

Chimpanzee Cognition and the Roots of the Human Mind

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The origins of the human mind have been a puzzle ever since Darwin (1871, 1872). Despite striking continuities in the behavior of humans and nonhumans, our species also exhibits a suite of abilities that diverge from the rest of the animal kingdom: we create and utilize complex technology, pass cultural knowledge from generation to generation, and cooperate across numerous and diverse contexts. Why do humans exhibit these abilities, but other animals (mostly) do not? This is a fundamental question in biology, psychology, and philosophy. This puzzle involves two main parts. The first is concerned with identifying the psychological capacities that are unique to humans. This phylogenetic question can be addressed through careful comparisons of humans and other animals to pinpoint the cognitive traits that are likely derived in our species. The second is concerned with the function of these capacities, and the context in which they arose. This evolutionary question examines why, from an ultimate perspective, we evolved these specialized capacities in the first place.

Solving these puzzles poses a special challenge because it is only possible to directly measure the cognition of living animals. The bodies of extinct species leave traces in the fossil record, and even some behavioral traits exhibit well-understood relationships with physical traits—such as relationships between dentition and dietary ecology, or mating system and sexual size

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dimorphism. These relationships provide important benchmarks when biologists infer the behavior of extinct species. Unfortunately, cognition does not fossilize, and neither do the brains that generate cognitive abilities. Even those features of neuroanatomy that do leave some trace in the fossil record—such as brain size or particular anatomical landmarks—are often related to the kinds of complex cognitive capacities potentially unique to humans in a coarse fashion. As such, identifying derived human cognitive traits requires reconstructing the mind of the last common ancestor of chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), and humans (*Homo sapiens*). This reconstruction then can be used to infer what cognitive characteristics have changed in the human lineage.

The best current model for the last common ancestor's psychology is the psychology of the living great apes. This review therefore aims to identify features of human cognition that differ from that of other apes, with a particular focus on our closest living relatives, chimpanzees and bonobos. Most research to date has been specifically devoted to understanding the capacities of chimpanzees, and when comparisons of multiple ape species do exist, there are often broad similarities in cognitive abilities across the extant great apes. Consequently, much of this chapter is focused on chimpanzee cognition. However, there are important exceptions to this generalization. For example, recent research comparing chimpanzee and bonobo cognition, with sufficient power to detect variation in their capacities, has revealed important variation in their skills in some domains (Hare et al. 2012; Hare and Yamamoto 2015). These differences clearly impact inferences about the last common ancestor's psychology, given that humans are equally related to both *Pan* species, who diverged from each other less than one million years ago (Won and Hey 2005; Prüfer et al. 2012). As such, differences in apes' abilities will warrant closer scrutiny through the chapter.

The first goal of the present review is to evaluate hypotheses for unique features of human cognition using empirical evidence on the psychological capacities of the living apes. In fact, there are several diverse hypotheses concerning potentially human-unique skills (Tomasello and Call 1997; Hermer-Vazquez et al. 1999; Pinker and Jackendoff 2005; Tomasello et al. 2005; Herrmann et al. 2007; Suddendorf and Corballis 2007; Penn et al. 2008; Hill et al. 2009; Hare 2011; Shettleworth 2012; Sterelny 2012), but here I will examine a subset of three hypotheses:

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1. **The social cognition hypothesis.** Humans have unique abilities to infer others' (unobservable) mental states from their superficial behaviors, as well as the motivation to share such mental states with others.
2. **The mental time travel hypothesis.** Humans are unique in our ability to engage in episodic memory and prospection, projecting a representation of the self into the past or future to solve problems.
3. **The executive function hypothesis.** Humans have specializations in self-control and decision-making capacities, which allow us to engage in flexible, goal-directed behavior across diverse contexts.

I propose that there is currently evidence for both deep similarities and profound differences in human and ape cognition across all of these domains, in contrast to approaches that focus on identifying a single core difference between humans and other animals.

The second goal of this review is to assess the evolutionary history of these unique cognitive capacities, illuminating the factors that engendered their emergence. To address this issue, I first show that the seemingly diverse cognitive abilities covered in the first part—social cognition, episodic mental time travel, and executive function—are in fact linked through shared psychological and neurobiological substrates. I then argue that one path to understanding the emergence of these skills is to examine what aspects of human behavior they actually support. In fact, many natural behaviors of deep and abiding interest to psychologists and biologists—such as hunting and foraging—require the seamless integration of skills that cut across typical cognitive distinctions. Consequently, I evaluate differences in the behavior of great apes and traditional human societies, with an eye toward the particular psychological capacities that may be necessary for individuals to engage in these behaviors. As human behavioral ecology is uniquely dependent on exploiting difficult-to-acquire food resources that are brought back to a central location and shared with others (following Kaplan et al. 2000, 2012; Marlowe 2005), I propose that successfully utilizing these types of resources requires multiple cognitive capacities, including prospection and memory to locate food in a large, complex home range; executive functions to avoid the temptation to eat that food on the go; and social cognition to engage in the cooperative acts that characterize human food sharing (see also Rosati in press). As such, I argue that human cognitive uniqueness is not

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defined by a single core difference. Rather, the behavioral problems posed by our species' behavioral niche require a suite of cognitive traits across psychological domains.

The First Puzzle: Identifying Unique Features of Human Cognition

How is human cognition similar to or different from that of our closest living relatives? This section will examine three hypotheses concerning human-unique cognition: our social cognitive abilities to think about others' behaviors and mental states; our episodic memory and prospection, linked capacities that allow individuals to project themselves backward or forward in time to simulate events; and finally, our executive function abilities, which allow us to flexibly update and control our responses to a changing world. It is important to note that understanding psychological processes requires controlled experiments that can rule out alternative explanations for observed patterns of results. As any given behavior can be psychologically implemented by many different possible mechanisms, observational research is inherently limited in terms of possible inferences about the cognitive abilities underlying that behavior (see also Tomasello and Call 2008). For example, studies of social cognition rule out the possibility that animals are utilizing the direct behavioral cues other actors provide, rather than actually inferring their (unobservable) mental states; studies of planning rule out that animals are acting to meet a need they are currently experiencing, rather than a future need; and studies of executive function rule out that animals learn simple rules without being able to flexibly adjust in new contexts. Such controlled experiments are pragmatically (and ethically) challenging to conduct in wild populations, and therefore quite rare (Zuberbühler 2014). Research aimed at understanding cognition in nonhuman primates is therefore conducted primarily in populations living in environments where such controlled experimentation is possible, such as in zoos or sanctuaries (see Figure 19.1).

Hypothesis 1: Social Cognition

One influential claim about cognitive differences between humans and other animals concerns the unique ways in which we think about other individ-

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FIGURE 19.1. Chimpanzees and the evolutionary origins of human cognition. Chimpanzees living in sanctuaries and zoos, such as these individuals living at Tchimpounga Chimpanzee Sanctuary in Republic of Congo, can be tested in controlled experiments that rule out different possible explanations for behavioral responses.

uals. Humans possess a complex belief-desire psychology that represents not only others' observable actions, but also others' internal and therefore unobservable psychological states. For example, imagine that your friend suggested several times that the two of you eat at a specific restaurant. An inference based on that person's behavior alone would allow you to predict that they will eat at that restaurant again. However, an inference about that person's mental state would illuminate that they *like* the restaurant and desire to eat a particular type of food—an inference that would allow you to make better predictions about your friend's actions in the future across others contexts—such as what kind of food they will order at a different restaurant, or what they will prepare at their own home. Many other animals clearly engage in complex social interactions, but what cognitive capacities do they use to do so? Several important theoretical views have argued that nonhumans can pick up on complex contingencies in others'

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behaviors, but do not represent subjective mental states (Cheney and Seyfarth 1990; Povinelli and Eddy 1996b; Tomasello and Call 1997; Heyes 1998; Tomasello 1999). That is, animals can learn about others' concrete actions ("she eats at that restaurant a lot") but do not infer the underlying mental state mediating those actions ("she likes French food"). However, increasing evidence indicates that apes also possess at least some theory of mind capacities.

Understanding Intentions, Perceptions, and Knowledge

What evidence supports the claim that apes can reason about mental states? First, they seem to conceive of others' actions in terms of their underlying goals, intentions, and desires. For example, chimpanzees and orangutans are sensitive to whether a human's behavior is purposeful versus accidental, even when different actions have similar qualities (Call and Tomasello 1998; Tomasello and Carpenter 2005; see also Warneken and Tomasello 2006). Similarly, when watching a human trying but failing to accomplish some task, chimpanzees tend to copy the (uncompleted) goal, rather than the observable (but failed) action sequence (Tomasello et al. 1987) (see also Horner and Whiten 2005; Buttelmann et al. 2007). That is, chimpanzees seem to conceive of these actions in terms of their underlying purpose, not just their visible components. Chimpanzees also modulate their responses to a human's behavior based on that person's intentions (Call et al. 2004). For example, when a human presents food but repeatedly does not give it, chimpanzees are more likely to stick around and beg for the food when the human is trying but failing to hand over the food, compared to when he is teasing the chimpanzee. Indeed, all four species of great apes can use contextual information to distinguish between the goals underlying completely identical actions (Buttelmann et al. 2012). Finally, apes predict that others will act in line with their desires. If a person initially responds more positively to one type of food, apes later predict that the person will choose to eat from a container with that food, rather than an alternative with different contents (Buttelmann et al. 2009).

Second, there is now strong convergent evidence that apes can reason about what others can see. Many primate species follow others' gaze, for example, by looking in a particular direction when they see another do so. Chimpanzees and other apes, in contrast, exhibit particularly flexible gaze-following behaviors that suggest that they are not just exhibiting a reflexive response, but rather that they understand that others look because they see

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something interesting (Rosati and Hare 2009). For example, all four great ape species will follow others' gaze—and even reorient to look around barriers or check back with the actor to verify the correct location of the target (Povinelli and Eddy 1996a; Tomasello et al. 1999, 2001, 2007; Okamoto et al. 2002; Braeuer et al. 2005; Herrmann et al. 2007, 2010; Kano and Call 2014). However, there seems to be some important variation in how different species of apes conceive of others' visual perspective. For example, chimpanzees and bonobos seem to have a richer understanding of others' line of sight when they have to infer what others are looking at in complex physical situations, whereas gaze-following responses in gorillas and orangutans are more reflexive (Okamoto-Barth et al. 2007). Similarly, chimpanzees are more successful than bonobos at using their knowledge about others' past experiences to infer what others are really looking at (MacLean and Hare 2012). Yet the strongest evidence to date that apes reason about what others can see comes from studies examining how chimpanzees behave when competing for food either with other conspecifics (Hare et al. 2000; Braeuer et al. 2007) or with humans (Hare et al. 2006; Melis et al. 2006a). For example, if a barrier prevents a competitor from seeing specific locations in space, chimpanzees will specifically pursue food hidden in that "safe" location. There is even some evidence that chimpanzees can infer others' auditory perceptions, indicating that this skill may extend across modalities (Melis et al. 2006a) (but see Braeuer et al. 2008).

Humans do not merely infer what others can and cannot see—we also can use our knowledge about others' perspective to assess what others do or do not know about the world. In fact, there is good evidence that at least chimpanzees do so as well. For example, chimpanzees realize that other conspecifics do not know about the presence of food that was baited out of their sight (Hare et al. 2001). Chimpanzees can also make sophisticated inferences about what choices others will make based on their knowledge. In one setup, two chimpanzees played a competitive back-and-forth game involving sequential choices for food locations in an array of three locations (Kaminski et al. 2008; see also Schmelz et al. 2011). Both chimpanzees might see one of those locations baited, whereas only the subject chimpanzee would see another location baited (while the competitor's view was blocked). If the subject then got to choose first, they were equally likely to choose either of the baited spots. Yet if the subject knew the competitor had already made one choice—but did not know what location the competitor had actually chosen—the subject

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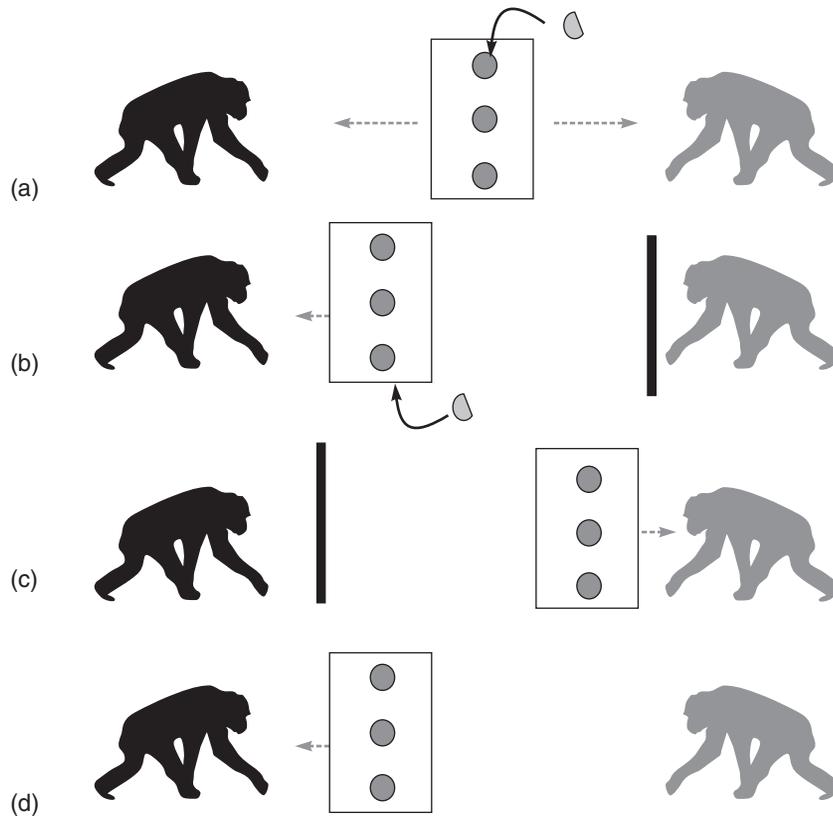


FIGURE 19.2. Understanding mental states: Chimpanzees infer how seeing leads to knowing. Setup for competitive back-and-forth game, adapted from Kaminski et al. (2008). (a) Both the chimpanzee subject (on left) and the competitor (right) watched as one container was baited with food. (b) Only the subject saw that a second location was also baited; the competitor's view was blocked. (c) In some trials, the competitor made the first choice, but their choice could not be seen by the subject. (d) If the subject chose second, they inferred that the competitor must have chosen the location that both had seen baited, and therefore chose the alternative location only they had seen baited.

could nonetheless deduce that the competitor must have already chosen the piece both had seen hidden (see Figure 19.2).

Despite these successes, there is currently limited evidence that other primates understand that other individuals can hold beliefs about the world that can be false (Rosati et al. 2010; Martin and Santos 2016). False-belief comprehension is sometimes treated as the benchmark test for human-like

theory of mind, and studies using competition paradigms have generally failed to show that apes attribute false beliefs (Call and Tomasello 1999; Krachun et al. 2007; Kaminski et al. 2008). For example, in the back-and-forth game described above, chimpanzees do not infer that others may have a false belief about the location of food if they observe it being placed in one location, but then it is subsequently moved (Kaminski et al. 2008). However, some recent work using eye-tracking methods suggests that apes may be at least implicitly sensitive to others' false beliefs (Krupenye et al. 2016). Here, apes watched short movies in which an actor viewed something hidden in one location, but then it moved while the actor was absent. The question concerned where apes thought the actor would search when they returned. In fact, chimpanzees, bonobos, and orangutans made anticipatory looks to locations that the actor (incorrectly) thought was the hiding place. Given that human children also succeed at such implicit looking tasks earlier in development than in explicit response tasks (Baillargeon et al. 2010), it may be that anticipatory looking measures reduce the executive function demands, as discussed in subsequent sections.

Overall, these results indicate that apes do not merely reason about the superficial qualities of other individuals' behavior. Rather, they can make surprisingly complex inferences about the goals, desires, and perceptions that motivate that behavior, although they may be relatively limited in their ability to attribute false beliefs to others (for reviews, see Tomasello et al. 2003; Call and Tomasello 2008; Rosati et al. 2010; Hare 2011; Martin and Santos 2016). However, there may be some important differences in how the four great apes reason about others' mental states. For example, chimpanzees and bonobos appear to have more sophisticated gaze-following capacities than other apes (Okamoto-Barth et al. 2007), but some of the best evidence that apes reason about others' visual perspective and knowledge comes from chimpanzees alone (Hare et al. 2000, 2006). While there is some evidence that other species such as rhesus macaques can infer perceptions and knowledge in competitive contexts (Flombaum and Santos 2005; Santos et al. 2006; Marticorena et al. 2011), there is currently little data addressing whether these capacities are more widely shared among primates.

Sharing Mental States

The particular tasks used to assess social cognitive capacities in apes highlight another important difference with humans: most successful demonstrations

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of theory of mind have focused on the cognitive skills animals use in competitive contexts to outwit conspecifics or humans. In fact, some theoretical views suggest that primates might show more sophisticated cognitive abilities in such contexts, given the importance of competition with others over food or other resources in many primate species' daily lives (Hare 2001; Hare and Tomasello 2004; Lyons and Santos 2006). In contrast, humans regularly engage in complex forms of cooperation in which individuals work together to reach collective goals. Consequently, recent proposals have begun to focus on differences between the social-cognitive abilities humans and apes utilize when multiple individuals are collaborating (Tomasello et al. 2012).

One proposal suggests that human-specific forms of cooperation require human-unique cognitive capacities. In particular, humans may be unique in our ability to represent joint activities as underpinned by shared goals or motivations that both individuals know are shared (Tomasello et al. 2005; Tomasello and Carpenter 2007). What constitutes such shared mental states? Take the example of gaze following. As noted previously, both humans and chimpanzees can expertly follow gaze ("I see you looking at something"). However, humans also exhibit joint attention—where both individuals knowingly share attention with each other toward the target ("You and I both know we are looking at something together"). While joint attention emerges within the first year of life in human infants, there is little evidence that chimpanzees engage in such triadic interactions (for review, see Carpenter and Call, in press). Indeed, this early difference in social cognitive development may result in later divergence in the trajectories of human and ape gaze-following skills into adulthood (Rosati et al. 2014).

The lack of "togetherness" in the way that other animals conceive of joint activities may have particularly important repercussions for cooperative behaviors. As is the case with joint attention in gaze following, young human children form joint intentions when engaging in cooperative actions. In particular, humans assume that the joint task needs to be completed together—and even act to help a partner achieve a successful outcome after their own individual needs have been met (Warneken et al. 2006; Greenberg et al. 2010; Hamann et al. 2011). That is, humans seem to act as though success at a joint task is not only about me getting my own reward, but both of us being successful together. Chimpanzees also engage in a variety of complex cooperative behaviors (Melis et al. 2006b, 2006c)—but they seem to con-

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ceive of their joint actions in terms of individual, but parallel, goals. Indeed, chimpanzees prefer to solve collaborative problems individually if possible (Bullinger et al. 2011; Rekers et al. 2011). To date, there is little evidence that chimpanzees or bonobos form joint intentions when engaging in cooperative activities (Herrmann et al. 2007, 2010; Wobber et al. 2013) (but see Pika and Zuberbühler 2008; MacLean and Hare 2013 for work with different criteria for shared intentionality). Importantly, these differences in human and ape social cognition may have quite far-reaching consequences for a wide variety of behaviors. For example, shared intentionality may support many forms of cultural learning (see Rolian and Carvalho, this volume; Henrich and Tennie, this volume) as well as human-specific forms of communication (Slocombe and Scott Philips, this volume). Thus, this cognitive difference may constrain the forms of social interaction that chimpanzees can engage in compared to humans (Tomasello et al. 2005; Herrmann et al. 2007; Wobber et al. 2013).

Hypothesis 2: Mental Time Travel

Another important proposal for human-unique cognition concerns our ability to recall the past and imagine the future (Suddendorf and Corballis 1997, 2007; Suddendorf and Bussey 2003). As is the case for theories of human social cognition, this hypothesis concerns whether animals share a specific cognitive mechanism with humans—not whether other animals generally lack memory or never act in accordance with future events. This hypothesis particularly focuses on whether animals possess episodic memory and prospection. In contrast to other forms of memory, such as semantic memory for facts about the world, episodic memory allows individuals to mentally reexperience life events—with the feeling of having been there personally (Tulving 1983). For example, imagine the difference between knowing the date of your birth, and knowing what happened on your most recent birthday—while you may know many details about the day you were born, you (probably!) only recall a set of facts that others have reported to you. In contrast, you likely can recreate your own personal experiences on your most recent birthday. This ability to mentally simulate past events is also involved in anticipating what is likely to happen in future (Buckner and Carroll 2007; Schacter et al. 2007; Suddendorf and Corballis 2007), and episodic memory and future planning are sometimes together referred to as

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mental time travel. Thus, the claim is that animals are mentally “stuck in time” (Roberts 2002): they can track intervals, remember semantic information, and tailor their behavior to likely future occurrences—but they cannot represent particular episodes occurring in the past, nor simulate new events that will occur in the future.

Episodic Memory

Theoretical claims about human-unique memory skills go back to Wolfgang Köhler (1927): in a major synthesis of his work with captive chimpanzees on Tenerife Island, he noted that their sense of time was “limited in past and future.” The issue of whether other animals can engage in mental time travel has been contentious ever since. Some theories about human episodic memory explicitly define this ability in terms of the phenomenal quality of these memories, in which individuals have conscious awareness of being engaged in the act of recollection (Tulving 1983, 1985; Tulving and Markowitsch 1998). This sort of definition obviously makes it quite difficult to test such abilities in nonlinguistic organisms. Consequently, comparative psychologists have developed behavioral criteria that animals must meet for the underlying cognitive abilities to be considered episodic memory. To meet this formal definition of episodic-like memory, animals must demonstrate knowledge of three pieces of information—what happened, when it happened, and where it happened—all structured into a single, coherent representation (Clayton et al. 2003; Hampton and Schwartz 2004). But it is also important to note that both episodic memory and spatial memory more generally depend on the hippocampus (Burgess et al. 2002), and hippocampal neuroanatomy is highly conserved across mammals (Manns and Eichenbaum 2006; see also Murray et al. 2017). Indeed, recalling the spatial context of in which items were previously encountered is an important component of human episodic memory (Davachi 2006). This suggests that evidence for shared mechanisms supporting spatial memory and navigation in humans and other animals can also illuminate the evolution of episodic memory.

To date, some of the strongest evidence for episodic-like memory in non-humans comes from studies of caching behavior in corvids (Clayton and Dickinson 1999; Emery and Clayton 2001; Clayton et al. 2003; see Martin-Ordas and Call 2013 for a review). What about apes? There is strong evidence that apes do use fairly sophisticated cognitive skills to encode spatial loca-

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tions. For example, chimpanzees can recall the locations of multiple items that were hidden in a large space, and use a “cognitive map” of the optimal route between these locations when retrieving food from these locations (Menzel 1973; Menzel et al. 2002). Moreover, these memories persist over long periods. In one study, a language-trained chimpanzee could communicate the type and location of food they had seen hidden in the enclosure up to sixteen hours earlier (Menzel 1999), and chimpanzees preferentially searched at locations where they had previously received food even three months previously (Mendes and Call 2014). This suggests that the apes’ representations of the spatial locations are quite temporally durable. However, there are some potential differences between ape spatial memory capacities. For example, while juvenile chimpanzees exhibit more accurate spatial memory than do infant chimpanzees, bonobos show no such developmental improvement over the same age range (Rosati and Hare 2012). This indicates that humans and chimpanzees, but not bonobos, may share similar patterns of ontogenetic improvement in spatial memory during early childhood (Newcombe and Huttenlocher 2006).

Is there evidence that apes can also recall specific events in the past by binding items with their context? One approach to answering this question has been to expose apes to unique events and then test their memory. For example, apes might be exposed to an unusual event—such as an unfamiliar person playing a guitar—and then later be asked to identify that person. In fact, gorillas are able to successfully select cards associated with that person and item after a delay (Schwartz et al. 2002, 2004). Another approach is to examine whether apes can recall unique episodes over very long timescales. For example, in one study chimpanzees and orangutans were presented with the unique room setup used in a tool-finding task the apes had completed three years previously. These situational cues were enough to trigger the apes’ recall of the location of specific tools hidden in the room (Martin-Ordas et al. 2013). Both of these approaches show that apes have sophisticated, temporally durable memories for unique events they experienced in their past. However, it is unclear whether they use episodic-like memory in these contexts, as they do not require bound representations of what, when, and where. For example, recalling an unfamiliar person who played a guitar required an association of “who” with “what” information, but it is not necessary to think about when specifically this event happened. Similarly, apes had to recall a unique event that had happened in the past to solve the tool-finding

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task, but not necessarily use information about *how long ago* the event happened.

The best evidence to date for apes binding what-when-where information comes from a study involving choices between foods that decayed over different timescales (Martin-Ordas et al. 2010). Chimpanzees, bonobos, and orangutans saw a container in one location baited with a preferred but perishable food (frozen juice), whereas another was baited with a less-preferred but nonperishable food (a grape). Apes were then given the opportunities to choose one of these containers before seeing their current contents (see Figure 19.3). When given the opportunity to choose after five minutes, apes selected the container with the frozen juice—the option that was generally more preferred. However, after one hour—a duration during which the frozen juice would have melted away—they preferentially selected the container with the grape. This shift in responses indicates that apes recalled what food was baited where, as well as how long ago these baiting events occurred. Yet it is important to note that these abilities may be somewhat fragile, unlike the more automatic encoding and recall of episodes that humans exhibit. For example, in a more complex situation in which food artificially decayed over

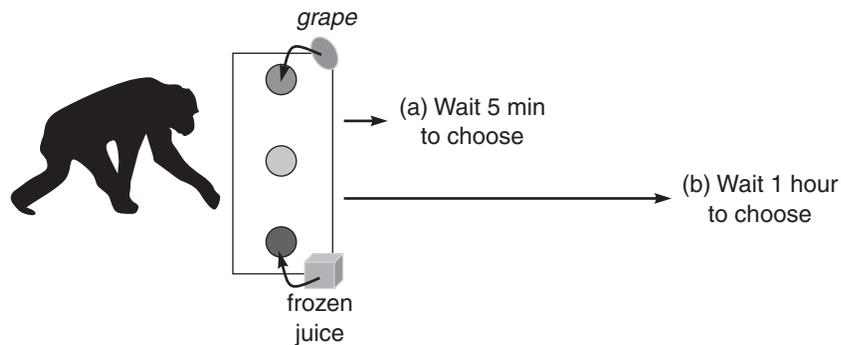


FIGURE 19.3. Episodic memory: Apes can remember where and how long ago different items were hidden. Setup for memory task, adapted from Martin-Ordas et al. (2010). Chimpanzees, bonobos, and orangutans chose between a location baited with a preferred but perishable food item (frozen juice, which melted and became inaccessible over time) and less preferred but temporally stable food item (a grape). Apes had to choose before observing the current contents of the containers. (a) If apes could make their choice after only a five-minute delay, they preferred the location baited with the perishable juice. (b) If apes could not choose until one hour after the baiting, they preferred the location with the grape.

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different timescales, chimpanzees failed to form such integrated memories (Dekleva et al. 2011). Thus, apes show durable long-term memories, robust recall of spatial information, and can encode at least some memories that integrate what-when-where information—but they do not always do so.

Future Planning

As is the case for episodic memory, comparative psychologists have developed fairly stringent behavioral criteria for what qualifies as evidence for future prospection in nonhumans. Animals may show many future-oriented behaviors that are not planning; this test concerns whether animals can act to satisfy their future rather than immediate needs. To understand this difference, imagine you are rushing between two meetings. If you are hungry when you leave the first meeting, you buy a snack—but if you are running late, you might not have a chance to eat it until after the second meeting. Contrast this with an alternative scenario where you feel fine after the first meeting, but know you tend to feel hungry in the middle of the afternoon—so you buy a snack in anticipation of how you will feel after the second meeting. In both cases, you completed the same actions (buying a snack and eating it later)—but in the latter case you planned for a future need, whereas in the former you acted due to your current state. Similarly, animals may seem to act for the future but actually be thinking only about their current motivational state. For example, chimpanzees have been observed to transport a tool some distance until they find suitable nuts to crack (Boesch and Boesch 1984), but this may be because their current hunger state is not yet satisfied. Thus, the most rigorous criteria for future prospection requires animals to anticipate a future need that they are not currently experiencing, termed the Bischof-Köhler criteria (Suddendorf and Corballis 1997; Mulcahy and Call 2006; Raby et al. 2007).

Studies of future planning in corvids have focused on food caching contexts, in which birds store food for retrieval at a later time (e.g., Raby et al. 2007). As apes do not store food, studies of ape future planning have focused on tool-selection tasks in which apes must select and save a tool in anticipation of a future opportunity to use it. In one influential study, both bonobos and orangutans were presented with an out-of-reach apparatus where they needed a tool to acquire food rewards (Mulcahy and Call 2006). In this situation, apes anticipated that they would have access to this apparatus, selected the correct tool from a set of possibilities in advance, and retained this tool

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for long periods. Indeed, some apes were even able to select the correct tool and hang on to it overnight, carrying it into their sleeping room and then back to the testing room in the morning. This shows that apes can select tools not only on the basis of their current need, but also in anticipation of the future. Indeed, both species showed similar performance, suggesting that this capacity might be widely shared among great apes.

However, some theorists have argued that this situation does not meet the strictest definition of the Bischof-Köhler criteria (Suddendorf 2006). Even though apes might have known they could not yet use the tool, they may nonetheless have experienced an internal desire for the food rewards throughout the duration of the test (at least while they were awake!). That is, it is unclear whether the apes were actually planning for a need they were not currently experiencing. However, some evidence suggests that apes can overcome immediate needs when faced with similar tool-selection choices (Osvath and Osvath 2008). For example, chimpanzees and orangutans were able to select between a tool (a straw) that would allow future access to juice, when also presented with an alternative of taking a preferred fruit that provided immediate benefit. Furthermore, if given a second choice between another tool and another fruit, apes then selected the fruit—indicating that the tool was merely an instrument for satisfying future desires, not motivationally equivalent to food. Indeed, even though apes do not normally store food in their natural behaviors, some evidence suggests that chimpanzees will spontaneously save raw food for several minutes, in order to place it in a device that appeared to transform it into a more desirable cooked item. In contrast, chimpanzees without access to this device in a control condition consumed all the raw food in their possession (Warneken and Rosati 2015).

Together with evidence of anticipatory tool selection, these studies provide clear evidence that apes can plan for their future states. However, there is still debate concerning whether these findings satisfy the more conservative Bischof-Köhler criteria, requiring that animals plan for future states that they are not currently experiencing (see Suddendorf et al. 2008; Osvath 2010 for this discussion). That is, while apes show a clear capacity to plan for future desires related to food or hunger, it is unclear whether they can plan for activities that are not strongly related to such central biological needs. Indeed, the challenge of devising valid tests for nonlinguistic organisms means that most studies thus far have focused on mental time travel specifically in food-acquisition contexts.

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Hypothesis 3: Executive Control

Social cognition and mental time travel are examples of specific cognitive domains where human cognition may differ from that of other apes. That is, these hypotheses suggest that humans may have special representational capacities: perhaps our species alone can think about certain types of mental states in others, or form coherent memories of what happened when and where. The final hypothesis discussed in this chapter is that humans exhibit exceptional executive function. In contrast to those discussed in previous sections, this hypothesis stems not from comparisons of cognition in humans and animals, but rather primarily from theories about human brain evolution. In particular, humans exhibit a suite of anatomical changes in the size and structure of our frontal cortex—a region of the brain that supports executive function and decision making (Goldman-Rakic 1996; Rilling and Insel 1999; Miller and Cohen 2001; Semendeferi et al. 2002; Schoenemann et al. 2005). However, this hypothesis is receiving increasing attention from comparative psychologists as well (Rumbaugh et al. 1996; Barkley 2001; Siegal and Varley 2008). Executive functions allow individuals to flexibly regulate and control their behavior and goals, overriding responses that would otherwise be carried out automatically. That is, executive processes encompass a diverse set of cognitive skills allowing individuals to consider relevant information, inhibit currently inappropriate responses, and shift to new responses when the rules of the game change (Rosati 2017). As such, executive functions encompass the cognitive skills that enable behavioral flexibility, and are an important regulator of many other behaviors.

Working Memory

One important component of human executive functioning is working memory (Kane and Engle 2002; Baddeley 2003). In contrast to the episodic memory skills discussed previously, working memory concerns the ability to consider and manipulate multiple pieces of information at once. That is, working memory is a system that processes information over the short term—and because attention is limited, this system inherently involves dealing with interference from multiple, possibly conflicting sources of information. In humans, working memory is thought to consist of storage systems for visual and auditory (or linguistic) information, as well as a central control process that organizes different information (Baddeley and Hitch

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1974; Baddeley 2000). Working memory can therefore constrain other aspects of executive control if individuals cannot access the necessary information to make an appropriate response. For example, humans might be able to make more flexible, context-appropriate decisions if they are able to consider greater amounts of information at any given point.

One approach to measuring working memory in apes has been to examine their ability to remember multiple items over short time spans. For example, in one set of studies chimpanzees briefly saw up to nine Arabic numerals that were located randomly on a touch-screen computer (Biro and Matsuzawa 1999; Kawai and Matsuzawa 2000). In order to receive a treat, the chimpanzees had to touch the numbers in their correct order. The trick was that the remaining numbers were masked after the chimpanzee first touched the number “1”—so they had to recall the location of the entire sequence from memory. In fact, chimpanzees were quite successful at completing this ordering task, sometimes able to recall all the remaining numerals after they were masked. One chimpanzee even outperformed adult humans when the numbers were presented for very short time periods (Inoue and Matsuzawa 2007). However, the chimpanzees may have benefited from their extensive experience, as people who receive additional training perform more like those chimpanzees (Cook and Wilson 2010). There may also be important individual differences in chimpanzees’ working memory abilities, as other chimpanzees recalled the location of only one numeral after the initial masking—despite similar experience with Arabic numerals (Beran et al. 2004). Together, this evidence suggests that apes and humans may have similar limits on working memory capacities, at least for visual information.

Response Control

Another important component of executive function is controlling responses—inhibiting actions when they are undesirable, and selecting the response that is appropriate given one’s current goals (Mostofsky and Simmonds 2008). While working memory is therefore critical for processing information in order to determine how to proceed in a given situation, response control concerns how this course of action is actually implemented. In fact, a plethora of studies have shown that many other animals can have quite difficult times inhibiting prepotent responses. For example, one task used to study response control is the A-not-B test, derived from a set of observations by Piaget (1954). Here individuals initially experience that a reward is repeat-

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edly hidden in one location (A), but on the critical test trials it is placed in a different location (B). In fact, even if they have seen the reward being placed in the second location, human infants and monkeys tend nonetheless to search at the old location (Diamond 1990). That is, they fail to inhibit their prepotent response to the spot that previously provided a reward. In contrast to the performance of these groups, apes and older children show near-ceiling levels of success on the A-not-B task (Barth and Call 2006). Moreover, two large comparative studies examining a wild variety of ape, monkey, and lemur species have indicated that apes are generally the most successful at inhibiting responses on the A-not-B task and related measures of response inhibition (Amici et al. 2008; MacLean et al. 2014). Thus, there is a clear difference in the level of control that apes have over their responses compared to primates more generally.

In terms of addressing human uniqueness, however, the question is whether humans nonetheless outpace nonhuman apes. In fact, in some contexts apes and human children exhibit similar levels of response control. In addition to their similar performance on the A-not-B task, apes and young children exhibit similarities in other reaching tasks. For example, apes and children both have some difficulty when they must inhibit direct reaching for a reward, but rather detour around the food to reach for it from another direction (Vlamings et al. 2010). However, when faced with more complex situations requiring the flexible inhibition of responses, children soon outpace apes. For example, when three-year-olds, six-year-olds, and chimpanzees initially learn to obtain a reward by raking it out of a tube or box, they can quickly acquire this skill. However, when they are then subsequently faced with a slightly different situation—where there is now a “trap” or hole in the bottom of the tube such that the reward will fall out of reach if they rake it out in the same way—six-year-olds are much more adept at shifting their response to acquire the reward with a new action than either three-year-olds or chimpanzees (Herrmann et al. 2015). Similarly, when the outcome of an event is ambiguous, such that a reward may come out of two possible locations, children rapidly outpace apes in preparing for both possible outcomes, rather than just one (Redshaw and Suddendorf 2016).

Even when human children and apes show similar performance, they may differ in the extent to which they can successfully inhibit their responses. For example, in one task individuals were faced with a reward trapped in a vertical maze (Voelter and Call 2014). Because the maze had

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various dead ends, apes and children had to plan their moves up to two steps in advance and inhibit prepotent actions in order to get the reward. Although apes performed similarly to children in terms of rate of success, apes had more difficulties than the children in inhibiting motor responses that led to dead ends. Another task tested how apes responded to a different vertical maze task in which individual had to move internal platforms so that a food reward would drop through to an accessible location at the bottom. Here, both bonobos and orangutans could succeed in situations where they could access the food by acting on the barrier that the food was initially resting on, but failed if they had to plan out an initial series of moves before touching to barrier with the food on it (Tecwyn 2013). That is, it was difficult for the apes to inhibit their prepotent response to reach toward the baited platform, even if doing so made it impossible to access the food subsequently. Together, these results indicate that, even though children and apes show similar performance on more simple reaching tasks, children may outpace chimpanzees in inhibiting motor responses in more complex contexts.

However, many of these tasks have only been implemented in a few species, making it difficult to make broader comparative claims. One response control test that has been widely studied across species is known as the reverse contingency task. Here an individual is faced with a choice between different value rewards—for example, one candy or five candies—but the trick is that they receive the item they *do not* choose. Thus, it is necessary to select the smaller reward in order to actually receive the larger reward (see Figure 19.4). This problem is challenging for chimpanzees and other primates, who generally cannot inhibit their tendency to approach or reach for the more valuable reward. In fact, primates are only able to overcome this prepotent response when faced with symbolic or nonconcrete representations of the rewards (Boysen and Berntson 1995; Boysen et al. 1996, 1999; Vlamings et al. 2006; Uher and Call 2008; Shifferman 2009). In contrast, children also improve when faced with symbolic rewards, but even many three-year-old children make the correct response when faced with real candy—and four-year-olds are even more successful (Carlson et al. 2005). That is, young children can easily solve an inhibitory control problem that is challenging (or impossible) for other primates.

Unfortunately, there have been few studies of chimpanzee performance in more typical cognitive neuroscience tasks used to assess response control in adult humans, such as the flanker task or Stroop task that examine how

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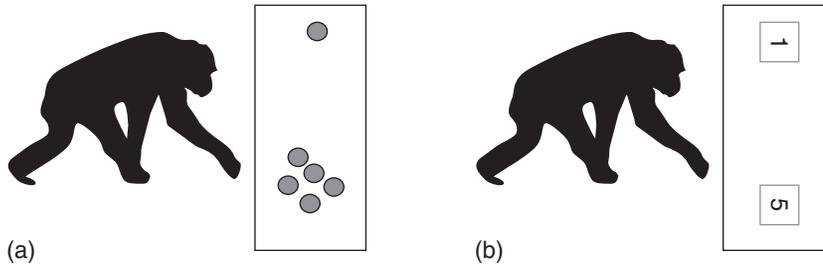


FIGURE 19.4. Response control: Symbolic representations improve primates' inhibition of prepotent responses. Setup for reverse contingency task, adapted from Boysen et al. (1996). Apes chose between a larger and smaller amount, but were given the option they did *not select*. (a) When apes saw different amounts of food, they had difficulty inhibiting choices for the larger amount, even though this resulted in their receiving the smaller amount. (b) When apes chose between symbolic representations of the food amounts (Arabic numerals), they were more successful at inhibiting. A variety of other species show similar improvements when faced with cues to the reward (such as color) rather than the concrete rewards.

individuals can control their responses under situations where there is conflict between different possible responses (Botvinick et al. 2004). For example, in the classic version of the Stroop task, individuals are asked to report the font color of a word they see, and the trick is that sometimes the word itself is a color term—that is, a person might see the word “brown” written in red font, so there is a conflict between correctly reporting the color written out (brown) and incorrectly reporting the actual color of the word itself (red). However, the little evidence that exists also suggests important differences between humans and apes. For example, a language-trained chimpanzee was tested on an adapted Stroop task in which she learned to associate geometric symbols with specific colors, and then had to report the color of stimuli she saw by choosing the associated lexigram (Beran et al. 2007). In fact, she made close to 50 percent errors when she faced conflicting stimuli—which is striking, as adult humans tend to make few actual errors in the Stroop task, but rather show slowed responses on trials involving response conflict (MacLeod and MacDonald 2000).

Strategic Control

Response control problems consist of decision-making situations in which individuals face conflict between different potential responses, as in the

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Stroop task. In this case, individuals face a conflict between producing different possible motor actions, such as pushing the button to indicate red, versus pushing a different button to indicate brown. The “correct” response is not under debate—the conflict concerns whether individuals can actually produce this response. Most studies of animal cognition often measure response control in tasks tapping into this sort of control over motor actions, such as which direction to reach or which container to point at in order to successfully acquire food. But this type of conflict between competing motor responses is not the only sort of conflict humans face when making decisions. Other situations involve a choice between different cognitive strategies—that is, the problem is not whether individuals can produce the (correct) motor response, but how they assess what the “correct” thing to do is in the first place. Many kinds of real-world decisions require that individuals decide which *strategy* to pursue, prioritizing different aspects of the available information (Venkatraman et al. 2009a, 2009b). Executive control systems play a critical role in this kind of decision-making by updating the strategies or rules guiding behavior when new information comes to light (Mansouri et al. 2009). The ability to change and adapt responses in a changing world is therefore a key skill underlying behavioral flexibility.

One important example of problems involving strategic control is intertemporal choices between rewards with different timings: individuals can pursue immediate gratification, or choose to wait for larger payoffs (Stevens and Stephens 2008). While humans often favor waiting for future gains—we can wait weeks or even months for larger rewards in some contexts (Frederick et al. 2002)—many other species seem quite impulsive and are willing to wait only a few seconds (Rachlin 2000). However, recent work suggests that chimpanzees and other apes can wait longer durations for future payoffs. For example, chimpanzees can sometimes wait over ten minutes in a delay of gratification task where rewards are accumulating over time (Beran 2002; Evans and Beran 2007). In fact, apes outwait monkeys and lemurs in accumulation situations (Stevens et al. 2011; Evans et al. 2012; Parrish et al. in press), when they make a series of repeated choices between immediate and delayed options (Stevens et al. 2005; Rosati et al. 2007; Amici et al. 2008; Addessi et al. 2011; Stevens and Muhlhoff 2012), and in exchange situations where smaller rewards can later be traded for larger ones (Ramseyer et al. 2006; Dufour et al. 2007; Pelé et al. 2010, 2011).

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Furthermore, although humans can outwait other species when faced with decisions about abstract rewards involving money (see Santos and Rosati 2015 for a review), chimpanzees and humans exhibit similar preferences when faced with matched choices involving delayed food rewards (Rosati et al. 2007).

These results indicate that chimpanzees can exert strategic control over their temporal choices, and sometimes even do so in ways comparable to humans. But can chimpanzees update and shift their strategies when faced with a changing world? A simple example of this is reversal learning, where individuals initially learn one rule (for example, that the correct response is to choose the blue item), but then the rule switches (now they should choose the red item). This situation therefore examines whether animals persevere in choosing the previously correct option, or update their representation of the rules of the game. Chimpanzees (and apes in general) outperform many other primate species in terms of picking up on the new contingencies (Rumbaugh and Pate 1984; Rumbaugh et al. 1996; Deaner et al. 2006). This suggests that apes exhibit a much more flexible ability to learn and apply new rules relative to other nonhuman primates—similar to their improved ability to control their motor responses.

It is also important to note that this type of reversal problem is markedly less complex than common tasks used to measure set shifting in humans. For example, one problem commonly used to assess human executive functioning is the Wisconsin card sorting task (Grant and Berg 1948; Milner 1968). Here individuals must sort modified playing cards, and the correct response changes once the player demonstrates initial learning of the rule. However, in contrast to primate reversal learning tasks, the images on these cards actually vary on multiple dimensions (such as number, color, and shape), and thus detecting the rule and updating responses is significantly more complicated. Grade-school children can already solve this task with the same level of accuracy as adults (Chelune and Baer 1986), but there has been no demonstration of how chimpanzees perform in a comparable task (but see Moore et al. 2005 for a simplified version developed for rhesus macaques). That is, many of the tasks developed to test these skills in nonhumans are quite simplified compared to problems that humans must solve. Consequently, future research comparing humans and apes on matched tasks will be critical to address the evolution of flexibility.

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The Second Puzzle: Evolving the Human Mind

Current comparative evidence indicates that humans may have specialized cognitive abilities across several domains, including social cognition, mental time travel, and executive functioning. Although chimpanzees and other nonhuman apes share many homologous capacities with humans, they also exhibit important divergences that point to derived features in our lineage (see Table 19.1 for a summary). This comparison is critical to address the phylogenetic problem of pinpointing which human cognitive traits are derived. But the second question about human cognitive uniqueness concerns why this suite of novel traits arose. In the following sections, I first argue that these diverse cognitive abilities—social cognition, prospection and memory, and executive control—are intrinsically connected, with overlapping psychological and neurobiological substrates. Then I argue that understanding the evolution of human cognition requires a careful examination of what aspects of human behavior they actually support. In fact, complex behaviors often recruit diverse cognitive skills, and many behavioral differences between great apes and humans cut across traditional cognitive distinctions.

Interrelationships between Abilities

The previous sections examined evidence for similarities and divergences between humans and chimpanzees in particular cognitive “traits” spanning the range of theories concerning human uniqueness (Shettleworth 2012). While social cognition is a classic example of a domain-specific skill that processes a particular type of information, executive functioning is a set of domain-general skills that influence a wide range of behaviors. Most of the experimental paradigms described in previous sections (necessarily) aim to tease apart discrete skills, while controlling for other possible influences on animals’ performance. Yet increasing evidence from psychology and neuroscience suggests that these skills are in fact linked. It is therefore important to understand which cognitive abilities share underlying mechanisms, and which covary across individuals or species, in order to understand how these abilities evolved.

In fact, even abilities that seem quite distinct can sometimes recruit shared underlying mechanisms. For example, skills such as theory of mind

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TABLE 19.1. Summary of empirical evidence for ape cognitive abilities.

<i>Domain</i>	<i>Skill</i>	<i>Chimpanzees and Other Apes</i>
Social cognition	Goal and intention understanding	Reason about behavior in terms of underlying goals, not just superficial actions
	Gaze following and perspective taking	Understand that others see things, and can track their line of sight
	Knowledge and beliefs	Reason about how seeing leads to knowing, but only implicit understanding of false beliefs
	Joint attention	Little evidence for human-like triadic gaze interactions
Mental time travel	Joint intentions and collaboration	Prefer to work alone, and seem to show parallel (not joint) goals with partner
	Spatial memory	Rich representations of location of items in their spatial context
	Long-term memory	Some evidence that apes can recall unique events for several weeks or even years
	Episodic memory	Can bind item with spatial and temporal context, but may be a fragile representation
	Save artifacts for the future	Can select and retain a useful tool for a future action over hours or overnight
	Plan for future needs	Some evidence that apes abstain from immediately eating food in order to obtain something more desirable in the future
	Executive control	Working memory
Simple response control		Flexible inhibition of undesirable reaching actions compared to other primates
Complex response control		Some control over undesirable actions, but less robust than humans
Temporal discounting		Greater capacity to delay gratification than other primates, but less robust than humans
Updating rules and set shifting		Greater capacity to update rules than other primates, but little research on more complex human tasks

and spatial memory might be considered distinct domains—one encompassing how we think about the social world, and the other encompassing how we think about the physical world (Tomasello and Call 1997; Herrmann et al. 2007). However, there is increasing evidence that social cognition and episodic memory or planning may actually share some core cognitive systems. For example, there is broad overlap in the brain regions supporting

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social cognition, episodic memory and prospection, and even spatial navigation and memory (Buckner and Carroll 2007). In fact, this proposal suggests that a key constituent process underlying these cognitive abilities is simulation: theory of mind involves simulating the content of another individual's mind; mental time travel involves simulating past or future events; and navigation involves simulating a path through a complex environment. That is, these diverse abilities may depend on a core computational problem of simulating events that are not directly witnessed in the moment.

Executive function systems, by their very nature, are concerned with regulating and controlling other cognitive processes, and there is clear evidence that executive control influences both social cognition and mental time travel. In terms of social cognition, developmental psychologists have long recognized that executive function may constrain theory of mind, preventing individuals from displaying the full extent of their abilities in complex tasks (Hughes 1998; Perner and Lang 1999; Carlson et al. 2002; Bailargeon et al. 2010). For example, correctly indicating that another individual has a particular false belief about the world with a clear behavioral response (such as a reach or a point) requires the ability to hold two conflicting versions of the world in mind at once, and then inhibit responses concerning the (true) state of the world. As such, one possibility is that apes' failures at explicit false belief tasks may be partially due to the high executive control demands posed by those situations (see Krachun et al. 2007; Kaminski et al. 2008). This may also explain why apes do exhibit sensitivity to false beliefs in anticipatory looking tasks (Krupenye et al. 2016). Executive function demands in such situations are reduced, given that individuals do not need to inhibit a direct response toward the true location of an object.

The relationship between executive function and mental time travel is perhaps even stronger, as many studies of prospection in nonhumans involve heavy inhibitory control demands. For example, planning for the future inherently requires that an individual exhibit inhibitory control, subsuming present needs for future gains (Osvath and Osvath 2008). While the previous sections explored whether apes can construct mental simulations of future events (Suddendorf and Corballis 2007), successful future planning could not occur without the ability to suppress immediate gratification in favor of delayed rewards. Similarly, increasing cognitive and neurobiological evidence indicates that successful recall of episodic memory engages multiple cognitive control processes in order to make an appropriate response (Baddeley

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2000; Dobbins et al. 2002; Wagner et al. 2005). Accordingly, apes may be more successful at some episodic memory tasks because they require less executive control resources.

Defining Cognitive Adaptations

A major challenge for understanding the evolution of uniquely human cognitive abilities concerns identifying what constitutes a cognitive adaptation in the first place. Given that even seemingly disparate cognitive abilities share underlying psychological and neurobiological substrates, defining a coherent functional unit in the mind is a tricky task. Beyond these intrinsic relationships between psychological processes, many complex natural behaviors require the seamless integration of multiple abilities. Experimental cognitive tasks are explicitly designed to disentangle the contributions of a particular capacity, but real-world behavioral problems often require the flexible deployment of multiple skills in tandem. In fact, some of the behaviors of the greatest interest to psychologists, biologists, and anthropologists span these cognitive domains. Consequently, understanding why human-unique cognitive abilities evolved requires understanding the role of those abilities in contexts in which they are actually used (Rosati in press).

Consider the example of chimpanzee hunting, a behavior that has long been a focus of both theoretical ideas and experimental research on the origins of human behavior (Boesch and Boesch 1989; Stanford 1999; Muller and Mitani 2005; Gilby and Wrangham 2007; Tomasello et al. 2012). What cognitive capacities do chimpanzees use when hunting? Hunting clearly has a strong social component: often only one chimpanzee captures the monkey, but other individuals also tend to get at least a little meat (Mitani and Watts 2001; Gilby 2006). These hunting behaviors have therefore inspired psychological insights into the social cognitive capacities that support cooperation. However, this sort of complex behavior likely recruits cognitive skills from other domains as well. For example, successful hunting clearly requires components of executive function, including working memory to track the different visual paths of monkeys and chimpanzees during the chase, or response control to stop oneself from lunging directly at a monkey when doing so might result in catastrophic falls. Chimpanzees' abilities to plan and anticipate the future location of monkeys as they are being chased could also impact their hunting success in the wild.

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From an evolutionary perspective, it is therefore critical to consider cognitive abilities in terms of the real-world behaviors. By integrating experimental comparisons of cognitive skills with information about different species' natural history, it is therefore possible to address *why* differences in cognitive traits may arise. In particular, the comparative method—one of the most powerful tools in evolutionary biology—can provide insight into the ultimate function of cognitive capacities. The comparative method illuminates the historical process of natural selection by examining the traits of different species in relationship to their socioecological context (Clutton-Brock and Harvey 1979; Mayr 1982; Harvey and Purvis 1991). Although such species comparisons are used widely for understanding the evolution of morphological characters, only more recently have they been applied to the problem of cognitive evolution (Balda and Kamil 1989; Clayton and Krebs 1994; Bond et al. 2003; Sherry 2006; Amici et al. 2008; MacLean et al. 2012). In terms of understanding human evolution specifically, this approach can assess whether the unique behavioral problems humans face in their natural world leave a recognizable psychological signature in our minds—much like the types of morphological signatures that can be identified in the dentition or other physical characteristics.

Human Cognitive Specializations

Human behavioral ecology differs from that of other great apes in several important ways (Marlowe 2005; Hill et al. 2009). First, human hunter-gatherers tend to consume higher-quality resources that are more difficult to acquire and may involve additional processing. For example, humans eat more meat, and consume more foods that involve extractive techniques such as nuts or honey than do chimpanzees (Cordain et al. 2000; Kaplan et al. 2000; Marlowe et al. 2014). Indeed, humans are well characterized as inhabiting a cognitive ecological niche in terms of their foraging behavior. Humans also uniquely depend on starchy foods such as roots that must be cooked to become palatable and energetically valuable (Wrangham et al. 1999; Marlowe and Berbesque 2009; Wrangham 2009). In contrast, while chimpanzees possess many of the basic cognitive capacities needed to cook, such as the ability to delay gratification and understand the causal transformation that occurs during the cooking process (Warneken and Rosati 2015), they do not engage

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in these kinds of cooking behaviors in the wild—possibly because of the social risk of theft associated with engaging in cooking.

Second, human hunter-gatherers have larger home ranges than other apes (Marlowe 2005). While chimpanzees and other apes are more reliant on fruits and leaves, humans' reliance on distant, patchily distributed resources means that they must travel farther to find them. Moreover, while apes tend to consume food on the go, humans exhibit a unique pattern of central-place foraging, in which foods are brought back to and shared at a central camp. Indeed, humans engage in several complex cooperative behaviors involving the redistribution of food. Importantly, a diet that focuses on high-quality, hard-to-acquire resources is a diet that carries great inherent risk (Hill and Hawkes 1983; Hawkes et al. 2001): foragers may have food supply that is superabundant on some days, but absent on others. Accordingly, although humans are relatively risk-averse when faced with decisions about money, some evidence suggests we are more risk-prone when making decisions about food (Rosati and Hare 2016). Food sharing may represent an additional mechanism for humans to reduce the inherent variability that results from exploiting a high-quality diet (Kaplan et al. 2012).

Successfully utilizing these complex resources—locating food, processing that food, and finally distributing that food within a social group—requires a diverse array of cognitive abilities. For example, hunting and food processing are complex behaviors that are often learned socially. Some activities, such as hunting, may also occur in social groups where members cooperate with others to be successful, and therefore involve social cognitive skills supporting collaboration (Gurven 2004). Utilizing distantly located food resources across humans' large ranges requires identifying the location of food and navigating between locations. Thus, memory and planning systems allow individuals to successfully recall the locations of food and plan a route between them and camp. Finally, all of these behaviors require that humans exert executive control. For example, central-place foraging patterns mean that individuals must successfully avoid the immediate temptation of consuming all the food once they have access to it, but rather carry major portions of food as they navigate back to camp in order to share it. Similarly, many behaviors that are necessary to process food—such as cooking—require that individuals inhibit immediate consumption. Critically, all of these skills must be used in order to successfully exploit human-specific resources. Thus,

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human cognitive uniqueness may be best conceptualized as a suite of capacities cutting across psychological domains (Rosati in press).

Comparative studies further support the hypothesis that these cognitive abilities can exhibit evolutionary coherence in their emergence—at least when an animal's socioecological niche requires the integration of these skills. In fact, many differences between human ecology and that of other apes also exist (albeit in less dramatic form) between chimpanzees and bonobos. For example, chimpanzees depend more on spatially dispersed food resources with greater seasonal variability, face higher levels of social competition, and engage in more costly hunting and extractive foraging behaviors than bonobos (Kano 1992; Wrangham and Peterson 1996; Hare et al. 2012). Accordingly, chimpanzees exhibit more accurate spatial memory (Rosati and Hare 2012), higher levels of temporal self-control (Rosati et al. 2007; Rosati and Hare 2013), and more consistently demonstrate robust theory of mind skills in competitive contexts (see Rosati et al. 2010 for a review). Some of these same skills also seem to emerge in tandem in other taxa. For example, corvids exhibit robust skills in both social cognition and episodic memory (Emery and Clayton 2004; Clayton et al. 2007)—and their natural caching behaviors likely require both sets of skills to successfully retrieve cached foods without theft by competitors. Unfortunately, to date there has been little research systematically investigating capacities across all these domains in other species of interest, such as elephants, cetaceans, or hyenas—all of which exhibit complex social cognitive abilities (Connor 2007; Holekamp et al. 2007; Plotnik et al. 2011). However, comparative studies of apes and corvids provide tantalizing clues that these abilities may emerge together phylogenetically. Together, this provides convergent evidence for hypotheses about why human and ape cognition differs, as well as how different cognitive skills are mechanistically linked across evolutionary history.

Summary

In contrast to theories focused on identifying a single fundamental difference between the cognition of humans and apes, I have proposed that there are important divergences across a suite of psychological abilities including social cognition, episodic memory and planning, and executive control. At

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first glance, this range of differences presents a challenging problem for understanding human cognitive evolution: if humans and other apes differ psychologically in so many diverse ways, how is it possible to identify the ultimate evolutionary roots of these differences? I have argued that it is important to consider cognitive capacities not in isolation, but in terms of their interrelationships as well as their contributions to evolutionarily relevant behaviors. In fact, even diverse skills like social cognition, memory, and executive function have clear links in the mind and brain—and often must be used in tandem for the implementation of complex human behaviors such as hunting, foraging, and food sharing. As such, these suites of cognitive traits may emerge together in phylogeny. Comparisons of cognition in humans and chimpanzees—when integrated with information about these species' natural socioecology and behavior—can therefore begin to identify the evolutionary origins of human cognitive adaptations. Consequently, understanding the evolution of human cognitive uniqueness must involve relating those cognitive traits to the behavioral problems that humans uniquely must solve in the natural world.

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