



Prospective memory in a language-trained chimpanzee (*Pan troglodytes*)

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ABSTRACT

Prospective memory involves the encoding, retention, and implementation of an intended future action. Although humans show many forms of prospective memory, less is known about the future oriented processes of nonhuman animals, or their ability to use prospective memory. In this experiment, a chimpanzee named Panzee, who had learned to associate geometric forms called lexigrams with real-world referents, was given a prospective memory test. Panzee selected between two foods the one she wanted to receive more immediately. That food was scattered in an outdoor yard where she could forage for it. Also outdoors were lexigram tokens, one of which represented the food item that remained indoors throughout a 30 min period, and that could be obtained if Panzee brought in the token that matched that food item. After foraging for the selected food item, Panzee consistently remembered to retrieve and return the correct token when food was available indoors, whereas on control trials involving no indoor food she rarely returned a token. This indicated that Panzee encoded information relevant to the future action of token retrieval after extended delays for one type of food, even when a more immediately preferred food was available.

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Do nonhuman animals show mental time travel? This is a fascinating and controversial question within comparative cognition, and one that grounds research in areas of inquiry looking at episodic memory, planning, prospective memory, and recall memory (e.g., Roberts, 2002, 2012). We accept that humans travel through time mentally, remembering their own unique pasts, anticipating themselves performing activities, and even re-experiencing their own unique past and their own imagined futures. For humans, the idea that such mental time travel occurs is tied to there being an experiential level that recreates not just the details of the event itself but also the subjective experience of living that event when one remembers a past event (e.g., Tulving, 1972, 1993). Humans travel forward in time and can plan for events that are minutes to years in the future (e.g., getting milk from the store, getting married next year, buying a retirement home). The anticipation of such future events can be intricately tied to experiential aspects that allow us to feel ourselves in that future (e.g., “can’t wait to see my friends this weekend”) or that perhaps instead just involve future needs that can be remembered without need of such experiential qualities (e.g., “need to get milk”). This latter case typifies what is often called prospective memory, and it is the focus of the present article. Humans use prospective memory whenever we plan an intended future action or event in a way that requires later remembering to implement that intended action (Einstein & McDaniel, 1990; Marsh, Hicks, & Cook, 2006; Marsh, Hicks, & Landau, 1998; McDaniel & Einstein, 2007; Smith, 2003, 2008). Such prospective memory and planning frees humans from the constraint of being stuck thinking of only what can be accomplished or obtained right now. Anticipation of the future also affords greater flexibility in behavior by allowing for responses that are not tied solely to

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present opportunity. Moreover, some have argued that accurate anticipation of the future may be even more advantageous than accurate memory of the past (Suddendorf, 2006; Suddendorf & Busby, 2003).

Despite the potential evolutionary advantages of mental time travel, scientists have long reserved this notion for humans (Atance & O'Neill, 2001; Köhler, 1925; Premack, 2007; Roberts, 2002; Suddendorf & Corballis, 2007; Tulving, 2005). Indeed, Tulving argues that autothetic awareness or self-knowing consciousness (assumed to be mediated by the episodic memory system) is required for mentally placing oneself forward in time and that it is a uniquely human ability. However, nonhuman animals (hereafter animals) may be capable of backward time travel, retrieving memories that are close to the episodic experiences of human memory (e.g., Babb & Crystal, 2005; Clayton & Dickinson, 1998, 1999; Eacott, Easton, & Zinkivskay, 2008; Hampton, Hampstead, & Murray, 2005; Naqshbandi, Feeney, McKenzie, & Roberts, 2007; Singer & Zentall, 2007; Zentall, 2005; Zentall, Clement, Bhatt, & Allen, 2001). Animals also may plan or anticipate future events and outcomes, although it is unclear whether such plans involve mental time travel of the kind described above (Chappell & Kacelnik, 2002; Clayton, Dally, Gilbert, & Dickinson, 2005; Mulcahy & Call, 2006; Osvath & Osvath, 2008; Zentall, 2006), and some theorists have argued that the requirement for conscious re-experiencing of the event is an unfair component in defining mental time travel (for more discussion regarding the role of consciousness in mental time travel, see Eacott & Easton, 2012). However, even when scientists have credited some form of planning to animals, they often stipulate that such behavior is restricted to events or outcomes that are presently preferred and desired (Suddendorf & Corballis, 2007) or limited to situations that capitalize on innate behaviors such as food caching (Shettleworth, 2007). This experiment attempted to go beyond such limitations and demonstrate components of future anticipation and planning in a chimpanzee (*Pan troglodytes*).

This is not an easy goal, as animals in laboratory tests often appear incapable of anticipating what they will need to do more than a few seconds or minutes later. For example, when given a choice between two sets of food items, long-tailed macaques (*Macaca fascicularis*) and chimpanzees did not choose amounts beyond those they could consume in the present, suggesting that they could not anticipate that they would be able to eat the excess food later (Silberberg, Widholm, Bresler, Fujita, & Anderson, 1998). In contrast, squirrel monkeys (*Saimiri sciureus*) did select the larger amount of food and consumed these large sets over extended time periods, indicating that choices were not the result of motivation to eat all items in the present time (McKenzie, Cherman, Bird, Naqshbandi, & Roberts, 2004). In a subsequent study, Naqshbandi and Roberts (2006) gave rats (*Rattus norvegicus*) and squirrel monkeys the choice between large or small amounts of food when water was not available but was returned at a later time (earlier if the smaller amount was selected, but later if the larger amount was selected). Monkeys, but not rats, learned to choose the smaller amount as if anticipating a future state of being thirsty. However, this result was not replicated with rhesus monkeys (*Macaca mulatta*; Paxton & Hampton, 2009). In other contexts, rats do seem to show some representation of a future outcome. Wilson and Crystal (2012) reported that rats showed one of the hallmark effects of prospective memory which is a detrimental effect on other ongoing activity. Rats that had learned that a meal was delivered after a consistent interval showed decreasing sensitivity in their ongoing judgments of time in a temporal judgment test, whereas rats that had no experience with this post-task meal showed no such detriment. This suggested that the rats were exhibiting time-based prospective memory, as evidenced by detrimental effects on the ongoing activity (see also Crystal, 2012, for more detailed information about this research with rats).

There are other kinds of tests where one might interpret the behaviors of animals as acting upon some sense of what can occur in the future versus in the present. This may be the case for tests of self-control (e.g., Beran, 2002; Beran & Evans, 2006; Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999; Dufour, Pele, Sterck, & Thierry, 2007; Evans & Westergaard, 2006; Grosch & Neuringer, 1981; Roberts, 2002; Rosati, Stevens, Hare, & Hauser, 2006; Stevens, Hallinan, & Hauser, 2005; Stevens, Rosati, Ross, & Hauser, 2005). However, one must be cautious about this interpretation because they could instead be responding on the basis of simple associations between delay and large reward versus no delay and small reward rather than anticipating its future delivery.

Although it remains unclear whether animals are capable of complex planning akin to that seen in humans (i.e., planning that requires mental time travel; Roberts, 2002), evidence for other forms of planning in animals has accumulated in recent years (see Roberts, 2012). When wild chimpanzees transport rocks to a distant site with nuts to perform nut cracking (Boesch & Boesch, 1984), this would seem to imply that the animals had the goal of cracking the nuts but could not presently do that, and so implemented the responses necessary to make that possible once rocks were brought near to the nuts. Non-primate species also show this behavior. Chappell and Kacelnik (2002) reported that crows (*Corvus moneduloides*) chose appropriate tools in anticipation of future food retrieval. Planning in animals also is not limited to tool selection, as chimpanzees and pigeons (*Columba livia*) appeared to plan sequences of responses during computerized tasks (e.g., Beran, Pate, Washburn, & Rumbaugh, 2004; Biro & Matsuzawa, 1999; Menzel & Menzel, 2007; Miyata & Fujita, 2008; Scarf & Colombo, 2010). These are just a few examples of apparent planning behavior where animals are motivated to obtain something they cannot get unless they perform an action (or sequence of actions) to obtain in the future that otherwise unattainable goal.

Despite this evidence, some have argued that planning in animals is limited to situations in which motivation at the time of the planned behavior (i.e., the present) matches that at the time of the later implemented response (i.e., the future) (Bischof, 1978; Roberts, 2002; Suddendorf & Corballis, 2007; Tulving, 2005). The Bischof-Köhler hypothesis states that animals cannot plan for future rewards that are not presently desired. As such, they cannot truly travel through time and represent a future reality or motivational state that differs from the present one. This restriction, if true, would mean that the human capacity for mental time travel relies on mechanisms that are unique to our species. This uniqueness could result from many factors, including language. Further, mental time travel may require, and may be indicative of, other sophisticated cognitive capacities including self-awareness, metacognition, theory of mind, perspective-taking, and imagination (Hesslow,

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