

CHAPTER 2

[lrh]Setting the Stage**[rrh]Future-Thinking in Animals****[cn]Chapter 2****[ct]Future-Thinking in Animals****[cst]Capacities and Limits**

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[ct epig]The brute is an embodiment of present impulses, and hence what elements of fear and hope exist in its nature—and they do not go very far—arise only in relation to objects that lie before it and within reach of those impulses; whereas a man’s range of vision embraces the whole of his life, and extends far into the past and future.

—ARTHUR SCHOPENHAUER, *Studies in Pessimism* (1851/1890)

[bodyni]Nonhuman animals (hereafter “animals”) do not harness the future to dominate their environments in the immediately obvious way that humans do (Suddendorf, 2006). It is therefore unsurprising that early thinkers such as Schopenhauer and others (e.g., Bergson, 1896/2004; Köhler, 1917/1927; Nietzsche, 1876/1998) regarded animals as being largely mentally bound to the present (but see James, 1890). Contemporary scientific theorists have also made cases for strong limits on nonhuman future-thinking (Roberts, 2002; Suddendorf & Corballis, 1997), and, driven by these claims, comparative psychologists have begun to document animal behaviors that appear in some way oriented toward the future (for previous reviews, see Cheke & Clayton, 2010; Roberts, 2012; Suddendorf & Corballis, 2007, 2010). Conflicting interpretations of the

CHAPTER 2

results has led to the formation of two camps within the literature: one that tends to emphasize the possible continuities between human and animal future-thinking (e.g., Clayton, Bussey, & Dickinson, 2003; Corballis, 2013; Osvath & Martin-Ordas, 2014; Roberts, 2012; Scarf, Smith, & Stuart, 2014; Zentall, 2005) and one that tends to emphasize the possible discontinuities (e.g., Cheng, Werning, & Suddendorf, 2016; Hoerl, 2008; Redshaw, 2014; Suddendorf, 2013a; Tulving, 2005).

Despite much heated debate, however, the dichotomy between the continuity and discontinuity camps is, in many respects, a false one. Both sides would agree, for instance, that animals often act in ways that increase their future survival and/or reproductive chances without mentally representing the future at all. Future-oriented behaviors need not necessarily require sophisticated planning, but instead can exist as purely innate processes (e.g., fixed action patterns) and/or arise via associative learning (Suddendorf & Corballis, 2007, 2010). Both sides would also agree that future-thinking is not an all-or-none process, an encapsulated cognitive module that an organism is either equipped with or not. Among humans, the various components involved in future-thinking come online at different ages during childhood (Suddendorf & Redshaw, 2013), and individual differences in the capacity persist into adulthood (e.g., Lebreton et al., 2013). Finally, both sides of the debate would agree that: (1) at least some animals can represent more than just perceptual information tied to the present, and (2) there are at least some differences between human and animal future-thinking (whether these differences be quantitative or qualitative in nature).

In defining future-thinking, various theoretical positions have placed differential emphasis on the subjective nature of the phenomenon and its behavioral consequences. Tulving (1985), for instance, initially put forward the notion of *autonoetic*, or “self-knowing,”

CHAPTER 2

consciousness to refer to the first-person awareness often implicated in mental access to past and future autobiographical events. Suddendorf and Corballis (1997) later coined the term *mental time travel* to refer to these declarative mental trips into past and future and also indicated that important differences may exist between the capacities of humans and animals. Specifically, they proposed the seminal Bischof–Köhler hypothesis (cf. Bischof-Köhler, 1985; Bischof, 1985; Köhler, 1917/1927), suggesting that animals may not be able to imagine and prepare for future desire states that conflict with their current states (see the section “Acting with future desires in mind,” later in this chapter). Subsequently, however, Suddendorf and Corballis (2007; 2010) emphasized how the behavioral consequences of this future-thinking might be discerned, reasoning that evolution can work only on the behavioral “output” or actions of an animal, and not on mental events per se. A number of researchers have since proposed that certain behavioral capacities (Raby & Clayton, 2009) or underlying mechanisms (Osvath, 2016; Osvath & Martin-Ordas, 2014) should be key to understanding the future-thinking of animals. The empirical goal of comparative psychologists, then, should perhaps not be to determine whether animals can mentally represent events that have not yet happened but, rather, to establish their capacities and limits in various future-oriented behavioral domains (Osvath, 2016; Raby & Clayton, 2009; Suddendorf & Corballis, 2007).

In the bulk of this chapter, we review and critique the evidence for future-oriented animal behavior from several lines of research. Future-thinking itself, of course, cannot be directly observed in nonverbal subjects, yet with careful controls simpler alternative explanations for their behavior can be ruled out with increasing confidence (Suddendorf & Corballis, 2010). Throughout our analysis, we highlight not only the achievements of animals on certain tasks, but also their failures, and suggest where their cognitive limits may lie. We then synthesize these

CHAPTER 2

findings and make the case for at least one overarching limit—namely, that animals (unlike humans) may not be able to reflect on their own natural future-thinking limitations and act to compensate for them to acquire additional benefits. Given that the vast majority of research has focused on primates, rodents, or corvids, we largely restrict our analysis to studies of these taxa. We do, however, point toward other branches of the phylogenetic tree that may be worth investigating.

[a]Animal Future-Thinking across Domains

[bodyni]In the following sections, we survey the behavioral evidence for animal future-thinking across six domains: (1) navigation and route planning, (2) intertemporal choice and delayed gratification, (3) preparing for future threats, (4) acquiring and constructing tools to solve future problems, (5) acquiring, saving, and exchanging tokens for future rewards, and (6) acting with future desires in mind. We then summarize animals' capacities and potential limits in each domain in Table 2.1.

[COMP: do NOT place Table 2.1 here—see later insertion]

[b]Navigation and Route Planning

[bodyni]It is not surprising that many animals should possess mental representations of their environments in order to navigate through them safely and efficiently. Indeed, classic behavioral research demonstrates that rodents (O'Keefe & Nadel, 1978; Tolman, 1948), chimpanzees (Boesch & Boesch, 1984; Menzel, 1973) and perhaps even bees (Gould, 1986) rely on "cognitive maps" to pursue both familiar and novel paths through known environments in order to attain rewards and avoid threats. Interestingly, recent research suggests that rodents may mentally preexperience such routes before they pursue them, both inside and outside of the simulated spatial context. This inference is based on recordings from hippocampal place cells, which show

CHAPTER 2

similar patterns of firing before the rodents take a path and then when they actually take the path (see, e.g., Dragoi & Tonegawa, 2013; Ólafsdóttir, Barry, Saleem, Hassabis, & Spiers, 2015; Pfeiffer & Foster, 2013).

If we grant the validity of hippocampal place cell recordings as evidence of phenomenological experience (cf., Suddendorf, 2013a), then the data do indeed suggest that rodents mentally represent specific navigational sequences before they take them (Corballis, 2013). Nevertheless, even if there is a correlation between mental representations and future behavior, it need not necessarily follow that rodents (or other animals) preemptively embed these representations within a specific future context (i.e., represent them *as* future representations). Among humans, representations of potential future events are often spontaneous and detached from awareness of the temporal location of these events (e.g., during mind wandering), even though such representations may influence actual future behavior (Baird, Smallwood, & Schooler, 2011; Stawarczyk, Cassol, & D'Argembeau, 2013). If similar cognitive processes occur in rodents, then it remains plausible that they experience navigational representations as an adaptive form of temporally detached mental imagery, rather than actively planning future routes as humans can (see Redshaw, 2014). Recent computational modeling suggests that offline sequential firing in rodent hippocampal place cells may even be generated randomly by neural network activity (Azizi, Wiskott, & Cheng, 2013).

Regardless of the underlying cognitive processes, neurological studies of rodent route planning have thus far focused only on navigation through very simple spatial fields. Ecological studies with great apes, on the other hand, have claimed to provide evidence of route planning through complex natural environments. Female chimpanzees in the Tai forest, for example, have been found to prefer sleeping in nests that are closer to breakfast sites containing ephemeral,

CHAPTER 2

high-calorie fruits than breakfast sites containing other fruits (Janmaat, Polansky, Ban, & Boesch, 2014). They also leave their nests earlier when they breakfast on ephemeral fruits, especially when these fruits are further away. These findings led the authors to conclude that the chimpanzees were flexibly planning their sleeping and nest-leaving behaviors with breakfast in mind (for similar route-planning claims in male orangutans, see van Schaik, Damerius, & Isler, 2013).

Ecological studies are extremely valuable for documenting the natural future-oriented behaviors of great apes and other species. The problem with drawing strong conclusions about future-thinking from such research, however, is that we cannot rule out whether the behaviors observed are the product of innate predispositions, learning processes, or a combination thereof (Thom & Clayton, 2015a). Future-oriented behavior is pervasive throughout the animal kingdom and need not necessarily require sophisticated temporal representations (Suddendorf & Corballis, 2007). It seems plausible, for instance, that natural selection would favor chimpanzees with an innate preference for sleeping closer to ephemeral, high-calorie fruits, even if these individuals were not specifically considering the next day's breakfast when doing so. Natural selection would also favor chimpanzees with a predisposition toward leaving earlier in their circadian cycle when traveling to breakfast sites that were farther away (according to their cognitive map). If chimpanzees are truly able to *flexibly* plan breakfast, then they should be able to do so in an experimental setting in which the natural contingency between proximity and ease of access to the next day's food is reversed (such that they must choose to sleep further away from a breakfasting area in order to more easily access it tomorrow).

[b]Intertemporal Choice and Delayed Gratification

CHAPTER 2

[bodyini]Animals often forgo immediate opportunities or incur immediate costs in favor of longer term benefits (Fawcett, McNamara, & Houston, 2012; Stevens & Stephens, 2008). When a spider builds a web that may later catch prey, for instance, energy must be expended to produce the silk and to spin the threads, and other opportunities (e.g., to mate) must be forfeited. Thus building a web, along with many other activities in the animal kingdom—from hibernating to caching food to searching for a mate—can be construed as intertemporal trade-offs between immediate and delayed outcomes (Stevens, 2010). Although these behaviors are typically referred to as “choices,” however, at least some of them likely involve no thinking about the future reward at all (Stevens, 2011). Few would attribute the spider in the above example with any mental representation of the rewards it stands to receive from its patience, for instance. On the other hand, larger-brained animals such as birds, rodents, and primates are also faced with intertemporal trade-offs, the underlying cognitive mechanisms of which are more contentious (Thom & Clayton, 2015b). Foraging is a classical case: An animal encountering an unripe fruit must decide whether to eat it now or wait for it to ripen in order to reap the benefits of improved taste and nutrition (Dasgupta & Maskin, 2005).

In standard laboratory intertemporal choice tasks, an animal is presented with two options: one that will trigger an immediate reward, and one that will incur a delay until reward onset. Although rats and pigeons generally exhibit a global preference for immediate reinforcement, they will sometimes choose to delay their gratification for a few seconds for a larger reward than an immediately available one in these tasks (Tobin & Logue, 1994). Both new-world and old-world monkeys tend to wait less than a minute for the larger reward (Santos & Rosati, 2015), whereas chimpanzees may wait up to 2 minutes (Rosati, Stevens, Hare, & Hauser, 2007). Other paradigms assess the related construct of delay maintenance—or how well

CHAPTER 2

an animal can hold out for a larger, later reward in the face of immediate temptation. In “accumulation” tasks, a small reward will gradually build up until the animal chooses to retrieve it, and chimpanzees have been shown to wait for up to 3 minutes for chocolate pieces to accumulate before consuming them (Addessi et al., 2013; Beran, 2002). In “exchange” tasks, on the other hand, a small reward must be kept in possession for a period of time before being traded back to the experimenter for a larger one. Chimpanzees may delay gratification for up to 8 minutes when the delayed reward is 40 times larger than the one initially provided (Dufour, Pelé, Sterck, & Thierry, 2007).

Although some authors have suggested that animals’ intertemporal choice behavior may rely on some form of future-thinking (Roberts, 2012; Santos & Rosati, 2015), there are a number of reasons to be skeptical. Standard dichotomous choice scenarios are usually presented in highly artificial environments in which many trials are used to teach the time lag associated with the delayed options (Mazur, 1987). For instance, it generally starts with the two rewards (large and small) both being delivered immediately, with a slight delay added to the larger reward every time it is chosen. Furthermore, because these studies often present both the delayed and immediate options simultaneously, with the only difference being the inferred wait that the animal has learned previously, it is possible for the subject to simply associate each of the options with the outcome it engenders if chosen (including the negative emotion associated with waiting for the larger reward), without necessitating a mental representation of the delay itself. In the accumulation task, this problem is somewhat abated, though the animal can still see the rewards building up and is therefore reinforced in its waiting behavior with every food item that is added. Successful performance on exchange tasks probably signifies the most convincing evidence of some degree of future reward representation, though such tasks typically still involve

CHAPTER 2

a long period of training to teach the trade behavior, and it is difficult to rule out the possibility that the subjects simply lose interest in the small reward and subsequently exchange it when it returns to their attention.

Sometimes it is more adaptive to select an immediate reward instead of a larger but delayed one, for example, when the environment is particularly harsh or uncertain (Fantino, 1995; Fawcett et al., 2012; Frankenhuis, Panchanathan, & Nettle, 2016). A capacity to *flexibly adjust* intertemporal preferences as a function of anticipated outcomes might therefore be a particularly informative avenue for exploring future-oriented thinking in the context of intertemporal choice (Bulley, Henry, & Suddendorf, 2016; Cheke, Thom, & Clayton, 2011). Bonobos have been found to adjust the amount of time they are willing to spend waiting for future rewards when the administering experimenter has proven to be unreliable, perhaps because they are “expecting” delayed rewards to be less likely to materialize (Stevens, Rosati, Heilbronner, & Mühlhoff, 2011). Similarly, squirrel monkeys have been found to gradually change their choice preferences to a smaller reward when they learn that this choice will eventually lead to a larger reward amount (McKenzie, Cherman, Bird, Naqshbandi, & Roberts, 2004). The animals in these studies, however, were taught that their food amounts would change as a function of their choices over a number of trials, so it is plausible that they learned to associate the two options with different outcomes. To test whether an animal could flexibly adjust intertemporal choices as a function of anticipated (rather than learned) outcomes, an experiment could be devised in which the reward options varied in perishability. For instance, if a chimpanzee first learned that 1 piece of food from Tray A would always be given immediately upon selection, whereas 10 pieces of the same food from Tray B would not be given until after a

CHAPTER 2

delay, then would it subsequently be less likely to select Tray B if the trays contained a quickly perishing food (e.g., flavored ice)?

[b]Avoiding Future Threats

[bodyni]The future holds the potential for abundant opportunities and rewards, but it also contains myriad potential threats. Whereas manifest threats tend to be responded to with a complex suite of processes collectively labelled as a “fear” or “defensive” response (LeDoux, 2014), many animals are also capable of responding to threats with a more advanced preparatory window. Such preparation for threats before they materialize is associated with a different set of physiological and cognitive reactions that together constitute an “anxiety” response (Bateson, Brilot, & Nettle, 2011; Damasio, 1995). This response entails the secretion of stress hormones and a change in heart rate, but also hypervigilance and precautionary behaviors oriented toward sampling more information and discerning the optimal reaction to the implied danger. In essence, the anxiety response can be thought of as extending the amount of time an animal has at its disposal to deal with potential threats before they eventuate. This response can be evoked both by specific cues of a possible threat, such as the smell of a predator, but also via an appraisal of “general vulnerability; for instance, based on interoceptive signals that indicate the current healthiness of the body (Bateson et al., 2011).

The threat reaction is thereby highly flexible, and its expression varies as a function of a number of variables pertaining to, among others, the state of the organism, its recent experiences, and ecological conditions (Bateson et al., 2011; Nettle & Bateson, 2012). Many prey animals, for example, exhibit vigilant “checking” behavior in open areas where they are susceptible to predation, and nocturnal animals show anxiety in bright light (Bednekoff & Lima, 1998; Burman, Parker, Paul, & Mendl, 2009; Underwood, 1982). Despite being impressively future-

CHAPTER 2

oriented and often flexible, however, such a preparatory anxiety response does not necessarily demonstrate mental representations of the future. Rather, this response may be largely dependent upon perceptible cues of specific or general threat in the immediate environment, alongside physiological signals about current vulnerability (Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005). It is possible that animals may also employ memory traces of aversive past events associated with such cues in modifying their responses. However, a capacity to think about and act against specific potential future threats without relying on external or vulnerability cues has thus far been demonstrated only in humans (Miloyan, Bulley, & Suddendorf, 2016).

Thus far, nearly all experimental research into animal future-thinking capacities has focused on preparation for future opportunities and rewards, rather than for future threats. In the previous section, however, we outlined how animals tend to be largely impatient and prefer immediately available rewards relative to larger, later ones; therefore, it may be somewhat unsurprising that animals fail certain future-thinking tasks in which they must pursue delayed rewards. Still, it remains possible that they could pass structurally similar tasks requiring them to plan for upcoming dangers. Indeed, threats to fitness are a potent source of selective pressure and likely played a critical role in the evolution of future-oriented cognition (Miloyan et al., 2016; Mobbs, Hagan, Dalgleish, Silston, & Prévost, 2015). Nevertheless, given the ethical concerns with experimental manipulations that have the potential to induce strong negative emotion, future research in this area may be largely confined to observational studies.

[b]Acquiring and Constructing Tools to Solve Future Problems

[bodyni]Some of the most commonly cited evidence of animal future-thinking comes from studies of great apes' capacity to select tools and use them after a delay to solve a problem and obtain a reward. In the earliest of these studies (Mulcahy & Call, 2006), bonobos and orangutans

CHAPTER 2

were first trained to use a tool to retrieve a food reward and were then presented with a free choice of tools (including the trained tool) to transport out of the room while the reward was unavailable. The apes transported the appropriate tool more often than inappropriate tools, and a few of them were more likely to bring the appropriate tool back to the room and use it when the reward became available again (either 1 or 14 hours later). A second study replicated these findings with chimpanzees and orangutans in a forced-choice paradigm (in which they could choose only one tool), while also showing that the subjects sometimes preferred the appropriate tool over an immediate small food reward (Osvath & Osvath, 2008). Impressively, the final experiment in this follow-up study found that the apes were more likely to choose *novel* tools that could solve the future problem than novel tools that could not.

Concerns exist over whether the apes' success in these paradigms could be explained by associative learning, given that the appropriate tools (or similar ones) had been previously reinforced during the training phases (Suddendorf, 2006; Suddendorf, Corballis, & Collier-Baker, 2009). Even setting aside this particular low-level explanation, however, such experiments can only go so far in demonstrating apes' future-thinking. It seems plausible, for instance, that seeing an appropriate tool would trigger an immediate representation of the reward it can retrieve (such representations are easily cued in humans; Tulving & Thomson, 1973); and so the apes could make their choice based on this immediate representation rather than any expectation of a specific future event in which the reward becomes available again. Then, when the reward does become available, they simply retrieve the tool to which they have convenient access. In this manner their initial representations would indeed be "future-oriented," but only from an objective perspective rather than from the apes' own perspective (Redshaw, 2014). Such explanations could potentially be ruled out by visibly destroying the reward apparatus (and then

CHAPTER 2

removing it from view) before testing whether the apes continued to choose the now useless tool. If they did not, it might suggest that they made their initial choices based on flexible representations of the future, rather than on rigid representations triggered by seeing the tool.

One recent study gave great apes the opportunity to construct tools that could be used to solve a future problem and obtain a reward (Bräuer & Call, 2015). Chimpanzees, bonobos, and orangutans were introduced to an apparatus that required them to bite off and insert pieces of wood into tubes in order to retrieve grapes. Once a piece of wood had been inserted into a tube, it could no longer be retrieved, such that the apes had to bite off multiple pieces of wood in order to retrieve grapes from multiple tubes. After learning how to do this, the apes' access to the apparatus was temporarily blocked by a transparent Plexiglas panel, and either zero, one, or eight of the tubes were baited with grapes. While waiting for the apparatus to become accessible again, the apes were more likely to prepare useful pieces of wood when grapes would be available in the future (for a limited time) than when they would not. They also prepared significantly more tools in the eight-grapes condition than the one-grape condition, but not excessively so (on average, they produced less than two tools in the eight grapes condition).

These results do indeed show that great apes can prepare tools that will enable them to obtain a currently unavailable reward in the near future, but they also point to important limitations. First, it remains to be seen whether apes could succeed at the task if visual access to the apparatus were blocked and the future availability of grapes (or lack thereof) had to be represented in working memory. Moreover, the pattern of responses suggests that the apes were not particularly sensitive to the specific contingencies of the problem. They showed no evidence of producing even close to the optimal number of tools in the eight-grapes condition, which suggests that they may have been producing them based on a rough rule (e.g., "more visible

CHAPTER 2

grapes = make more tools”) rather than the precise requirements of the task (i.e., “make one tool per visible grape”). The apes’ difficulty with the eight-grapes condition and the more general capacity to produce multiple tools to solve multiple future problems may be related to limitations in number representation (Matsuzawa, 2009).

[b]Acquiring, Saving, and Exchanging Tokens for Future Rewards

[bodyni]Money is a powerful reinforcer for humans primarily because we recognize that it can be exchanged for desirable items and experiences in the future. Researchers have investigated whether nonhuman primates, too, can acquire, save, and eventually exchange tokens for future rewards. In one of the earliest of these studies (Dufour & Sterck, 2008), chimpanzees were first trained to return a colorful straw to an experimenter in order to receive peanuts. In the subsequent test phase, they were given the opportunity to collect straws and two types of distractor objects, transport them to another room when ushered away, and then come back to the first room an hour later and exchange the straws for peanuts. The distractor objects were also associated with rewards (a branch that could be used to retrieve honey and a stick that could be used to retrieve fruit pieces), but not in an exchange context, in order to rule out the possibility that the subjects simply preferred the straws because of their previous positive reinforcement. The results showed that the chimpanzees often transported the straws and distractor objects out of the room when ushered away but that they rarely returned and exchanged the straws for peanuts (the best performer exchanged straws on 2 of 10 trials). Critically, the subjects showed no significant preference for returning to the testing room with straws compared with the distractor objects, suggesting that they were not specifically considering the future exchange task when returning to the room.

CHAPTER 2

A similar study produced contrasting results, although there was one important methodological difference. Osvath and Persson (2013) showed that chimpanzees and orangutans preferred to transport, return with, and exchange the previously reinforced token instead of distractor objects, and they also preferred to select the token over distractors in a forced-choice paradigm. Unlike in the earlier study, however, the distractor items were novel and not positively associated with rewards in any context. Prior to training, the subjects showed no inherent preference for selecting the correct token instead of the distractors, but it seems likely that the apes would have quickly acquired a preference for the token after they had been taught to return it for food. It therefore cannot be ruled out that the subjects preferred to select and transport the correct token instead of the distractors simply because of the token's unique association with rewards. A final study showed that bonobos and orangutans also acquired, transported, and later exchanged items for rewards (Bourjade, Call, Pelé, Maumy, & Dufour, 2014), but these results are also equivocal, as there were no distractor objects for the apes to select.

The differential pattern of responding across these studies elegantly illuminates where apes' limitations in exchange tasks may lie. Specifically, it appears that they may select and transport tokens based on their *past utility*, rather than representing and reasoning about the specific future exchange context in which they will become useful. In Dufour and Sterck's (2008) study, the distractor items also had past utility (albeit in a nonexchange context), and so they were preferred equally to the tokens. In the later studies, however, the tokens were preferred based on their unique past utility, regardless of the fact that they would become useful in the future. The preference for past utility could be based on simple associative valence (Suddendorf, 2006; Suddendorf et al., 2009), or it could be based on cued mental representations (i.e., episodic

CHAPTER 2

memory traces) of previous occasions when the token was useful (Cheng et al., 2016; Redshaw, 2014).

[b]Acting with Future Desires in Mind

[bodyni]For nearly two decades, animal future-thinking researchers have been trying to falsify the Bischof–Köhler hypothesis (Suddendorf & Corballis, 1997), which proposes that animals cannot imagine and prepare for a future motivational state that conflicts with their current motivational state (e.g., they cannot imagine and prepare for future hunger when sated). As Suddendorf and Corballis (2007) point out, animals incapable of anticipating future drive or need states would “have little reason to concern themselves with a remote future” (p. 306), on account of the fact that only present needs would matter to such animals. Early observations suggested that animals had great difficulty imagining future desires (e.g., Roberts, 2002), but more recent studies have produced some provocative findings.

In the earliest study that claimed to falsify the Bischof–Köhler hypothesis, Naqshbandi and Roberts (2006) gave two squirrel monkeys a choice between selecting one piece of date with water available after 30 minutes, or four pieces of date with water available after 180 minutes. The monkeys eventually began to prefer the former option, with the authors arguing that they made their selection in order to reduce future thirst levels (as dates induce thirst). Nevertheless, the fact that the monkeys gradually began to prefer the one date over many trials suggests the involvement of associative learning; and, moreover, if they were truly acting for future desires, then they should have selected the four pieces of date and simply waited until water became available before eating them (Suddendorf & Corballis, 2010). The result could not be replicated in a sample of six rhesus monkeys (Paxton & Hampton, 2009).

CHAPTER 2

One of the most interesting lines of evidence in this area comes from a pair of observational studies with a male chimpanzee, Santino. Zookeepers and researchers witnessed him storing piles of stones on some mornings before hurling them at zoo visitors later (Osvath, 2009; Osvath & Karvonen, 2012). These observations were met with claims that Santino may have been preparing for future occasions when he would desire to display his dominance toward the zoo visitors (the stone-collecting behavior appeared to occur in a calm state, whereas the hurling behavior typically occurred in an aroused state). Nevertheless, it remains unclear just how oriented toward specific future events his stone-storing activities were, rather than being driven by more general mental representations (i.e., episodic memory traces) of zoo visitors appearing (Redshaw, 2014). These observational findings must be replicated in an experimental setting before they can begin to seriously question the Bischof–Köhler hypothesis.

Perhaps the strongest challenge to the Bischof–Köhler hypothesis comes from a clever line of research with birds from the *Corvidae* family, which have a natural proclivity for caching and retrieving food (e.g., Correia, Dickinson, & Clayton, 2007; Raby, Alexis, Dickinson, & Clayton, 2007). The most convincing of these studies (Shettleworth, 2012) exploited the fact that corvids and other animals prefer not to eat a specific food (in comparison with other foods) once they have become satiated on that food. Eurasian jays were first fed a particular food (e.g., peanuts) to the point of satiation, and they subsequently preferred to store that food in a specific cache that would be available to retrieve from only when they would prefer the food again in the future (Cheke & Clayton, 2012). Thus it appeared the birds were ignoring their current distaste for the food in order to act for their future preference. Nevertheless, the authors conceded that the jays could have simply learned to associate an emotional preference for the food with the appropriate storage location during the training phase, with this preference becoming reactivated when the

CHAPTER 2

birds were given the opportunity to cache. In other words, the birds might have not been acting based on a “future” desire state but rather a cued current desire state that just happened to match the future desire (Redshaw, 2014).

Emotional states seem particularly susceptible to such reactivation in that they can be cued by environmental factors and experienced in the present to motivate behaviors with incidental future benefits (see Boyer, 2008; Damasio, 1989; Osvath & Martin-Ordas, 2014). So-called interoceptive states (e.g., general hunger, thirst, temperature sensitivity), on the other hand, arise more directly from the peripheral nervous system (Craig, 2002) and may be less susceptible to reactivation. Tests of the Bischof–Köhler hypothesis should perhaps therefore focus on whether animals can act for future interoceptive states if they wish to rule out associative reactivation as an explanation. Nonetheless, acting for such states may be genuinely beyond the capacity of animals. Among humans, children struggle to act for future thirst levels until at least age 7 and possibly beyond (Atance & Meltzoff, 2006; Mahy, Grass, Wagner, & Kliegel, 2014). Indeed, even adults struggle to preexperience future interoceptive states (try to “experience” hunger the next time you finish a very large meal, for example), and so our capacity to act for such states may be largely based on an abstract understanding of temporal shifts in motivation rather than any analogue representation of the states themselves. If there is truth to the Bischof–Köhler hypothesis, then, it may be that animals cannot represent desire states in a propositional fashion in the way that humans can.

[a]Synthesis

[bodyni]The previous sections have described evidence for animals’ future-oriented behavior in a number of domains (see Table 2.1 for summary). In each section we have presented examples of animals acting in ways that make future events more pleasurable and/or less painful. It is not

CHAPTER 2

surprising that such behaviors would be apparent in the animal kingdom, given that natural selection can clearly act on how a behavior affects an animal's future survival or reproductive chances (Klein, 2013; Schacter & Addis, 2007; Suddendorf & Corballis, 2007). It is also not surprising that some of these behaviors would be underpinned by cognitive processes, in that certain animals can represent states of reality that correlate with actual future events and subsequently behave in a manner that provides tangible fitness benefits. Indeed, some of the most influential unified theories of neuroscience propose that brains are essentially “prediction machines” that, through a continuous, potentially Bayesian-like process of comparing expected and actual outcomes, become ever more optimal at anticipating events in the immediate environment (Bar, 2007; Clark, 2013; Friston, 2010). And at least some of the predictions generated by the brain may be based on episodic memory traces triggered by the presence of relevant external cues (Cheng et al., 2016; Redshaw, 2014). In this particular sense, animal future-thinking may be basically continuous with the human capacity.

[COMP: Insert Table 2.1 about here]

In each domain, however, we have also encountered important potential limitations. Some of these potential limitations may eventually require reconsideration; future research may well demonstrate that animals are capable of more complex future-thinking and behavior than is currently known. On the other hand, in comparison with human future-thinking at least, it seems almost certain that some genuine limits exist. Moreover, some of these limits may be overarching, in that they restrict future-oriented behavior across several domains. A recurring theme throughout our analysis, for example, has been the lack of any evidence that animals represent future representations *as* future representations—a form of “metarepresentation” that may be critically important in various flexible human future-oriented behaviors (Redshaw, 2014;

CHAPTER 2

Suddendorf, 1999). In fact, Schopenhauer (1818/1909) first proposed this fundamental discontinuity between humans and animals nearly 200 years ago, when he claimed that the principal component missing from animal minds was “distinct consciousness of the past and of the eventual future, *as such*, and in connection with the present” (p. 229, emphasis in original).

Metarepresentation is important for future-thinking not necessarily in that it enables more vivid future imagery but, rather, because it allows agents to represent the *properties* of future imagery, such that potential future events can be explicitly contrasted with both current reality (Kappes & Oettingen, 2014; Oettingen, 2012; Redshaw, 2014) and with other potential future events (Gollwitzer, 2014). A predictive brain may indeed be ideally suited to representing likely outcomes of an event, but some future events cannot be anticipated with any certainty by even an optimal predictive brain (consider, e.g., the often erratic behavior of predators and prey). An agent with an additional capacity for forming metarepresentations, on the other hand, can reflect on the natural representational limits of his or her own mind and flexibly compensate for these limits. The human ability to develop and enact contingency plans, for instance, relies on an understanding that future events do not always unfold as expected or desired, and so it pays to also prepare for mutually exclusive alternatives. A traveler may imagine and prepare for a dream overseas holiday, but he or she may also purchase insurance in case something goes wrong and his or her original plan must be abandoned. On a broader scale, governments and other institutions are tasked with guiding human societies toward prosperous versions of the future, but they must also plan for potential large-scale emergencies and disasters.

One recent study examined the capacity to simultaneously prepare for two mutually exclusive outcomes of a very basic, immediate future event in 2- to 4-year-old children and a sample of eight great apes (Redshaw & Suddendorf, 2016). Subjects were given the opportunity

CHAPTER 2

to catch a desirable item that was dropped into a forked tube with one opening at the top and two possible exits at the bottom. The apes (like 2-year-olds) typically covered only one exit when preparing to catch the item, whereas most of the 4-year-olds consistently covered both exits from the first trial onward. The apes thus failed to provide evidence for an insightful capacity to consider and prepare for multiple, mutually exclusive future event outcomes. Nevertheless, it remains possible that future studies with other subjects, species, and/or paradigms will discover some competence.

Another domain in which humans often reflect on and compensate for their future-thinking limitations is prospective memory, which involves remembering to perform an action at some particular future occasion. Because we recognize the chance that we will forget to perform the action, many of us use calendars, alarms, lists, and other external reminders as aids (Gilbert, 2015; Risko & Gilbert, 2016). Indeed, many human institutions would collapse entirely if it were not for future-oriented record-keeping procedures that preclude the need for perfect memories (e.g., consider legal and financial systems). There have been some claims for prospective memory in great apes (Beran, Perdue, Bramlett, Menzel, & Evans, 2012; Perdue, Evans, Williamson, Gonsiorowski, & Beran, 2014), with experiments showing that they remember to request or exchange a token for food after completing another irrelevant task (for similar claims in rats; see Crystal, 2013). Nevertheless, it remains possible that no future-thinking was involved in these studies but, instead, that the apes were simply cued into action after completing the irrelevant task. There is nothing to indicate that great apes or other animals spontaneously set their own reminders in order to improve their likelihood of remembering to perform future actions.

CHAPTER 2

Certain species naturally act on their environments to store information that will be useful in the future. Consider, for example, ants that leave a pheromone trail between their nest and a food source (Sterelny, 2003). The question here, however, is whether any animals can do so in various novel contexts, as humans can. This would indicate a domain-general, flexible capacity for strategic reminder setting rather than an instinctual fixed action pattern confined to a narrow domain (for more general arguments along these lines, see Premack, 2007; Suddendorf & Corballis, 2010). One could examine this ability, for instance, in a delayed object permanence paradigm, in which an animal has to wait a specified period of time before it can select (from some options) the location where an experimenter has hidden food. Would the animal spontaneously and consistently mark the correct location with a body part (or scent) or other object during the waiting period in order to increase its chances of remembering the place?

To summarize, there remains no evidence that animals metarepresent future representations *as* future representations, as mere possibilities that could be otherwise because of the mind's inherent inability to predict some aspects of future events with certainty. Humans, on the other hand, reflect on and flexibly compensate for their future-thinking limitations to acquire enormous benefits. Nevertheless, it is important to remember that an absence of evidence is not the same as evidence of absence, and thus future studies should give animals more opportunities to demonstrate such a capacity. Here we have given two possible lines of evidence to pursue: (1) the ability to spontaneously and simultaneously prepare for multiple, mutually exclusive versions of the future and (2) the ability to spontaneously set reminder cues in prospective memory tasks. Any results suggesting that animals did or did not possess these abilities would likely inspire debate and alternative interpretations, but with increasing refinement of experimental manipulations, it is certainly possible to make progress on such important questions.

CHAPTER 2

[b]The Phylogeny of Future-Thinking

[bodyni]Absence of evidence is not only a specific problem for certain domains of animal future-thinking but also more a general problem when considering the relatively minuscule number of species that have been tested in controlled settings. The performance of great apes and other primates is of particular interest, of course, given the potential for shedding light on the evolution of human-like future-oriented mechanisms by studying closely related species. Nevertheless, by examining patterns of capacities and limits across vastly different taxa, one could potentially reason about the biological and environmental factors responsible for the emergence of future-thinking in general (whether that be “mere” predictive cognition or higher order capacities). For example, does future-thinking tend to arise as a by-product of domain-general cognitive specialization? Or does it tend to emerge in response to critical environmental pressures, such as highly uncertain future rewards or threats that precipitate a need for advanced preparation? And what roles do overall brain size, neocortex ratio, or other neurological factors play? These questions will remain moot, however, until more studies are carried out with nonprimate taxa other than corvids and rodents. Prime research candidates include taxa that have demonstrated impressive cognitive skills in other domains, such as elephants (e.g., Foerder et al., 2011), cetaceans (e.g., Marino et al., 2007), domestic dogs (e.g., Range, Viranyi, & Huber, 2007), and parrots (e.g., Pepperberg, Willner, & Gravitz, 1997). Even certain invertebrates, such as coleoid cephalopods (i.e., octopuses, squid, and cuttlefish), are worthy of investigation, given their notable problem-solving and tool use capacities (Vitti, 2013).

Importantly, although discussions of “animal” future-thinking are traditionally confined to extant species other than modern humans, we must also consider that *Homo sapiens* are only the last survivors of a rich hominin lineage. Indeed, archaeological evidence suggests that

CHAPTER 2

hominin future-thinking has undergone radical changes in the last few million years. Over one million years ago in east Africa, for example, our *Homo erectus* predecessors were making many more Acheulean tools than were necessary for everyday use (Kohn & Mithen, 1999). Given that such tools are notoriously difficult to craft, it is possible that these early humans were deliberately practicing tool manufacture with future expertise in mind (Rossano, 2003)—a behavior that may be out of reach for extant animals (Suddendorf, Brinums, & Imuta, 2016). Other novel future-thinking capacities are likely to have emerged in our more recent ancestors, such as *Homo heidelbergensis*, as the ability to harness the future continued to be a prime mover in human evolution (Suddendorf & Corballis, 1997). If any of our recently extinct cousins were still walking the earth—such as *Homo neanderthalensis* or the Denisova hominin—then the potential limits column in Table 2.1 would likely be considerably bare (see Suddendorf, 2013b).

[a]Conclusion

[bodyni]Contemporary comparative psychologists have shown animals to be capable of far more complex future-oriented behaviors than was once thought possible. Here we have reviewed the available evidence and suggested that at least some of these behaviors are based on mental representations that go beyond the here-and-now. Such representations probably function to motivate present action that provides tangible future benefits across various domains.

Nevertheless, there remain important questions regarding just how much insight animals have into their own future-thinking processes. There is no current evidence to suggest that animals metarepresent and behaviorally compensate for their natural future-thinking limits—an overarching capacity that enables humans to acquire additional and substantial benefits. Much further research is needed to shed light on the continuities and potential discontinuities between

CHAPTER 2

human and animal future-thinking capacities and on the evolutionary circumstances that give rise to these capacities.

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