Topics in Cognitive Science 2 (2010) 407–419

ISSN: 1756-8757 print / 1756-8765 online
DOI: 10.1111/j.1756-8765.2010.01099.x

Primate Cognition

Amanda Seed, Michael Tomasello

Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology

Received 16 April 2009; received in revised form 22 September 2009; accepted 23 October 2009

Abstract

As the cognitive revolution was slow to come to the study of animal behavior, the vast majority of what we know about primate cognition has been discovered in the last 30 years. Building on the recognition that the physical and social worlds of humans and their living primate relatives pose many of the same evolutionary challenges, programs of research have established that the most basic cognitive skills and mental representations that humans use to navigate those worlds are already possessed by other primates. There may be differences between humans and other primates, however, in more complex cognitive skills, such as reasoning about relations, causality, time, and other minds. Of special importance, the human primate seems to possess a species-unique set of adaptations for ''cultural intelligence,'' which are broad reaching in their effects on human cognition.

Keywords: Primates; Cognition; Culture; Causality; Theory of mind

1. Introduction

Thirty years ago, in 1980, we knew almost nothing about the cognitive skills of our nearest primate relatives. The study of animal behavior in the middle of the 20th century was dominated in America by behaviorism and in Europe by ethology, neither of which was much interested in cognitive processes. Indeed, the study of cognition was suspect in both paradigms, considered by many to be an inherently anthropomorphic enterprise. And so the cognitive revolution came only slowly to the study of nonhuman animals.

In 1980 what we knew about primate cognition was essentially as follows: (a) a few things about their problem-solving skills from the studies of Köhler (1925) and others conducted before the rise in behaviorism and ethology; (b) a fair amount about their skills of discrimination learning from the behaviorists (e.g., Harlow, 1944); (c) some interesting facts

Correspondence should be sent to Michael Tomasello, Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04102 Leipzig, Germany. E-mail: tomas@eva.mpg.de

about their behavior in the wild concerning such things as tool use and making (e.g., Goodall, 1968); and (d) a few other isolated facts that could be interpreted cognitively (e.g., on communication: Menzel, 1971; Seyfarth, Cheney, & Marler, 1980). However, there were few if any systematic cognitive investigations going on at this time. In 1980 most of the discussions about primate cognition in the cognitive sciences were focused on how to interpret the newly emerging ''ape language'' studies (e.g., Terrace, Petitto, Sanders, & Bever, 1979) and the single ape ''theory of mind'' study (Premack & Woodruff, 1978), but this was work done with special ape individuals who were highly trained by humans.

In the past 30 years, new theoretical paradigms have emerged that seek to investigate the natural cognitive skills of primates and other nonhuman animals in their evolutionary context, and many different programs of systematic research into primate cognition have been, and are being, conducted within these paradigms. The most significant developments theoretically have been the following: (a) the recognition in such relatively new paradigms as cognitive ethology and evolutionary psychology that specific cognitive skills evolve in response to specific ecological challenges—and so ethologically valid tests in the context in which those skills probably evolved are the best way to tap into them; and (b) the recognition that a primary ecological challenge in the evolution of cognitive skills is the complex social world of competition and cooperation that individuals must learn to navigate (Humphrey, 1976). These theoretical developments rest, of course, on the basic Darwinian assumption that cognitive skills are not the exclusive province of humans, but rather they are phenomena of the natural world that may arise under certain specifiable conditions in any animal species. A particularly dramatic illustration is recent work uncovering surprisingly complex cognitive abilities—including everything from flexible tool use to rudimentary mindreading—in some species of birds (reviewed in Seed, Emery, & Clayton, 2009). These skills arose evolutionarily in complete independence of primate and human cognition, but they show many of the same characteristics, including mental representation and flexible decision making.

Starting from these modest empirical beginnings and with the gradual emergence of these new theoretical paradigms, research into primate cognition in the past 30 years has flourished. It has established beyond a reasonable doubt that many of the most basic skills of human cognition are already possessed by our living primate relatives—although there are still some controversies, of course, and many species still need to be tested. At the same time, the human primate displays a number of species-unique cognitive skills that very likely have evolved only relatively recently from these general primate beginnings, as humans have developed their distinctively cultural way of life.

2. Primate cognition of the physical world

Virtually everyone who has studied the matter would agree that all primates, including humans, perceive the same basic physical world of objects (and at least some categories and quantities of objects) arrayed in space. There is more controversy about their understanding of events arrayed in time and possible causal interconnections among them. In what follows we look at the most recent research (for background, see Tomasello & Call, 1997).

2.1. Objects and space

All primates perform well on Piagetian object permanence tasks up to Stage 4 or 5, demonstrating an understanding that objects continue to exist in their last seen location even when they are no longer perceived—and some even follow an object's invisible movements as its container moves to new locations (Barth & Call, 2006; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007). The primates that have been tested (apes and rhesus macaques) also show an understanding of object identity based on property/kind information (perhaps evidencing sortal concepts): If they see an object hidden in a location, they continue to search for it after they have retrieved a different kind of object from that location but not after they have retrieved an object of the same kind from that location (Mendes, Rakoczy, & Call, 2008; Phillips & Santos, 2007; Santos, Sulkowski, Spaepen, & Hauser, 2002). Combining these two skills, orangutans are able to quickly learn which of 20 different locations contain which of two different types of food (Scheumann & Call, 2006).

There is also evidence that primates (and many other animals) form perceptual categories. They typically demonstrate this after much training, but rhesus monkeys are able to sort novel photographs into ''animals'' and ''food'' spontaneously with a level of accuracy similar to that of humans (Fabre-Thorpe, 2003). Nonhuman primates also quantify objects, going well beyond perceptual subitizing. For example, they can identify the larger quantity of two sets of objects (food) even if the two sets are formed by an experimenter placing the items into opaque buckets one at a time—so that their choice of bucket must be based on a memory of the placing events (e.g., Evans, Beran, Harris, & Rice, 2009; Hanus & Call, 2007; Lewis, Jaffe, & Brannon, 2005). Some ape species also recognize that continuous quantities are conserved across transformations of container shape (e.g., Beran, 2008; Suda & Call, 2005).

2.2. Causality

The notion of causality encompasses many different things. The primate literature has focused mainly on the understanding of how the use of a tool brings about its effect. In many studies a variety of primate species differentiate—through visual inspection alone without any direct learning experiences—between effective and ineffective tools for obtaining an out-of-reach object (for a review, see Seed & Call, in press).

However, Povinelli (2000) conducted a series of well-known experiments with chimpanzees in which they failed on several tasks to transfer their tool-use skills to novel variations in a way that suggested they were using perceptually based strategies to solve the task rather than a knowledge of the causal role of object properties (such as solidity, connectedness, and rigidity). However, more recent experiments have used modified methods (mostly aimed at reducing inhibition demands) and found that at least in some contexts chimpanzees do have such knowledge. One modification removed the tool-using component entirely and found that chimpanzees quickly learned to move a reward along a solid surface rather than over a trap, and transferred this solution when the perceptual cues in the original task were confounded or changed, implying the use of abstract causal knowledge rather than arbitrary perceptual cues (Seed, Call, Emery, & Clayton, 2009). Similarly, wild capuchin monkeys, which prefer to use large heavy stones to break open nuts, were able to select the heavier of two artificial stones in an experiment when the stones were the same size and even when the heavier stone was the smaller of the two (Visalberghi et al., 2009).

Other studies have used novel problems involving other kinds of causal principles. For example, in one study chimpanzees inferred the location of food based on an understanding that its ''weight'' should cause one end of a balance beam to move lower down—with no previous experience of balance beams (Hanus & Call, 2008). The use of strategies based on perceptual regularities could not account for their performance because they did not choose the lower cup when, after hiding the food, the experimenter tipped the balance by hand. In another study, several species of great apes knew that a piece of food was most likely under a tilted board rather than one that was lying flat, suggesting some knowledge of ''support'' relations (Call, 2007). Finally, apes and capuchin monkeys were able to infer which of two cups contained a single piece of food on the basis of hearing no sound when one was shaken. This is a kind of reasoning by exclusion (analogous to disjunctive syllogism in formal logic): (a) the food is in one of the cups; (b) it is not in this one (inferred from lack of sound—causal reasoning); (c) so then it must be in the other one (Call, 2004; Sabbatini & Visalberghi, 2008). Again, they did not find the food when given an auditory cue that was reliably but arbitrarily linked to the location of food, ruling out a task-specific learning account. Overall, taken together these studies suggest that many primate species have an understanding of at least some causal principles, without extensive learning experiences in particular tasks.

2.3. Time

Many theorists believe that nonhuman animals are ''stuck in time'' in the present moment and cannot recall specific past experiences (episodic memory) or anticipate future states (future planning; e.g., Suddendorf & Corballis, 1997, 2008). However, in a recent study orangutans and bonobos learned very quickly to save a tool in anticipation of future use (i.e., take it with them and save it for up to 14 h; Mulcahy & Call, 2006). A subsequent study reinforced the case for planning, showing that chimpanzees and orangutans reliably chose a novel tool over a grape, and brought it back 70 min later to obtain a larger reward (Osvath & Osvath, 2008). It would thus seem that at least some primate species have the ability to mentally represent possible future events and so to plan for them.

2.4. Beyond the information given

Nonhuman primates have the same basic perceptual organs and brain organization as humans, and so it is only natural that they live in the same basic phenomenal world as do humans. And there is also little disagreement that they also go beyond this to cognitively represent absent objects, spatial relations, and some categories and quantities. A number of researchers want to draw the line at an understanding of abstract causal and temporal relations and so explain nonhuman primates' impressive performance in some experiments in terms of evolved, domain-specific expectations about what perceptual features are likely to be salient in a given context. However, we see no evidence in the data for any such clear line at precisely this place.

3. Primate cognition of the social world

In the study of primate social cognition (‘‘theory of mind,’’ broadly construed) pretty much everything is controversial. A number of researchers (most recently, Penn & Povinelli, 2007) believe that nonhuman primates do not understand anything about the mental states of others; they operate with perceptually based rules—‘‘behavior rules’’—based on associations between antecedent and consequent behavioral events and tuned by inborn predispositions. These rules, they argue, may be abstract in the sense that a general principle is drawn from several exemplars, for example, ‘‘if a competitor is out of sight when food is hidden he will not try to get that food,’’ but crucially these rules do not involve attribution of mental content of the sort ‘‘if a competitor is out of sight when food is hidden *then he has not seen that food*, and will not try to get it.’’ However, we believe this position is untenable, and that many nonhuman primates understand the behavior of others in terms of underlying (a) goals and intentions, and (b) perception and knowledge.

3.1 Goals and intentions

In a number of different studies, several primate species (most of the research is on chimpanzees) demonstrate an ability to assess and react not just to another’s overt behavior, but rather to the goal they are attempting to achieve—and in some cases the behavioral plan (intention) of the other as well.

There are two very different types of studies, from a variety of different experimental paradigms, requiring at least five different behavioral responses, most of which have also been used with human infants, that support this contention. First are studies in which the subject reacts not toward the behavior of the other but toward his goals. For example, chimpanzees react differently to very similar behaviors when a human is refraining from giving food because he is unwilling versus unable to do so (Call, Hare, Carpenter, & Tomasello, 2004). They (and other apes) also react differently when a human does something on purpose versus by accident (Call & Tomasello, 1998). They also discern that another’s goal is to reach an out-of-reach object and then they either help him to reach it (Warneken, Chen, & Tomasello, 2006; Warneken, Hare, Melis, Hanus, & Tomasello, 2007) or grab it first if it suggests the location of food (Hare & Tomasello, 2004). And having reliably anticipated an experimenter’s movement to a feeding station when he stands and turns in a certain direction by going there to meet him, they hesitate when novel contextual cues change the goal he is probably pursuing (D. Buttelmann, S. Schütte, M. Carpenter, J. Call, & M. Tomasello, unpublished data). Recent research on capuchin monkeys has found that they too help a human experimenter to gain an out-of-reach reward and distinguish between unwilling and unable acts (Barnes, Hill, Langer, Martinez, & Santos, 2008; Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009). It is important to note that in some of these studies, the behavior at the time the subject must react is identical in experimental and control conditions, with the only difference being in the immediately preceding context, which is the only cue that can be used to infer the different goals involved. Given the range of behaviors and contexts investigated, predicting outcomes based on rules abstracted from past experience which do not involve attributing goals to other individuals seems unlikely.

A second set of studies show converging evidence that chimpanzees infer goals from surface action: Chimpanzees act out what they understand the other to be attempting to do, not what he is actually doing. In these three studies (all modeled on similar studies with human infants), chimpanzees imitated what the human was trying to do, not what he actually did (Tomasello & Carpenter, 2005); they imitated his purposeful rather than his accidental actions (Tomasello & Carpenter, 2005); and they selectively imitated his actions based on an understanding of why he chose this particular behavioral means toward his goal (Buttelmann, Carpenter, Call, & Tomasello, 2007)—which may be construed as understanding his intention, in the sense of the action plan chosen for pursuing a goal. These actions and contexts were novel, as is usual in studies of social learning, and so rules based on likely behavior in given contexts do not apply.

The only reasonable conclusion to be drawn from these studies, in our opinion, is that chimpanzees, and perhaps other nonhuman primates, understand the actions of others not just in terms of surface behaviors but also in terms of the underlying goals, and possibly intentions, involved.

3.2 Perception and knowledge

To understand how another works as a goal-directed agent, an observer would benefit from understanding not just his goals but also his perceptions—as what he sees and knows helps to determine what he does. Again in the current case, the main alternative hypothesis is that nonhuman primates use others' surface behaviors in different contexts to predict how they will behave next—without any understanding of their perception or knowledge.

In two sets of studies, using several different experimental paradigms, a number of primate species (most of the research is on great apes) demonstrate an ability to assess and react not just to another's orienting behaviors, but to what she is actually perceiving or has just perceived. A first set of studies involves gestural communication, with the general finding being that great apes take into account whether a potential recipient can see their gesture. They do this in their natural gestures with one another (for a review, see Call & Tomasello, 2007), as well as in experiments on humans. Of particular importance, Kaminski, Call, and Tomasello (2004) found great apes much more sensitive to the recipient's ability to see them than did Povinelli and Eddy (1996) in a similar paradigm. Other studies have found that several species of great ape even move themselves around in front of a potential recipient to gesture so that he can see it (Liebal, Call, & Tomasello, 2004).

A second set of studies has used a food competition paradigm. The basic finding is that when competing with others for food, chimpanzees strategically assess what their competitor can and cannot see—for example, due to the placement of barriers (Bräuer, Call, & Tomasello, 2007; Hare, Call, Agnetta, & Tomasello, 2000). In some cases they even attempt to influence what the other is able to see, or what she is able to hear, by actively concealing their own approach to contested food either visually or auditorily (Hare, Call, & Tomasello, 2006; Melis, Call, & Tomasello, 2006). The fact that this concealing is similar in two different perceptual modalities suggests abstract cognitive representation. Chimpanzees in some studies also know what others know, in the sense that they keep track of what the other has just seen a moment before (even if he can no longer see it now; Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008). Some of these results have also been replicated with rhesus macaques (see Flombaum & Santos, 2005; Santos, Nissen, & Ferrugia, 2006).

Again in the case of perception and knowledge, then, there are many different methodologies involving different experimental paradigms and response measures all leading to the same conclusion: Nonhuman primates do not just react to the orienting responses of others but rather an understanding of what the other sees or has seen provides a more parsimonious explanation of the results.

Importantly, despite all of the evidence consistent with the idea that at least some nonhuman primates understand the perception and knowledge of others, there is no evidence that any nonhuman species understands false beliefs; that is, there is no evidence of one individual predicting what another will do based on what that other believes when the subject knows something else to be the case. First are the negative findings of Call and Tomasello (1999) using a nonverbal version of the standard change locations (Sally Ann) task with chimpanzees and orangutans. Second are the supporting negative results from a competitive version of this same task (Krachun, Call, & Tomasello, 2009). Third, in the Hare et al. (2001) study chimpanzees knew when their competitor had not seen the hidden location of food previously, but they could not predict what a competitor would do if the food's location was switched when he was not watching. And finally, Kaminski, Call, and Tomasello (2008) found that in a single experimental paradigm chimpanzees differentiated between knowledge and ignorance, but they did not predict another's behavior based on a false belief. Of course, explaining negative results is always perilous because it is possible that the problem here is one of inhibiting what one knows in assessing what others know (the ''curse of knowledge'').

3.3 Beyond behavior reading

Nonhuman primates (chimpanzees) do not just read and react to another's surface behavior but predict how agents are likely to behave in novel circumstances based on, we argue, an understanding of at least some of their mental states. Even if they do not understand false beliefs, they almost certainly understand others as goal-directed agents who mentally represent desired states of affairs (i.e., goals and intentions) and possess information about the world (i.e., perception and knowledge; for a fuller review, see Call & Tomasello, 2008).

4. The human primate

As humans have brains three times larger than their nearest primate relatives—and share so many basic cognitive skills with them—one proposal to explain uniquely human cognition is that humans' extra-large brains simply enable them to perform cognitive operations of all kinds, across the board, better and faster than other primates—what we may call the general intelligence hypothesis. A variant of this hypothesis suggests that the main difference between human and nonhuman cognition is based on a unique ability to reason about abstract relations, that is, relations of all kinds across all domains, including both physical and social (Penn, Holyoak, & Povinelli, 2008). However, both of these domain general hypotheses are problematic. Neither provides a satisfactory evolutionary account for the purported differences, and both are beleaguered by studies of nonhuman primates behaving in ways entirely contradictory to predictions drawn from their principles. A much more promising hypothesis for what distinguishes human cognition from that of other primates is that it is those cognitive abilities that provide them an entrée into culture.

Evidence for this proposal comes from an extremely large-scale comparative study. Herrmann et al. (2007) administered a comprehensive battery of cognitive tests to chimpanzees ($n = 106$), orangutans ($n = 32$), and 2.5-year-old human children ($n = 105$). The battery consisted of 16 different nonverbal tasks assessing all kinds of cognitive skills involving both physical and social problems. The tests related to the physical world consisted of problems concerning space, quantities, tools, and causality. The tests related to the social world consisted of problems requiring subjects to imitate another's solution to a problem, communicate nonverbally with others, and read the intentions of others from their behavior. If the difference between human and ape cognition is based on domain general cognitive skills such as relational reasoning across the board, then the children in this study should have differed from the apes uniformly across all the different tasks. However, this was not the case. The finding was that the children and the apes performed very similarly on tests dealing with the physical world, but the children—old enough to use some language but still years away from reading, counting, or going to school—outstripped both ape species in tests dealing with the social world. Factor analysis of individual differences revealed that only the human children showed a distinct, coherent factor of social cognition (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2010).

Human cultural groups can be distinguished from cultures seen in nonhuman primates because of their highly cooperative nature. Although apes acquire new behaviors through social learning both in the wild and captivity (Byrne, 2009; Whiten, in press), in contrast to such passive or ''exploitative'' social learning in nonhuman primate groups, human cultural traditions are propagated through unique levels of imitative learning (Horner & Whiten, 2005) and teaching. Whatever pressures favored the evolution of such cooperative cultural living, the hypothesis is that it favored a unique set of cognitive skills—a kind of species-specific cultural intelligence. More specifically, the kind of perspective shifting in which humans engage when interacting and communicating with others socially is internalized during ontogeny to create perspectival and symbolic cognitive representations, which enable humans—and, by hypothesis, no other primates—to shift flexibly in the ways they construe one and the same situation for different purposes (Tomasello, Carpenter, Call, Behne, & Moll, 2005). In this way, selective pressure to participate and thrive in a cultural environment could also impact physical cognitive skills. In addition, participating in a cultural group will then further enhance children's cognitive skills, as children, for example, imitate others' tool use, acquire a language and all its conceptual and causal categories, learn mathematical symbols and operations via instruction, and so forth and so on. Children's cultural intelligence thus bootstraps other cognitive skills by enabling them to collaborate with, communicate with, and learn from others and their artifacts in the cultural group (Tomasello, 1999).

5. The next 30 years

As the cognitive revolution was slow to come to the study of animal behavior, the vast majority of what we know has been discovered in the last 30 years. Scientists are notoriously poor at predicting the future, but—as per our instructions—here are some speculations about the next 30 years: the first three about specific research areas, and the second two about broader theoretical themes and agendas.

1. We will clear up the uncertainties about whether nonhuman primates understand causality. The answer will be that they do, but there will still be significant differences with the human version. It would be nice if in addition we make progress in testing the hypothesis of Bermudez (2003) that the causal reasoning of animals in terms of antecedent-consequent events is a starting point for the counterfactual ''if–then'' reasoning of humans.
2. The debate surrounding mental attribution will be resolved. Explanations invoking the use of rules based on past experience with no encoding of mental content are hard to falsify, but there are two avenues that could be explored. First, their exponents should look for positive evidence to support them, perhaps using controlled rearing experiments. Could subjects extrapolate an arbitrary rule from behavior that violates natural logic (such as that seeing leads to ignorance)? Second, we need more experiments capitalizing on experience projection, in which one's personal knowledge (for example, of the transparency of a barrier) is used to predict another's behavior, which have been long suggested to directly counter the behavioral rules account (Heyes, 1993).
3. We will substantiate that nonhuman primates cannot understand false beliefs. The reason will involve to some degree problems of inhibition, but more generally nonhuman primates will show an inability to simultaneously take the perspective of others and compare it with their own in any domain (because they do not have cognitive skills of ''shared intentionality'').
4. We will be paying increasing attention to processes of convergent evolution. For example, a number of bird species have cognitive skills very similar to those of nonhuman primates, and these clearly do not derive from any common ancestor (indeed there are significant differences in primate and avian brain organization). This gives us the opportunity to discover the ecological conditions that favor the evolution of complex cognitive skills from various behavioral and neural starting points. To such an end it will also be important to extend our studies to more primate species.

5. Finally, we will make progress in specifying exactly what makes human cognition a special form of primate cognition. The answer will be that behavioral and brain adaptations for cultural life are crucial, especially as they become elaborated during ontogeny. In particular, taking the perspective of others and the human way of communicating will turn out to be the origin of many humans' more specific abilities such as reasoning cooperatively with others in the context of normative rules and institutions, and their use of symbolic conceptual reasoning to enhance their knowledge of the physical world.

Acknowledgments

The authors thank Josep Call for helpful discussion and Laurie Santos for comments on an earlier version of the manuscript. AMS gratefully acknowledges the Royal Commission for the Exhibition of 1851 for funding.

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