cognition required for cooperation to function, it is clear from studies of other species that quite complex cooperation can exist with little-to-no cognition, as, for instance, among the castes of eusocial species or among cleaner fish mutualisms.

Decision-Making

Primates make myriad decisions on a day-to-day basis. They must decide, for instance, how to allocate their time, where to forage, and which foods to consume, and which partners to seek out and which to avoid. All of these decisions require individuals to evaluate costs and benefits, but many may also require them to explicitly include risk or relative payoff in their decision calculus. Below we discuss two of the better studied situations in which decision-making requires these additional considerations, inequity and 'irrational' decision-making.

Although it has been known for years that humans dislike situations of inequity, only recently has this been demonstrated for other species. This behavior is closely linked to contrast effects, or violation of expectation, but in this case, the expectation is based on what a conspecific received, rather than one's individual experience. In studies comparing how individuals respond when they receive a less good outcome than that of a conspecific, both capuchin monkeys and chimpanzees often refuse foods they typically like if a partner receives better food. This response occurs only in the context of a task of some sort and is limited to differences in outcome; differences in the effort required to achieve an outcome do not lead to these negative responses. This response is also affected by an individual's sex, rank, and relationship to their social partners. Inequity is hypothesized to be a mechanism which functions to support cooperation by allowing individuals to identify partners who are not sharing the outcomes.

Of course, on the surface, turning down an outcome because it is less than a partner's seems irrational, or counter to one's immediate interests. Other behaviors, such as loss aversion and the endowment effect also meet this criterion, leading to a surge in research on irrational decision-making and cognitive biases in primates. For instance, several species of apes and monkeys show an endowment effect, or a tendency to value what is in their possession more than they valued the same item prior to ownership. Primates' interest in increasing their outcomes interacts with risk, likely causing them to value what they have (a certain outcome) over what they could obtain (a risky one). This response occurs for foods, but not for nonfoods, indicating that the evolutionary salience of the item affects decision-making. This may explain some of the variation in the effect in human studies. Supporting this, capuchin monkeys also show loss aversion, a tendency to avoid gambles framed as losses, but not those framed as gains. In these decision-making situations, studying other species may help us better understand how these responses evolved in all primates, including humans.

Social Learning

Primates learn a great deal of information from others. Learning from conspecifics allows individuals to obtain information quickly, without potentially costly trial-and-error. This may include learning basic information, such as the relevance of a specific location or stimulus (local or stimulus enhancement) or more detailed information, including procedures (copying) and goals (emulation). At its most basic, social learning exists among all of the primates, including prosimians, as well as many nonprimate species. The most complex form of social learning is argued to be imitation, in which individuals learn others' goals and the procedures used to reach these goals. In fact, comparative studies indicate that humans do more imitation than other species (who rely on emulation or less cognitively complex mechanisms). Humans appear to have been selected to imitate exactly, perhaps due to our proportionally greater reliance on socially transmitted information.

Social learning may also lead to more advanced phenomena, such as culture and teaching. There is little evidence for teaching among species other than humans; the mechanism for social acquisition among other species seems to be primarily up to the learner, rather than the model. However, there is evidence for social traditions or cultures in primates, including both monkeys and apes. There are now studies on several species, including nonprimates, showing evidence for behaviors which differ between groups, and cannot be explained by genetic or environmental factors. This leads to the assumption that the behavior must be transmitted socially. For instance, different chimpanzee populations have their own methodology for ant fishing, and some crack nuts while other groups, with the same opportunities for nuts and the availability of potential tools, do not. More recent studies implicate mechanisms such as conformity and prestige in affecting social transmission in primates, as they do in humans.

Communication

Communication is an integral part of daily life in socially grouped primates; it is used to convey information and to influence others' behavior. Primates communicate about many things, from the location of food and the presence of predators to an individual's emotional state and intentions. Communication occurs through several modalities, and different modalities can be used in combination (e.g., vocal and nonvocal communication). Nonvocal communication involves transmission of information through gestures, body posture, or facial expressions. One of the major facilitators of nonvocal communication in primates is the face, which provides information on age, sex, individual identity, underlying emotions, and impending behavior. Recent studies on face perception indicate similar perceptual processes in nonhuman primates and humans, suggesting perceptual mechanisms in facial recognition are preserved throughout the primate lineage.

While faces may be particularly expressive, much communication also takes place through gestures. Some have even argued that gestural communication was the first means of communication in our early human ancestors. Extensive gestural communication seems to be limited to apes and humans, suggesting a shift toward a more flexible and intentional form of communication in the Hominoidea lineage. Gestures are predominately produced together with another form of communication, either facial expressions or vocalizations. This multimodal communication is beneficial because individuals gain greater flexibility, more amplification, and greater complexity in signal output. Multimodal communication in which gestures are produced along with vocalizations is also seen in human children, and seems to precede language development.

Finally, much primate communication is vocal. There are three primary views on the evolution of vocal communication. The first of these is the classical ethological view that vocalizations evolved because they could change a listener's behavior by acting on the salience of acoustic events and the listener's capacity for affective learning. A second view is that signals act as representations of objects or external events, rather than conveying a signaler's motivational state. This view was prompted by Cheney and Seyfarth's work which indicated, among other things, referential alarm calls in vervet monkeys. Finally, the affect-induction view is that nonlinguistic vocal communication influences the behavior of others through changing their affective state. In this case, calls are not always associated with particular contexts and may not have a meaning-based interpretation. Unlike the previous two theories, this theory puts the focus on the listener's affective state, rather than the vocalizer's. Thus far, all of these theories have at least some support.

There is extensive debate over the presence of language or language-like skills in other species. As discussed previously, the gestural origins of language theory suggests that gestures were the starting point for human language. It is also suggested that language emerged from referential vocal signaling in primates. At the most basic level, language evolution may go even further back than the primates. Recent evidence using looking-time tasks indicates that other species, including birds and primates, can understand basic grammar-like structures. However, humans are unique with respect to language. Historical attempts to teach language to other species, including nonprimates, indicate that while they can learn to communicate using symbols or sign language and achieve quite impressive outcomes, including vocabularies of hundreds of words and syntax comprehension, their language never reaches the degree of proficiency seen in humans.

Deception

Deception allows individuals to manipulate another's behavior for their own gain. In tactical or functional deception, an individual produces a signal outside of its typical context in order to affect listeners' behavior. While deception is meant to change others' *behavior*, it is not clear if the signaler intends to create false *thoughts or beliefs* in others. Deception is, by definition, rare if it is to be effective, making it rather difficult to study experimentally. Nonetheless, good evidence exists for at least functional deception in primates.

Deception can be passive or active. In passive deception, an animal refrains from a particular behavior so others will not detect their presence or actions, for example, hiding facial expressions or erections, or withholding food calls. Although such behavior is 'passive,' it may indicate that the animals have awareness that they can manipulate their communicative displays. On the other hand, individuals may also actively mislead or provide false information to others. False alarm calls are a common form of active misleading. Cheney and Seyfarth report a vervet monkey giving an alarm call in the middle of an intergroup encounter (but in the absence of a predator) that stopped the dispute when the combatants fled. Capuchin subordinates use alarm calls to distract more dominant individuals during competitive situations, reducing some of the costs associated with competition for food in the wild. Although these forms of deception function to manipulate others' behavior, there is no evidence that the intention is to manipulate their psychological states.

Finally, there is some evidence for counterdeception, or individuals taking active countermeasures against a conspecific's deceptive act. For instance, others may learn to avoid the calls of deceptive callers in food or aggressive contexts. In an experimental study involving chimpanzees, one chimpanzee in a group knew the location of hidden food and soon learned to keep the food's location a secret to avoid having it stolen by her ignorant partner. The ignorant chimpanzee then began to follow the knowledgeable chimpanzee, ignoring her attempts at misleading, indicating that he anticipated her attempts at deception. In other experimental procedures, chimpanzees have learned to withhold information – and even provide false information – to competitive human experimenters who do not provide food to the subject in experimental tasks.

Theory of Mind

Theory of mind is the ability to reason about the mental states of both the self and others. The attribution of mental states allows one to know about other's beliefs, emotions, and intentions. Individuals capable of attribution have a competitive advantage because they can predict future behavior, generalize their knowledge, recognize ignorance in others and choose to reveal or withhold information. In a primate's world, the better social strategist, who used their knowledge to their own and their kin's benefit, would have the advantage. Whether or not primates actually know about the psychological states of others is heavily debated.

A basic prerequisite for theory of mind is self-awareness, or viewing the self as a social agent. There is a distinction between conscious self-awareness and self-recognition. Self-awareness is being aware of one's own state of mind and using this to predict and explain one's own and others' behavior. Self-recognition is distinguishing self from others but does not imply any awareness of doing so. Initial research focused on self-recognition. First developed by Gallup, the mirror self-recognition (MSR) test gauges self-recognition in young children and primates. The individual in question receives a painted mark on his/her forehead and then is shown a mirror. If they recognize themselves, they should show behavior directed at the mark, such as touching it, when exposed to the mirror. Critically, they must also act differently than when a 'sham' mark that they cannot see has been placed on their head, to rule out the possibility that tactile, olfactory, or other cues are at work. These studies have demonstrated that chimpanzees and other apes recognize themselves in the mirror, as do elephants and dolphins. Monkeys do not show evidence of self-recognition; however, they can use mirrors to solve problems and they do not treat their mirror image in the same way as they treat a stranger.

Initial attempts to test for further abilities were negative. A series of studies were run to test whether chimpanzees would recognize when a human was and was not able to help them in a task (e.g., would they be able to understand the experimenter's view of the world). These studies presented chimpanzees with two containers, one of which contained a hidden food item, and allowed them to choose between experimenters to obtain the food for them. One of the experimenters was in a position to know where the food was, while the other was not (e.g., their face was covered, their eyes were averted, or they were facing backwards). Chimpanzees consistently failed to discriminate between the experimenters.

On the other hand, others have found evidence that nonhuman primates, especially chimpanzees, go beyond behavioral rules and understand others' goals and possibly intentions, thus possessing aspects of theory of mind. First, these initial studies have been run in situations which do not rely on the chimpanzee expecting the human to collaborate, to very different results. For instance, when chimpanzees are trying to steal food, they fail to do so more often when the experimenter is able to see them versus unable to see them. Moreover, when the experimenters back is turned, chimpanzees reliably choose options which do not alert the experimenter (e.g., a door which does not squeak), indicating an understanding that nonvisual cues may also alert a competitor. Moreover, additional studies demonstrate that chimpanzees, like human children, understand others' intentions by reacting to a goal rather than the actual behavior of the human experimenter. For instance, chimpanzees will help an experimenter reach an out of reach object, and both chimpanzees and orangutans react differently to a loss of food when it appears to be intentional versus accidental.

No monkey has been shown to succeed in any of these theory of mind related tasks. Although monkeys seem to have a sense of self within their social group, they do not impute motives to others, cannot imitate, do not actively teach, show no evidence for self-awareness (they do not pass mirror tests) and do not appear to reflect upon their own knowledge. On the other hand, they can deceive each other, although functional deception may not require an understanding of others' minds (see section 'Deception'). However, apes possess elements of a theory of mind; they appear to know others have beliefs and they can alter those beliefs, understand others' goals and motives (can imitate), deceive, understand others' knowledge and lack thereof, but cannot attribute false beliefs, and do not engage in active pedagogy. Thus, humans' full theory of mind appears to be an extreme along a continuum, rather than a uniquely human trait.

Conclusion

The study of primate behavior is vital to our understanding of the evolution of cognitive mechanisms. Primates must adapt to both their physical and social worlds and do so flexibly by employing cognition. In order to thrive in their physical environment, primates must be able to successfully manipulate their resources, which can include problem solving and planning. They must also successfully coexist in social groups and maintain relations with conspecifics. By delving into the minds of our close evolutionary cousins, we learn not only how they navigate in their own world, but how we evolved to navigate in ours.

See also: Animal Cognition; Comparative Primate Psychology; Episodic Memory; Equity Theory; Gestures; Memory; Nonverbal Communication; Social Cognition.

Further Reading

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http://www2.gsu.edu/~wwwcbs/research.html – Dr. Sarah Brosnan's CEBUS lab at Georgia State University.

http://www2.gsu.edu/~wwwlrc/ – Language Research Center at Georgia State University.

http://www.eva.mpg.de/english/index.htm – Max Plank Institute for Evolutionary Anthropology in Leipzig, Germany.

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