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Monkeys exhibit prospective memory in a computerized task

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ABSTRACT

Prospective memory (PM) involves forming intentions, retaining those intentions, and later executing those intended responses at the appropriate time. Few studies have investigated this capacity in animals. Monkeys performed a computerized task that assessed their ability to remember to make a particular response if they observed a PM cue embedded within an ongoing learning-set (LS) task. At a break in the LS task, monkeys selected one of two icons indicating that they had or had not encoded the occurrence of the PM cue (the latter icon resumed the LS task). Critically, during this response period, the PM response icon appeared after a delay during which monkeys could self-initiate the PM response prior to receiving any external prompt. Monkeys selected the PM and LS icons when each was the optimal response, illustrating that they could encode, store, and respond appropriately to a stimulus event in the future. Critically, some monkeys self-initiated the PM response prior to that icon's appearance, indicating that they could retrieve the PM and act on their intention to make that response without the aid of a prompt. These monkeys appeared capable of using PM in this task. Thus, this capacity appears not to be limited to humans.

1. Introduction

Humans travel through time, although not in the way envisioned by science fiction writers. We remember past events, in some cases at an experiential level that recreates not just the details of the event itself, but also the subjective experience of living that event (Tulving, 1972, 1993). Humans travel forward in time as well and plan for events that are minutes to years in the future. The ability to anticipate future events allows an organism greater flexibility in its current behavior by allowing for responses now that are not solely responsive to present stimuli. In fact, some have suggested that it is more advantageous to anticipate the future than to remember the past (e.g., Suddendorf, 2006; Suddendorf & Busby, 2003).

Humans use prospective memory (hereafter PM) to take advantage of anticipated events and to aid in planning and decision-making by remembering things that must be done later (Einstein & McDaniel, 1990; Marsh, Hicks, & Landau, 1998; Marsh, Hicks, & Cook, 2006; McDaniel & Einstein, 2007; Smith, 2003, 2008). Everyday life examples of PM range in importance from remembering to attach a file to an email before sending it to remembering to take one's blood pressure medication before going to sleep. Although PM is easily disrupted and fragile, and PM failures can sometimes have devastating consequences, humans routinely use it as a tool to aid in planning and remembering future behavior (Einstein, McDaniel, Manzi, Cochran, & Baker, 2000; Einstein, McDaniel, Smith, & Shaw, 1998; Graf & Uttl, 2001; Kliegel, Mackinlay, & Jager, 2008; Kliegel, McDaniel, & Einstein, 2000; McDaniel, Einstein, Graham, & Rall, 2004; McDaniel, Einstein, Stout, & Morgan, 2003; Smith, 2003, 2008).

PM refers specifically to the processes of encoding, storage, and delayed retrieval of a future response. Laboratory paradigms of human PM are designed so that the PM is embedded within ongoing activity (to prevent continuous rehearsal of the PM) and so that there is no explicit external prompt to make the future response (to

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prevent participants from searching their retrospective memory store at that time; McDaniel & Einstein, 2007). In an example of a standard human PM paradigm, participants must remember to make a response (e.g., press a key) whenever a particular target item (e.g., the word "green") occurs in the context of an unrelated task (e.g., rating words for pleasantness). These studies have focused on the ability to remember that a response is needed while other activities are ongoing (Kvavilashvili & Ellis, 1996; Thorpe, Jacova, & Wilkie, 2004) and have tended to deemphasize the difficulty of the retrospective memory component (i.e., the number of different target events and the complexity of the response) in order to isolate the processes that are involved in prospective remembering (McDaniel & Einstein, 2007; Riley, Cook, & Lamb, 1981). Thus, in the example given above, the retrospective memory challenge (remembering the action and the target word) is simple, and the real interest is in seeing whether participants will switch from seeing green as a word to be rated for pleasantness to seeing it as a cue for performing the PM action. Further, this is assessed without direct prompting to search memory for the significance of "green" when it occurs (e.g., by asking "is this the target word" each time a word is presented to the participant), so as to not make it a retrospective memory task (e.g., a cued recall task).

Few studies have directly investigated human-like PM in nonhuman animals (hereafter animals), despite the evolutionary advantage it could provide within the context of planning and decision-making. For example, it would be beneficial for monkeys to use PM to remember to visit a distant fruit tree at a later time as a result of just having encountered evidence that a particular fruit species is ripe (e.g., a discarded fruit pit or a similar fruit tree; see Menzel, 1991). Instead, animal studies typically focus on the ability to encode information for future use (often called prospective coding), without the added requirements of storage and retrieval of the PM within an ongoing task. For example, using a 12-arm radial maze, Cook, Brown, and Riley (1985) found evidence for within-trial flexible coding by rats. Each arm was baited and rats were allowed to visit the arms and collect food. At some point, rats were taken out of the test with food still remaining in some arms (after 2, 4, 6, 8, or 10 correct arm visits). After a delay, rats were given only two choices – an arm that had not yet been visited and one that had been visited. Inserting this delay early in trials, when only a few arms had been visited, or late in trials, when many arms had been visited, resulted in good choice behavior of the still-baited arm. However, when the delay occurred after an intermediate number of arms had been visited (e.g., 6), performance was much lower. These data seem to indicate that rats used a dual response strategy. Early in trials, they appeared to remember where they had already been in the trial, but late in trials they appeared to remember where they still had to go to find the remaining food. Zentall, Steirn, and Jackson-Smith (1990) also found evidence for this kind of prospective coding in pigeons using a radial maze analog. However, DiGian and Zentall (2007) did not find similar results, and Klein, Evans, and Beran (2011) reported that monkeys did not show evidence of a dual-coding strategy in a computerized analog of the radial arm maze, relying instead on retrospective coding alone. Thus, there is mixed evidence as to whether or not animals prospectively code information in that experimental paradigm. Even if animals do use prospective coding in that task, because their responses are not embedded within ongoing activity, the possibility remains that animals are continually rehearsing the goal locations, rather than storing that information for later use.

Another limitation of most animal PM studies is that they only assess whether animals remember the correct future response, but do not require spontaneous initiation of that response. Instead, a cue is given when it is time to make the delayed response, and this allows for the possibility that animals then rely on retrospective memory to recall what they were supposed to do. For example, during a sequential paired association task, monkeys first learn an association between two stimuli. Next, they view one member of the pair, and after a delay, they view the second stimulus. The monkeys must respond differently depending on whether or not the second stimulus is the one associated with the first or is not. Researchers have suggested that during the delay, monkeys are remembering what the associated (second) stimulus *should be* when it is presented later and not what the first stimulus *was* (e.g., Colombo & Graziano, 1994; Genovesio, Brasted, & Wise, 2006; also see Rainer, Rao, & Miller, 1999). Although this suggests that monkeys use PM, explicit prompting of animals to respond via presentation of the second stimulus (and the opportunity to continuously rehearse during the delay) has prevented such studies from directly assessing human-like PM (see also Murphy, 2009, for another prospective paradigm that allows for similar alternative explanations in a study of horse memory). For these reasons, Thorpe et al. (2004) argued that most PM studies with animals actually show capacities that, in human memory research, would be identified as retrospective.

A more recent study has provided other suggestive evidence that animals can remember to make future responses. Wilson and Crystal (2012) reported that rats anticipating a future event exhibited reduced performance on an ongoing task, which is an effect that sometimes accompanies prospective memory (e.g., Smith, 2003). Rats that had learned that they would receive a meal if they poked their nose into a trough after a consistent interval showed decreasing sensitivity to time in an ongoing bisection test that took place during the delay interval. This suggested that the rats were exhibiting time-based prospective memory. However, rats made the nose poke response throughout the test interval (albeit at increasing frequency), and so their reduced performance on the ongoing task could have been attributed to the rats dividing their attention between the test trials and their responses to the food trough, rather than their actually memory for the future feeding. Nevertheless, this study demonstrated that rats would anticipate a future event, and so this methodology may lead to other insights with regard to future-oriented behavior in animals.

In the present study, to address the issues mentioned above, we designed a PM study to assess whether animals