

3.23 The Evolution of Primate Executive Function: From Response Control to Strategic Decision-Making

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3.23.1	Introduction	423
3.23.2	Response Control	424
3.23.2.1	Inhibiting Reaching Responses	424
3.23.2.2	Controlling Complex Motor Actions	425
3.23.2.3	Dealing With Response Conflict	426
3.23.3	Strategic Decision-Making	426
3.23.3.1	Delaying Gratification and Future-Oriented Choice	426
3.23.3.2	Accounting for Uncertainty	427
3.23.3.3	Sensitivity to One's Own Knowledge	428
3.23.4	Learning and Updating	429
3.23.4.1	Detecting Contingencies	429
3.23.4.2	Updating Rules	430
3.23.4.3	Adjusting for Context	431
3.23.5	The Roots of Human Executive Control	431
3.23.5.1	The Evolutionary History of Executive Function	432
3.23.5.2	Cascading Effects of Executive Control on Other Domains	432
3.23.5.3	Linking Executive Control to Human Brain Evolution	433
3.23.6	Conclusion	434
	Acknowledgments	434
	References	434

Abstract

Human cognition is permeated by self-control: the ability to engage in complex, goal-oriented behaviors rather than just react to the moment at hand. This chapter examines the evolutionary roots of these abilities by comparing the psychological capacities of humans and other primates. In fact, there is marked variation in how different primate species control their motoric responses to inhibit prepotent but ineffectual actions, engage in strategic decision-making to determine the best course of action, and learn and update their responses when contingencies change. Understanding how and why this variation emerged can shed light on the origins of human cognition.

3.23.1 Introduction

Intelligent behavior is one of the hallmarks of the human species: we do not merely react reflexively to the stimuli presented to us in the moment, but can rather engage in complex, goal-oriented behaviors that we carry out over extended periods of time. This ability to engage in such controlled behavior is often called executive function, an umbrella term for a diverse set of regulatory cognitive capacities that monitor other cognitive processes. These control processes allow individuals to flexibly regulate their behavior, overriding responses that would otherwise be carried out automatically. Executive control is central to behaviors that require incorporating new information, inhibiting currently inappropriate responses, or shifting to new responses when the rules of the game change—and therefore enables the sort of flexibility that defines intelligent behavior.

Our species' ability to engage in such seemingly purposeful or "willful" behavior presents a puzzle for both psychologists and biologists. At the proximate level, what psychological processes engender this sort of cognitive control? At the ultimate level, what are the origins of these capacities, and are there any that are unique to our species and therefore might help explain why human behavior is strikingly different from that of other animals? This sort of debate about continuity (or discontinuity) between human and animal minds originated with Darwin (1871, 1872) and continues to this day. Several prominent hypotheses about critical differences between humans and other primates are rooted in cognitive experiments (Tomasello et al., 2005, 2012; Suddendorf and Corballis, 2007; Penn et al., 2008), but the proposal that humans possess a uniquely well-developed set of executive function capacities has its bases in ideas about human brain evolution. Humans have long been noted to 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 (Semendeferi et al., 2002; Rilling and Insel, 1999; Goldman-Rakic, 1996; Schoenemann et al., 2005; Miller and Cohen, 2001). Yet this proposal is receiving increasing attention from comparative psychologists as well (Siegal and Varley, 2008; Rumbaugh et al., 1996; Barkley, 2001). Disentangling the psychological capacities that are shared or unique across species will play a critical role in linking these structural changes in the brain to their mental function.

In addressing the origins of human cognition, primates are of special interest because they are our closest living relatives. Comparative studies of primate cognition can therefore provide insights into the phylogeny of human psychological traits by identifying which human capacities are ancestral—inherited by common descent with other primates—versus which are uniquely derived traits that arose on the human lineage. Recent comparative research on self-control and decision-making in primates has generated a wealth of new information concerning how diverse species solve problems that tap into executive functions, so it is now possible to apply this comparative approach to understanding executive control. Integrating these empirical results with information about the natural history of different primate species—their ecological niche and social structure—can begin to illuminate why more sophisticated executive functions may evolve in the first place.

This chapter has four main parts. In the first section, I examine patterns of control over motor responses across primates—a basic form of executive function that allows individuals to inhibit prepotent responses when producing them is undesirable. In the second section, I examine patterns of value-based decision-making across primates. Decisions about whether to delay gratification or accept variation in reward payoffs require that individuals assess the value of different possible courses of action and then select the best one. Consequently, strategic decision-making inherently involves psychological processes that are central to executive function, such as acting toward future goals and inhibiting some possible responses. In the third section, I examine evidence concerning how primates learn, update, and shift their behaviors when the rules of the game or context change—key capacities for flexible behavior. Across these three sections, I will focus primarily on executive control problems where there is evidence from many diverse primate taxa, rather than a single model species. This broader comparative view will then underpin the final section examining the evolutionary origins of flexible executive control across primate species, including in our own.

3.23.2 Response Control

A foundational 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). The ability to control motoric responses in this fashion is a critical precondition for flexible behavior. Several standard tasks have been developed to examine how humans can control their responses under situations where there is conflict between different possible courses of action (Botvinick et al., 2004). However, most of these tasks have not been widely implemented across nonhumans, hindering systematic comparisons across species. Moreover, as shall be detailed in the following sections, current evidence suggests that nonhuman primates can have serious problems with inhibiting even simple reaching responses that prove minimally challenging for humans.

3.23.2.1 Inhibiting Reaching Responses

The ability to inhibit a direct reach toward a target is one of the simplest forms of response control. One of the most widely used tasks to probe response control in nonhumans is the A-not-B test, derived from a set of observations by Piaget (1954). In the basic setup, individuals initially experience that a reward is repeatedly hidden in one location (A), but on the critical test trial it is placed at or moved to a different location (B; see Fig. 1A). When confronted this problem, younger infants struggle to inhibit their prepotent reaches to the A location that previously provided a reward—even if they directly observed that the reward was moved to the second location (Diamond, 1990). A variety of features may influence performance on the A-not-B task, including visual attention to the reward's path, memory for the baited location, and motor control over reaching (see Jelbert et al., 2016; Smith et al., 1999 for reviews). However, humans show fast development of this suite of executive function skills, as toddlers begin to successfully solve this problem around their second birthday (Piaget, 1954; Call, 2001; see Rosati et al., 2014 for a review of this developmental sequence).

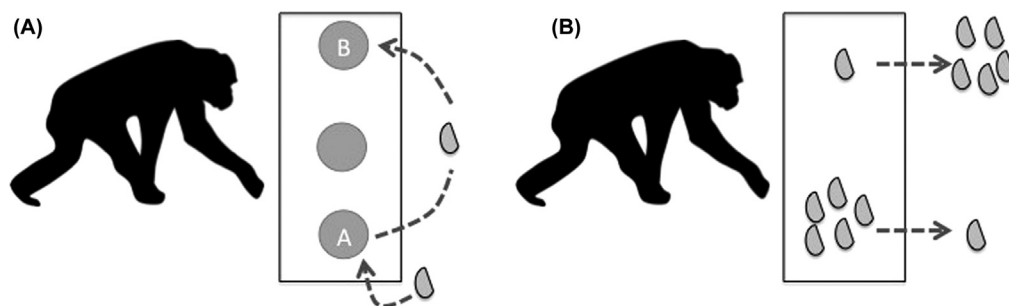


Figure 1 Controlling motor responses. (A) In the A-not-B task, individuals watch as a reward is repeatedly hidden in one location (the A container). In the test trial, the reward is first hidden under A, but then moved in full sight of the subject to the B container. (B) In the reverse-contingency task, individuals see a smaller and larger reward, but they receive the opposite of what they choose—so they must reach for the smaller reward to receive the larger one.

Current evidence indicates that many nonhuman species find the A-not-B problem to be quite difficult and often fail to inhibit prepotent motor responses in this situation. Two large comparative studies have directly compared a variety of primate species on the A-not-B task (MaClean et al., 2014; Amici et al., 2008). This includes all four species of great apes—chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo pygmaeus*); six Old World monkey species—rhesus macaques (*Macaca mulatta*) and other macaque species, hamadryas baboons (*Papio hamadryas*), and golden monkeys (*Rhinopithecus roxellana*); five New World monkeys including golden lion tamarins (*Leontopithecus rosalia*), marmosets (*Callithrix jacchus*), and capuchins (*Cebus apella*); and eight lemur species from a variety of genera including *Lemur*, *Eulemur*, *Propithecus*, and *Varecia*. These large-scale phylogenetic comparisons found wide variation in how different primate species deal with these kinds of challenges. For example, all four species of great apes show near-ceiling levels of success on the A-not-B task—similar to children tested on the same setup (Barth and Call, 2006). In contrast, several monkey and lemur species have much more difficulty inhibiting their prepotent reaching.

Similar evidence showing that apes generally have more robust motor control than do other primates comes from other sorts of problems where animals must also inhibit a reaching response. For example, in “detour” tasks, individuals have to refrain from reaching directly for a reward they can see, because it is blocked by a clear barrier. In one version of this problem, individuals must inhibit directly reaching for a visible reward because it is located on a ledge behind a clear plastic flap—a direct reach would knock the food out of reach when the flap is lifted. To get the reward, individuals must therefore detour around the flap to reach for the reward from the side. Human children and some ape populations show similar performance on this version of the detour task (Amici et al., 2008; Vlaming et al., 2010). In another variant, the reward is simply placed inside a transparent container with open ends (such as a box or cylinder): the subject’s direct reach is blocked, but they can access the food by going through the side opening. Even though animals can initially succeed at detouring to reach from the side when the barrier is opaque—a situation attenuating the desirability of the prepotent reach because the food is not visible—a variety of primate species struggle to detour when they can see the food (Diamond, 1990; MaClean et al., 2014, 2013; Santos et al., 1999; Lakshminarayanan and Santos, 2009). Yet as with the A-not-B task, apes generally show more control over their reaches in this situation than do monkeys and lemurs.

3.23.2.2 Controlling Complex Motor Actions

Apes may have more control over inhibiting simple reaching responses, but what about more complex forms of response control? Here the natural behavior of primates provides a hint that there are important differences across primates in degree of motoric control. Great apes (including humans) are much more proficient tool users than are monkeys, with the exception of a few species such as capuchins (Sanz, 2013; van Schaik et al., 1999). Along the same lines, humans have very dexterous hands with independent control of fingers when manipulating objects (Edin et al., 1992; Haeger-Ross and Scieber, 2000). While there is some evidence for similarly dexterous control of fingers in other apes, there is less evidence for this sort of fine motor control in monkeys (Byrne et al., 2001; Crast et al., 2009; Scheiber, 1991; Spinozzi et al., 2007).

Given apes’ sophisticated abilities to solve tool-use problems, many studies have focused on comparing the capacities of great apes in comparison to human children. While children and apes may show similar performance in some situations, children soon outpace apes when faced with more complex situations requiring the flexible inhibition of responses. For example, three-year-olds, six-year-olds, and chimpanzees can all initially learn to obtain a reward by raking it out of a tube or box. However, differences emerge when they are then subsequently faced with a slightly different situation—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. Here, 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., 2014).

Even when human children and apes show similar overall success in a task involving complex manual responses, they may differ in the extent to which they can specifically inhibit prepotent responses. For example, in one task, individuals were faced with a reward trapped in a vertical maze. Because the maze had various dead ends, participants had to plan their moves up to two steps in advance and inhibit prepotent actions to get the reward. Although apes and children had similar overall success at obtaining the reward, apes had more difficulty than children specifically in inhibiting motor responses that ultimately lead to dead ends (Voelter and Call, 2014). There is converging evidence from similar motor planning studies that apes struggle with this sort of sequential action planning. For example, in another task, apes had to move internal platforms so that a food reward would drop through to an accessible location at the bottom. While 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, they failed if they had to plan out an initial series of moves before touching the barrier with the food (Tecwyn, 2013). That is, it was difficult for the apes to inhibit their prepotent response toward the baited platform, even if doing so made it impossible to access the food later.

Together, these results indicate that even though children and apes show similar performance on more simple reaching tasks, children may outpace other apes in inhibiting motor responses in more complex contexts. More generally, nonhuman primates seem to have greater difficulty than humans in inhibiting their own reaches toward visible rewards or locations that have been routinely rewarded with food. Across a variety of setups, many primates species exhibit a strong tendency to reach directly toward rewards, even if doing so causes them to lose access to those rewards. One possibility as to why this occurs is that situations involving food may pose an especially challenging inhibitory-control problem for many nonhumans, as further detailed in the next section.

3.23.2.3 Dealing With Response Conflict

While *inhibiting* prepotent responses is a critical component of response control, many situations require that individuals *select* between different possible responses. This sort of ability is another foundational process supporting complex behavior. Several standard tasks have been developed to examine how humans control their responses under situations where there is conflict between different possible responses (Botvinick et al., 2004). For example, in a classic version of the “Stroop” task, individuals are asked to report the written color word they see. In some cases all the words are written out in a neutral font color (such as black), whereas in others the word itself is printed in a colored font. 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). This sort of response conflict can be invoked in a variety of ways, including by asking individuals to identify the number of words on the screen and then presenting words that are number terms themselves, or by asking individuals to identify the direction that an arrow is pointing (up or down) and altering whether it is located on the top or bottom of the screen.

Unfortunately, these sorts of tasks have not been widely used across many nonhuman primates species. What little evidence there is has often come from special populations of primates that have been extensively trained on artificial communication systems or numerical competencies (Beran et al., 2007; Washburn, 1994). However, the little evidence that exists also suggests important differences between humans and other primates. 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; see also Allritz et al., 2016). In fact, this chimpanzee made close to 50% 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). Overall this suggests that nonhumans may have a much more difficult time dealing with response conflict than do humans.

A different response control test that has been more widely studied across multiple species is known as the reverse-contingency task. Here, an individual is faced with a choice between different value rewards—for example, between one and five pieces of food. The trick is that they receive the item they *do not* choose (see Fig. 1B). Thus, it is necessary to select the smaller reward to actually receive the larger reward. 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 generally unsuccessful at this task when faced with real food rewards, and can only overcome this prepotent response when faced with symbolic representations of the amounts (such as Arabic numerals, for individuals who have been previously trained to understand these symbols) or other nonconcrete representations of the amounts (such as following training that a certain color cues a given amount). These representations seem to reduce the appeal of the larger reward, allowing a variety of primates to successfully choose the smaller reward (Boysen and Berntson, 1995; Boysen et al., 1996, 1999; Uher and Call, 2008; Shifferman, 2009; Vlamings et al., 2006). While children also improve when faced with symbolic rewards compared to real candy, even many 3-year-old children make the correct response when faced with candy—and 4-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.

3.23.3 Strategic Decision-Making

The previous section examined problems where the best response was clear, at least in principle. Individuals must inhibit their prepotent motor responses to reach their goal, but what goal they should actually be pursuing—acquiring the more valuable reward—is not in question. Another key type of executive control concerns the regulation of what that goal should be in the first place. That is, the problem is not whether individuals can produce the correct response, but how they assess what the “correct” thing to do actually is. In fact, many kinds of real-world decisions require that individuals decide which *strategy* to pursue (Venkatraman et al., 2009a,b). In these sorts of decision-making contexts, a particular choice is not necessarily yoked to a particular kind of motor response (for example, all choices might involve some sort of approach or reach toward the relevant option). Rather, the question at stake is how animals decide which of a set of possible options is actually the best.

3.23.3.1 Delaying Gratification and Future-Oriented Choice

Intertemporal choices—or decisions that involve trade-offs between the reward accrued and the time spent waiting for them—are ubiquitous in both human and animal lives. Decades of research have revealed that people can often have a potent bias toward immediate gratification—in situations ranging from dieting and health to saving for retirement, people tend to devalue, or discount, the future (Frederick et al., 2002). Yet a comparative perspective on intertemporal choice suggests that, despite the temptation that immediate gratification can present, humans are actually quite skilled at waiting for future payoffs: we can forgo payoffs right now to wait weeks or even months for larger rewards in some contexts (Rachlin, 2000). Humans’ relative prowess in delaying gratification in these sorts of decision-making contexts has provided crucial support for several prominent theories that humans are unique in our ability to consider the future impact of our decisions (McClure et al., 2004; Roberts, 2002; Stevens and Stephens, 2008; Suddendorf and Corballis, 1997). For example, some proposals argue that animals are psychologically “stuck” in the present, incapable of thinking about their future selves (Roberts, 2002).

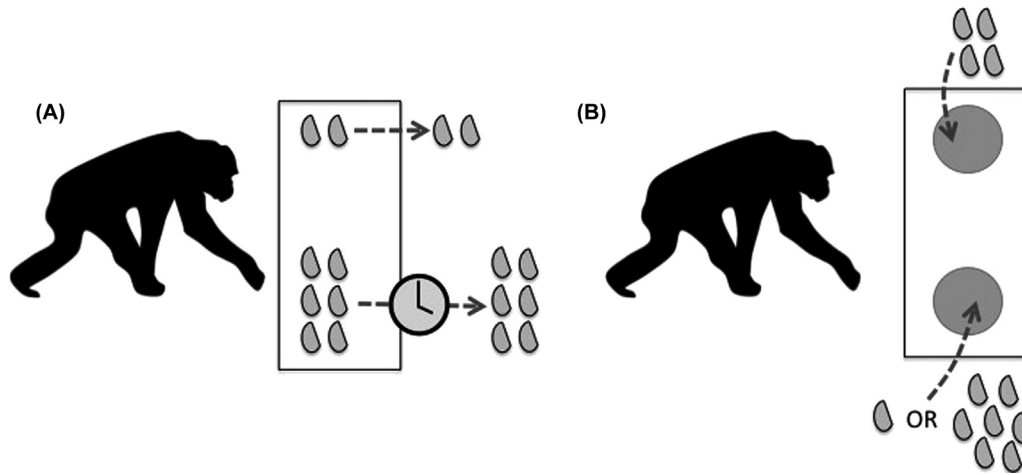


Figure 2 Decision-making. (A) In intertemporal choice tasks, individuals must choose between a smaller reward they could have right now, and a larger reward that they must wait some delay to receive. (B) In risky choice tasks, individuals choose between options that differ in the variance in outcomes they provided. In this example, the subject can choose between two options that provide equivalent average amounts of food, but one provides a constant reward whereas the other varies across trials.

In fact, there are major differences in the temporal preferences that different species exhibit. Early studies examining temporal decision-making in nonhumans found that when various birds or rodents were offered a choice between a smaller reward they could have immediately and a larger, delayed reward, they generally preferred to wait for the larger payoff only when the delay was very short (see Fig. 2A). However, if the delay was increased, they switched to preferring the immediate option—even if the delay imposed was in the range of 10 s (Mazur, 1987; Green et al., 1994, 2004; Tobin and Logue, 1994). Similar studies of intertemporal choice in nonhuman primates showed that while some monkeys were willing to wait a bit longer than pigeons or rats, they nonetheless switch to preferring the smaller reward in the range of 10s to 40s (Tobin et al., 1996; Stevens et al., 2005a). In general, these results supported the idea that other species do not think about the future consequences of their choices in a very rich way.

Yet the picture with great apes is quite different. More recent evidence has shown that when apes are presented with a delay-of-gratification task where a reward is accumulating over time—and accessing the reward halts the accumulation—some individuals were willing to wait more than 10 min to increase their payoffs (Beran, 2002; Beran and Evans, 2006; Beran et al., 1999). This basic result—that great apes are more patient than other species when delaying gratification to obtain more valuable future rewards—seems to hold across many diverse contexts (Addessi et al., 2013). For example, apes are consistently more willing to wait than other primates on accumulation delay-of-gratification tasks (Evans and Beran, 2007b; Evans et al., 2012; Parrish et al., 2014); apes exhibit a higher indifference points—or the delay attached to the larger reward at which they switch to preferring the smaller, sooner reward—in delay-adjusting tasks (Amici et al., 2008; Tobin et al., 1996; Stevens et al., 2005a; Rosati et al., 2007; Stevens and Muhlhoff, 2012; Addessi et al., 2011); and apes even wait longer durations in exchange situations in which they must give up a smaller reward to acquire a larger reward after some time has passed (Ramseyer et al., 2006; Dufour et al., 2007; Pelé et al., 2010, 2011).

Moreover, apes seem to use some of the same cognitive control capacities as humans to make future-oriented decisions. For example, chimpanzees will spontaneously distract themselves when waiting to access a desirable reward, such as by looking away from an accumulating reward or playing with toys (Evans and Beran, 2007a)—much like children trying to avoid the pull of immediate temptation (Mischel et al., 1972, 1989; Mischel and Ebbesen, 1970). Some evidence further shows that apes can envision and plan for future events, such as by saving a tool for several hours in anticipation of future tool-using opportunities (Mucalhy and Call, 2006). In these situations, apes can override immediate needs when planning for the future, choosing the tool that will be useful in the future even if the alternative is current access to a desirable fruit (Osvath and Osvath, 2008). Apes even apply these skills to novel contexts such as saving food items. Even though apes do not normally store food in the wild, chimpanzees will spontaneously save raw food for several minutes, to place it in a device that transformed it into a more desirable cooked item. In contrast, they will consume all the raw food in their possession when they lack access to this transformational device (Warneken and Rosati, 2015). Yet there is little evidence that monkeys or lemurs can plan for the future in this way (see Roberts, 2002)—suggesting that great apes have the most humanlike capacities for future-oriented behaviors among primates.

3.23.3.2 Accounting for Uncertainty

Decisions about risk, or probabilistic variation in payoffs, are also a pervasive problem across both human and animal lives. For example, the challenge of deciding the best course of action when outcomes are uncertain is one often faced by foraging animals: individuals have to decide which patch of food to exploit without knowing precisely how much food they will extract from

different patches. Humans generally exhibit a strong aversion to options with variable payoffs, at least when making decisions about monetary rewards (Kahneman and Tversky, 2000). Do other animals exhibit similar responses? Most studies have probed animal decision-making under risk by presenting them with decisions about variability in the amount of reward that they receive (eg, Heilbronner et al., 2008; Kacelnik and Bateson et al., 1996, 1997; Platt and Huettel, 2008). For example, an animal could choose between gambling on the chance that they receive seven pieces of food (or loose and only get one), or play it safe and take four pieces for sure. The average payoff is the same for both of these options, but there is great variability in the possible outcomes from the risky option. Other tasks have examined responses to risk where the variance in outcomes stems not from the amount of the reward, but rather the quality or desirability of the different potential payoffs (Rosati and Hare, 2011, 2012, 2013).

In these situations, a wide variety of nonhuman species ranging from insects to birds and mammals are broadly risk-averse for gains when making decisions about food (Kacelnik and Bateson, 1997). This suggests that humanlike patterns of risk-aversion might be a widely conserved foraging strategy. However, there is also accumulating evidence that even closely related primate species can show significant variation in their responses to risk. For example, rhesus macaques (Platt and Huettel, 2008; McCoy and Platt, 2005), capuchins (De Petrillo et al., 2015), and chimpanzees (Heilbronner et al., 2008; Rosati and Hare, 2012, 2013; Haun et al., 2011) have all been shown to be fairly risk seeking. While preferences in any given study can depend on a variety of contextual variables (such as the specific payoffs in play), this preference for risk seeking in some species is notable given that other (often closely related) species show risk aversion in similar or identical contexts. For example, chimpanzees were more risk-prone than bonobos across several directly matched comparisons (Rosati and Hare, 2011, 2012, 2013; Haun et al., 2011). Indeed, humans are also more risk-prone for food rewards when making decisions about food rewards in the same experience-based setup the necessarily must be used to examine decision-making in nonverbal animals (Hayden and Platt, 2009)—showing patterns similar to chimpanzees in matched comparisons (Rosati and Hare, 2016).

How do different species decide whether to play the odds? One important type of information that might influence these sorts of risk preferences is what happened in the past. For example, individuals might exhibit a win-stay lose-shift strategy across trials, showing a greater propensity to gamble again after a previous choice where they gambled and won, compared to those trials where they previously gambled and lost. Many diverse primates exhibit these sorts of trial-by-trial strategies, including monkeys (McCoy and Platt, 2005; Barraclough et al., 2004; Hayden et al., 2008), apes (Rosati and Hare, 2013), and humans in similar iterated tasks (Hayden and Platt, 2009; Worthy et al., 2013). However, not all species respond to feedback in the same way. For example, bonobos use a win-stay lose-shift strategy, adjusting their strategies depending on the outcome of their previous choice—but chimpanzees prefer to gamble regardless of whether this strategy paid off on their last choice (Rosati and Hare, 2013). This suggests that even very basic mechanisms for adjusting responses based on feedback can vary across species.

In more complex situations, decision-makers can use several different sources of information when deciding how to act. For example, individuals could integrate feedback about whole sequences of decisions over time to form expectations about future outcomes. Along these lines, humans seem to expect that winning will come in streaks—a phenomenon called the hot-hand bias (Nickersons, 2002; Ayton and Fischer, 2004). People generally tend to perceive (illusory) streaks in sequences of random outcomes, and people with a higher propensity to perceive such streaks are more likely to take risks (Wilke et al., 2014). At least some other primates also integrate information about sequences in this way. For example, when rhesus monkeys saw sequences of visual stimuli and had to correctly guess what symbol would occur next, monkeys tended to guess that the next symbol would match the previous one—and consequently fared worse at guessing the next image when faced with sequences specifically designed so that the outcomes did not occur in streaks (Blanchard et al., 2014). An open question, however, is whether animals merely predict that sequences of outcomes will match, or if they also form expectations about how their own behavior can influence these outcomes, like humans do.

3.23.3.3 Sensitivity to One's Own Knowledge

When faced with choices involving risk, decision-makers do not know the specific outcome of any given trial, but the likelihood of the potential outcomes is known. In other situations, however, decision-makers may not even have good knowledge about the possible outcomes in the first place. That is, the likelihood of different outcomes is not known in situations involving ambiguity. Although classical economic theories predicted that people make decisions based on expected value regardless of their confidence in their knowledge (Savage, 1954), subsequent empirical research has shown a person's knowledge or confidence in their judgments can have a profound impact on how they choose to act. In particular, people do not like choosing options where the potential range of consequences is unclear, showing a robust aversion to ambiguity above and beyond their aversion to risk (Camerer and Weber, 1992). Do nonhuman primates exhibit similar sensitivity to their own knowledge when making decisions, avoiding the unknown like humans? In fact, several explanations for ambiguity aversion in humans invoke quite complex forms of reasoning, including the possibility that people want to be able justify their choices to others (Curley et al., 1986), or that people want to avoid embarrassment (Heath and Tversky, 1991)—psychological processes that are unlikely to be shared with most other species. Moreover, ambiguity aversion requires some degree of sensitivity to one's own knowledge, yet whether nonhumans shared these sorts of metacognitive abilities to think about their own thoughts has been heavily debated (Terrace and Son, 2009).

Despite the potentially complex cognitive mechanisms that may underlie ambiguity aversion, some recent evidence suggests that at least some nonhuman primates show also this bias. One study tested this by presenting rhesus monkeys with a choice between a gamble with a known probability of winning a large reward, and an ambiguous option with an unknown probability of winning. Although these two options are equivalent in their average payoffs across trials, monkeys preferred the risky option with known

probability—much like humans facing the same problem (Hayden et al., 2010). Apes also exhibit ambiguity aversion when faced with gambles of unknown payoffs. Chimpanzees and bonobos made choices across four situations: in three trial types, they always saw the set of possible outcomes in advance, and therefore knew the probability of winning the high-value payoff (100%, 50%, or 0%). In the fourth type, however, the apes' view of the potential outcomes was blocked, so they lacked this knowledge. Although the average payoff from this ambiguous option was identical to the average payoff of the risky option (50% chance of winning), apes were less likely to choose this ambiguous option (Rosati and Hare, 2011).

Given that at least some primate species seem to recognize their own lack of knowledge when making decisions, will they go a step further and try to remedy this situation by seeking out new information before making a choice? There is evidence suggesting that some will. When apes and some monkeys do not initially know where a reward is located, they will engage in information seeking by changing their visual perspective to locate the reward by peering from a new angle (Call, 2010; Call and Carpenter, 2001; Rosati and Santos, 2016). Further evidence shows that apes will also exhibit this kind of information-seeking response specifically when it allows them to acquire more information about reward payoffs. In one study, a treat was hidden under one of several containers out of the apes' sight, but they had to select just one. The trick was that they could acquire more information about their likelihood of winning by peering under the containers from below, because the table the containers were supported on was made of transparent plastic. In fact, they were more likely to seek information in this way when their likelihood of selecting a baited container by chance was low (because more containers were present), than when it was higher (Marsh and MacDonald, 2012). Given that there are clear species differences in the basic propensity to engage in information seeking—some monkey species do not do so as readily as apes (Hampton and Schwartz, 2004) or in some cases at all (Paukner et al., 2006)—there may also be important differences in how animals seek information when faced with uncertainty.

3.23.4 Learning and Updating

Both basic control of motor responses and more complex forms of decision-making require that individuals learn about the costs and benefits associated with different courses of action. Moreover, the world is not static, so even once a set of contingencies is learned, it may be necessary to update the strategies guiding behavior when the rules of the game change or new information comes to light. Executive control systems play a critical role in allowing individuals to detect appropriate responses and flexibly adapt to a changing world.

3.23.4.1 Detecting Contingencies

In many of the decision-making paradigms discussed previously, animals first gain experience with potential options before they start making choices. For example, animals might sample all available options in an initial exposure phase involving “forced choice” or “exposure” trials, where only one option is available at a time to ensure that the individual has had the opportunity to learn about different reward distributions. Similarly, foraging animals must often learn about payoff distributions by sampling different courses of action over time, for example, by eating food from different patches (Dall et al., 2005)—so these learning mechanisms likely impact real-world behavior.

What processes shape this kind of learning, and are there differences between humans and nonhumans? It is clear that experience-based learning plays an important role in human decision-making (Hertwig and Erev, 2009). In some contexts these same sorts of learning mechanisms shape other species as well. For example, when humans and pigeons are presented with structurally identical decisions and learn about their options through direct experience, they exhibit similar risk preferences (Ludvig et al., 2014). Metaanalyses examining larger numbers of species similarly suggest shared underlying psychological processes (Weber et al., 2004). These kinds of direct comparisons between humans and nonhumans provide strong evidence that at least some substrates for learning about costs and benefits in a dynamic situation may be widely shared.

However, animals and humans may show important differences in how they learn about more complicated distributions. One example comes from the Iowa Gambling Task, a more complex reward-learning situation that has been the focus of increasing comparative work (see Fig. 3A). In the original version of this task developed for humans (Bechara et al., 1997), individuals could choose between four decks containing cards, with each representing either a win or a loss of money. Importantly, these decks differed both in their average payoffs over time and in their variance: two of the decks produced average losses over trials but occasionally resulted in a very big payoff, whereas the other decks did not pose as much risk and resulted in average gains over time, but did not provide the highly salient large payoffs of the “bad” decks. Although people have no initial knowledge about these decks' payoffs, most learn to prefer the higher-value, lower-risk decks by sampling the different available options over time.

Several studies have adapted this basic setup to examine how other species learn about rewards. Yet these results suggest that other species may not always be as sophisticated as humans doing this. For example, humans, chimpanzees, and capuchins were directly compared on a simplified version of this task involving only two decks (Proctor et al., 2014). Across several conditions that differed in the relative variance and mean payoffs of two options, capuchins generally showed less evidence of learning the optimal response compared to humans or chimpanzees. Similarly, several rodent adaptations of this setup involving operant tasks suggest that rodents may also fail to converge on the optimal response (see de Visser et al., 2011 for a review). These results suggest

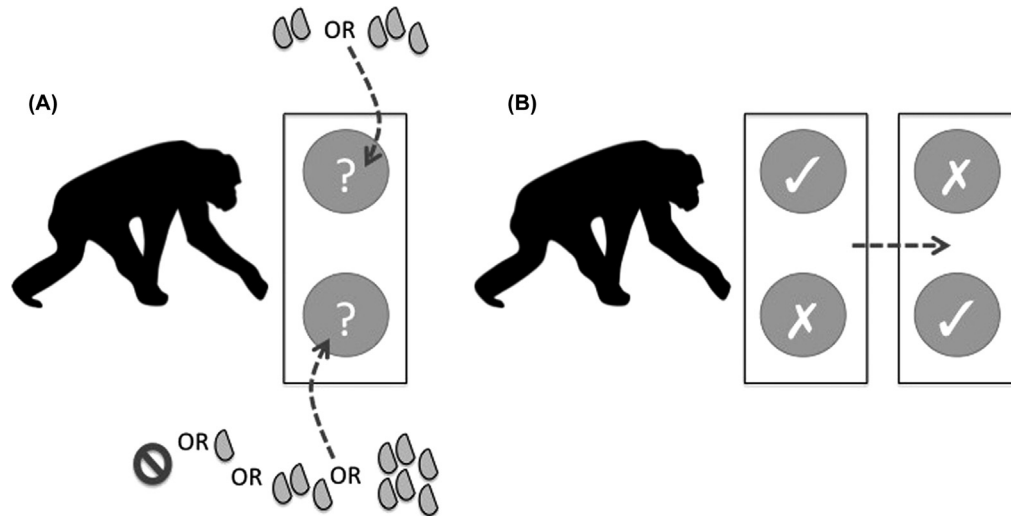


Figure 3 Learning and updating. (A) In a modified Iowa gambling task, individuals must learn about the contingencies of two options: one that is less risky and has a higher expected value over trials, and another that is riskier, sometimes provides very high payoffs, but also results in lower rewards across trials. (B) In reversal learning tasks, individuals first learn that one course of action is desirable, and then these contingencies are flipped to examine how quickly they update and adjust their responses.

that while other species can learn about reward variance by sampling unknown options, there may be differences in how fast other species learn or what aspects of the payoffs are most salient compared to humans.

3.23.4.2 Updating Rules

In the real world, a given behavioral strategy is unlikely to always be ideal because environmental contingencies are stochastic: a course of action that pays off now may no longer do so in a day or a year. Consequently, animals must be able to not only learn what behavioral strategy to pursue initially, but also update that strategy when the rules of the game change. The simplest example of updating behavioral strategies is reversal learning—how individuals respond when a previously valid response is now incorrect.

In the basic setup for a reversal learning task, individuals initially learn one rule (for example, that the correct response is to choose the blue container, and the incorrect response is to choose the yellow container). Once individuals repeatedly respond in accordance to that rule, the rule then switches (so now the yellow item is the correct response). This situation therefore examines whether animals perseverate in choosing the option that used to be correct, or can instead update their representation of the rules of the game (see Fig. 3B). Reversal learning tasks have been implemented across many diverse nonhuman species, so they provide a good benchmark for tracking variation in executive control across primates. In fact, chimpanzees and other apes generally outperform monkey and lemur species in their ability to pick up the new contingency and adjust their behavior when the correct response switches (Rumbaugh et al., 1996; Deaner et al., 2006; Rumbaugh and Pate, 1984). This suggests that apes exhibit a more flexible ability to learn and apply new rules relative to other nonhuman primates—similar to their greater control over motor responses.

For all its usefulness in examining executive control across many nonhuman species, it is also important to note that reversal problems are markedly less complex than common tasks used to measure set shifting in humans. For example, one situation commonly used to assess human executive functioning is the Wisconsin card sorting task (Milner, 1968; Grant and Berg, 1948). As in reversal learning tasks, this situation requires that individuals learn a rule, and the correct response changes once the player demonstrates initial learning of the rule. In contrast to primate reversal learning tasks, the card-sorting tasks requires that people detect and classify the images on the cards that vary on multiple dimensions such as shape, color, and number—much like a typical card deck has cards that can show different suites, red or black colors, and different card values. Consequently, detecting the rule and updating responses in this situation is significantly more complicated than in typical primate reversal learning tasks.

While there is no direct analog of this card-sorting task designed for nonhumans, some simplified versions of this problem have been developed. For example, rhesus monkeys completed a touchscreen task where they categorized stimuli that differed along two dimensions, such as color and shape. On each trial, the monkey would see three stimuli that varied across these two dimensions and were rewarded for choosing the matching item. The target dimension would then shift to see if the monkeys could pick up the new contingency (Moore et al., 2005). For example, items might initially be classed based on color, but then shape would become the relevant dimension. In fact, older monkeys showed impairment at this kind of updating (Moore et al., 2003), paralleling shifts in executive function seen in humans. Similar declines in reversal learning have been noted in chimpanzees in a simpler reversal learning task (Manrique and Call, 2015), suggesting the potential for shared mechanisms underlying these declines. However, to date there has not been direct comparisons of performance on a sorting task across different primate species. Importantly, grade

school children can already solve versions of the Wisconsin card sorting task with the same level of accuracy as adults (Chelune and Baer, 1986), suggesting that this is a form of executive function that emerges before adulthood in human development. Consequently, future research directly comparing humans, apes, and monkeys when faced with this kind of problem will be critical to address the evolution of flexibility.

3.23.4.3 Adjusting for Context

A final critical component of learning and updating is the ability to modulate behavioral strategies according to context. In some ways this is an extension of the previous ideas. For example, the ability to inhibit prepotent reaching can be construed as an adjustment based on context: reaching directly for a reward is generally a successful strategy, but sometimes it backfires because the reward is actually behind a barrier. Similarly, reaching for the larger of two possible rewards is generally a reasonable response—but not if an individual faces a reverse-contingency problem. Consequently, being able to recognize when context shifts the desirability of different courses of action is a key component of executive control. Along these lines, there is increasing evidence that a variety of nonhumans are sensitive to context when making decisions (see Rosati and Stevens, 2009; Santos and Rosati, 2015 for reviews).

One such example comes from examining how primates make trade-offs between costs and benefits when pursuing resources. As described earlier, both humans (Frederick et al., 2002; Loewenstein et al., 2003) and other primates tend to devalue rewards that involve a temporal cost and are therefore delayed in time. Yet sometimes decision-makers do not just pay costs not in terms of time, but in terms of the amount of effort or work that is required to gain the reward (Rudebeck et al., 2006; Walton et al., 2007). Although many real-world situations conflate time and effort costs, careful experiments teasing them apart show that some primates will shift their patterns of decision-making depending on which type of cost they face. For example, when monkeys face intertemporal choices about delayed rewards, cotton-top tamarins (*Saguinus oedipus*) are less willing to passively wait for larger rewards than are marmosets (Stevens et al., 2005a). Yet when monkeys must expend effort by traveling to acquire larger but spatially distant rewards, tamarins are more willing than marmosets to pay this sort of cost—even though the time it took them to reach the reward was less than in the passive waiting situation that marmosets prefer (Stevens et al., 2005b). This reversal of preferences across species indicates that the monkeys' preferences shifted across temporal versus effort contexts.

Another well-studied example of context sensitivity is the framing effect. Work from psychology and behavioral economics shows that humans treat rewards differently depending on how they are presented: a relative loss seems different than a relative gain, even if the actual outcome is equivalent (Kahneman and Tversky, 2000; Tversky and Kahneman, 1981). Several primate species show this tendency as well. For example, in one simple test of the framing effect in primates, individuals can choose an option initially consists of one reward, but it is sometimes augmented to two pieces if after their choice. This *gain frame* is contrasted with a *loss frame* where the option initially consists of two pieces but sometimes is decreased to one. Even though both of these options provide the same average payoff—1.5 pieces of fruit—framing that amount as a relative gain makes it seem more attractive than if it appears to be a relative loss. Capuchins, chimpanzees, and bonobos all are more likely to prefer this option when it is presented in the gain frame (Chen et al., 2006; Krupenye et al., 2015, 2016). Whether rewards are perceived as losses or gains further shifts how capuchins respond to decisions about risk: monkeys are more likely to gamble if the rewards in play appear to be relative losses, but more likely to play it safe when the rewards are relative gains (Lakshminarayanan et al., 2011, see also Marsh and Kacelnik, 2002).

Finally, decision-making in some nonhumans is sensitive to social context. In humans, there is emerging evidence that social context can shift a decision-maker's goals or emotional state. For example, people are more likely to make risky choices if it improves their status relative to a hypothetical competitor (Hill and Buss, 2010; Ermer et al., 2008). People may further weight potential losses more heavily when alone, but focus on the possibility of winning more than others in social contexts (Bault et al., 2008). Mechanistically, competitive social contexts may shift people's mood states (such as anger) and thereby increase risk-seeking behaviors (Fessler et al., 2004). Competition is also a pervasive component of social interactions across primate species, so being able to adjust decision-making strategies to deal with social context has a similar logic. In one study, chimpanzees and bonobos become more risk seeking following a competitive interaction compared to a neutral one, much like the evidence from humans (Rosati and Hare, 2012). In contrast, the apes' preferences did not change following a positive (play) interaction, suggesting some specificity of this shift to the competitive context. This sort of evidence suggests that social context can influence economic decisions that involve individual-level strategies such as in risky choice—possibly because social context can be an important cue as to the value of various resources in the current environment.

3.23.5 The Roots of Human Executive Control

The previous sections have shown that there are systematic differences in the executive control capacities seen across different primate species. Whenever matched comparisons exist between apes, monkeys, and lemurs, great apes consistently show more flexible control over their motor responses, show greater ability to delay gratification and incorporate information about their own knowledge state into decision strategies, and are faster to update their behavioral patterns when contingencies shift. Moreover, humans exhibit more flexible behavior across these same dimensions when compared to apes. Indeed, often these direct comparisons contrast other great apes with young human children, suggesting that the gap may widen even more substantially if this comparison involved human adults. This final section will therefore examine the evolutionary origins of these human capacities, as well as the consequences of these differences for the human mind and brain more generally.

3.23.5.1 The Evolutionary History of Executive Function

Although humans show important cognitive similarities with other primates, the previous sections showed that we also have many abilities that markedly differ from other species. Why did such differences in cognitive capacities emerge? One way to answer this question is to use the comparative method to relate different species' traits to evolutionarily relevant characteristics such as social structure or feeding ecology. This comparative approach is one of the most powerful tools in evolutionary biology for illuminating the historical processes of natural selection (Clutton-Brock and Harvey, 1979; Harvey and Purvis, 1991; Mayr, 1982). Recent cognitive comparisons of different primates have begun using this approach to examine patterns of executive control across taxa, and there is increasing evidence indicating that closely related primates vary in executive control capacities in accordance with their wild ecological niche.

For example, marmosets are more willing to passively wait delays, whereas tamarins are more willing to travel distances to acquire larger rewards (Stevens et al., 2005a,b; Rosati et al., 2006). Although these species have similar body sizes and social group structure, there is an important difference in their wild diets: marmosets are obligate gummivores who spend much of their time waiting for sap to exude from trees (Stevenson and Rylands, 1988), whereas tamarins only feed on gum opportunistically but have larger home ranges to exploit more ephemeral fruit and insects (Snowdon and Soini, 1988). Thus, marmosets' greater willingness to wait temporal delays maps onto their behavioral need to acquire gum, whereas tamarins' greater willingness to expend effort maps onto the larger distances they must travel to exploit their typical food resources.

There is similar evidence for differences in executive control in apes. Despite their close evolutionary relatedness (Won and Hey, 2005), chimpanzees and bonobos live in regions with important differences in the ecology (Kano, 1992; Wrangham and Peterson, 1996; Malenky and Wrangham, 1993; White, 1989, 1998; White and Wrangham, 1988; Wrangham, 2000). In particular, chimpanzees are thought to face higher temporal costs to obtain food, as evidenced by longer search times between patchy resources and their use of temporally costly extractive foraging techniques; face more risk in their resources, as evidenced by more seasonal variation and a greater dependence on risky hunting; and face greater feeding competition, which may have resulted in relaxed selection on aggressive behaviors in bonobos and contribute to differences in these species' social structure (Hare et al., 2012). Along these same lines, chimpanzees and bonobos exhibit target differences in executive control. Although chimpanzees and bonobos generally show quite similar patterns of cognitive skills (Herrmann et al., 2010), chimpanzees are more patient when waiting for future rewards, more risk-prone, and better able to inhibit undesirable reaching in social contexts than are bonobos (Rosati et al., 2007; Heilbronner et al., 2008; Rosati and Hare, 2012, 2013; Haun et al., 2011; Wobber et al., 2010). This indicates that variations in executive control in apes may be tailored to these species' natural history.

Several large comparative studies of different executive control capacities, controlling for the phylogeny of these species, further support the link between ecology and executive control. For example, a comparison of intertemporal choice patterns in 13 primate species found that one important predictor of willingness to delay gratification was home range size: species that typically had longer search times in the wild were more willing to wait in experimental tasks. Comparisons of response control in a sample of 23 primates showed that dietary breadth—the number of distinct categories of food items in their diet—predicted the abilities of different apes, monkeys, and lemurs to inhibit prepotent reaching in the A-not-B and detour tasks (Maclean et al., 2014). In contrast, neither of these analyses found that common metrics of social complexity such as group size predicted temporal preferences (Stevens, 2014) or response control (Maclean et al., 2014, 2013). It may be that more specific measures of social complexity—such as whether different primates have a fission–fusion social structure where smaller subsets of individuals spend time together and then rejoin the larger group—may also support the emergence of stronger inhibitory control (Amici et al., 2008). However, to date most evidence has highlighted the importance of ecological variables in shaping these skills.

This evidence suggests that more sophisticated executive control capacities may evolve in response to complex ecological problems across primate species. Is this also true for humans? In fact, human feeding ecology differs from that of other great apes in several important ways that parallel the ecological differences already highlighted in other primates. For example, human hunter-gatherers have larger home ranges than other apes and exhibit a unique pattern of central place foraging where individuals return to a centralized location to prepare and consume food they have gathered (Hill et al., 2009; Marlowe, 2005). That is, humans are more reliant on distant food sources that are more temporally (and effortfully) expensive to exploit. Moreover, humans must inhibit eating food in their possession to bring it back to the central camp—similar to the sorts of response control problems explored in earlier sections. These observations suggest that, evolutionarily, humans may exhibit especially robust executive function to support this human-specific pattern of foraging.

3.23.5.2 Cascading Effects of Executive Control on Other Domains

These evolutionary differences in human executive control systems likely have pervasive impact on other domains of behavior. Executive functions are inherently concerned with regulating and controlling other cognitive processes, so changes in executive functions will have cascading effects on other domains. In fact, some proposals suggest that executive control may constrain or enable other sophisticated cognitive skills that are critical for understanding human cognitive uniqueness—and there is increasing evidence supporting these claims. For example, some influential proposals suggest that humans and other animals have critical differences in sociocognitive capacities (Tomasello et al., 2005; Tomasello and Call, 1997; Tomasello and Carpenter, 2007)—how we think about other individuals' minds—or our memory and planning capacities (Suddendorf and Corballis, 2007;

Suddendorf, 2006; Suddendorf and Bussey, 2003)—how we thinking about the past and the future. Both of these skill sets seem intimately related to executive control.

In terms of social cognition, humans possess a complex belief-desire psychology that represents not only other's observable actions, but also others' internal and therefore unobservable psychological states. Current evidence suggests that apes and some other primates can also make surprisingly complex inferences about the goals, desires, and perceptions that motivate other's behavior (for reviews, see Call and Tomasello, 2008; Hare, 2011; Tomasello et al., 2003; Rosati et al., 2010). However, there are also some salient differences in how other primates reason about mental states. For example, while some species can infer the perceptions and knowledge of others, there is currently no evidence that any nonhuman can understand that others can hold false beliefs about the world (Marticorena et al., 2011; Kaminski et al., 2008; Krachun et al., 2007; Martin and Santos, 2016). One explanation for this pattern of results concerns the high executive function demands posed by situations involving false beliefs, versus other kinds of mental content such as perceptions and knowledge. Developmental psychologists have long recognized that executive function may constrain theory of mind abilities (Hughes, 1998; Carlson et al., 2002; Perner and Lang, 1999): representing that another individual has a particular *false* belief about the world actually requires that two conflicting representations of the world (the true one, and the false one) are held in mind at the same time, and making responses consistent with others holding a false belief further requires that the representation of the true state of the world is then inhibited when making a response. As such, primates' consistent failures at false belief tasks may be due to these high executive control demands.

The role of executive functions in episodic memory and future planning (together often referred to as "mental time travel") is also clear. Many situations involving prospection in nonhuman studies inherently require robust inhibitory control of the sort discussed previously, such as inhibiting ineffective motor responses or delaying gratification. For example, in one study, apes were given a choice between taking a tool (a straw) that would allow future access to highly preferred juice, or a piece of fruit that provided immediate benefit; apes in fact preferred the straw (Osvath and Osvath, 2008). This sort of successful future planning could not occur without the ability to suppress immediate gratification in favor of delayed rewards. Along the same lines, increasing cognitive and neurobiological evidence from humans indicates that the recall of episodic memory engages multiple cognitive control processes to make an appropriate response (Dobbins et al., 2002; Baddeley, 2000; Wagner et al., 2005). Accordingly, humans may show outstanding mental time travel capacities at least partially because our executive functions allow us to mediate between these conflicting behavioral options.

3.23.5.3 Linking Executive Control to Human Brain Evolution

Comparative studies of executive control in other primates suggest that ecological complexity may be an import predictor of these capacities across species. That is, wild feeding ecology may be the ultimate cause of differences in these capacities. But this same research has also highlighted that evolutionary changes in executive function are linked to evolutionary changes in the brain. Humans have an especially large brain, and more recent studies examining the architecture of specific regions in humans and other apes highlight there are important differences in the regional organization and connectivity of the human brain as well.

In terms of general patterns of brain evolution, several large comparative studies have highlighted that the absolute brain size of different primate species is a strong predictor of executive control capacities. For example, the study examining performance on the A-not-B task and detour task found that dietary breadth predicted performance on these motor inhibition problem, but absolute brain volume did as well. However, differences in relative brain volume (controlling for each species body size) did not predict a given species' success (Macleán et al., 2014). Similarly, in the comparative study of intertemporal choice, both home range size and absolute brain size predicted great willingness to delay gratification, whereas relative brain size did not (Stevens, 2014). Along these lines, the human brain that is both larger than would be expected for a primate of our size, and absolutely larger than that of other apes: 1300 cc compared to 300–400 cc for chimpanzees, bonobos, gorillas, and orangutans (Rilling and Insel, 1999; Schoenemann, 2006). While the number of neuronal cells in the human brain scales with the expected number for a primate of our size, the *absolute* number of neurons in the human brain is nonetheless the highest among primates (Herculano-Houzel, 2012). These results highlight the importance of absolute brain size when considering cognitive functions such as executive control across primates. Although relative brain size has long been a preferred index used by evolutionary biologists and anthropologists when examining the evolution of the brain, absolute brain size might be a better predictor of many relevant cognitive skills because changes in absolute size seem to go hand-in-hand with changes in the underlying structure and connectivity of brain regions supporting specific cognitive capacities (Striedter, 2005). However, it is important to note that this relationship may not hold across more distantly related taxa with different patterns of brain organization. For example, while elephants have larger brains than humans, they actually have less cortical neurons—suggesting that scaling relationships seen in primates do not necessarily hold in other taxonomic groups (Herculano-Houzel, 2012; Herculano-Houzel et al., 2014).

Absolute size may also be important for understanding the evolution of frontal cortex, which is especially important when considering the origins of humanlike decision-making and executive control (Passingham and Wise, 2012). Although it was previously thought that humans have a disproportionately enlarged frontal cortex compared to other apes, this claim was primarily based on early studies involving a few incomplete samples of nonhuman ape brains. More recent analyses, however, have challenged this view. The relative size of human and nonhuman ape frontal cortex is similar (Semendeferi et al., 2002); humans rather have an absolutely larger frontal cortex. As with overall brain size, this shift may be associated with changes in the organization of specific regions or the connectivity between regions. For example, a comparison of humans and other apes shows

that humans have more white matter in the frontal lobe than expected based on ape data (Schenker et al., 2005). Detailed histological studies of specific parts of the frontal cortex have also revealed important differences in absolute size, regional subdivisions, and cytoarchitecture between humans and other apes (Semendeferi et al., 1998, 2001). This kind of evidence can begin to link evolutionary changes in cognition to changes in their underlying neural substrates.

3.23.6 Conclusion

The ability to engage flexible, goal-oriented behavior is a hallmark of our species. Recent comparative evidence from across primates has begun to illuminate the evolutionary roots of human executive control. At the proximate level, there is increasing evidence for important differences in the degree to which different primates can inhibit prepotent but ineffective motor responses; how primates make decisions about the timing and uncertainty associated with benefits; and finally in how primates learn, update, and shift their preferences across contexts. Phylogenetically, these comparisons also reveal that humans show more controlled responses than other primates whenever matched comparisons exist—but also nonhuman apes show more control than monkeys or lemurs. At the ultimate level, there is increasing evidence that environmental complexity—such as species' typical wild feeding ecology and home range size—predicts species' executive control capacities. Thus, linking comparative cognitive studies with information on species' natural behavior can begin to address why differences in cognitive control evolve, including in our own lineage.

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