Behavioural Processes 112 (2015) 88–99

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Prospective memory: A comparative perspective

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ARTICLE INFO

Article history:
Available online 4 August 2014

Keywords:
Prospective memory
Time-based prospective memory
Event-based prospective memory
Animal models
Primate
Rodent

ABSTRACT

Prospective memory consists of forming a representation of a future action, temporarily storing that representation in memory, and retrieving it at a future time point. Here, we review the recent development of animal models of prospective memory. We review experiments using rats that focus on the development of time-based and event-based prospective memory. Next, we review a number of prospective-memory approaches that have been used with a variety of non-human primates. Finally, we review selected approaches from the human literature on prospective memory to identify targets for development of animal models of prospective memory.

This article is part of a Special Issue entitled: "Tribute to Tom Zentall".

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http://dx.doi.org/10.1016/j.beproc.2014.07.016
0376-6357/

1. Introduction

Memory serves two functions, namely to remember the past and plan for the future (Schacter and Addis, 2007; Schacter et al., 2007). The repertoire of experimental techniques available to investigate memory for past events in nonhumans is well developed (Roberts, 1998; Wasserman and Zentall, 2012). However, the range of techniques available to investigate the role of memory in planning for the future in animals is less well developed. While considerable recent interest focuses on this relatively new problem, the conclusions are widely debated as to whether non-humans are capable of forming representations of the future and whether newly developed paradigms sufficiently demonstrate this capability (Corballis, 2013; Crystal, 2012, 2013b; Eacott and Easton, 2012; Roberts, 2002, 2012; Suddendorf, 2013; Suddendorf and Corballis, 1997; Zentall, 2005, 2006, 2010). This article focuses on one approach toward investigating an animal's representations about the future. *Prospective memory* focuses on our intentions to act in the future. Because our intentions to act are often interrupted by other immediate needs, these interruptions often displace active processing of the intention. Thus, our intentions are temporarily put on hold – stored in memory – meaning that we need to reactivate or retrieve these memories at an appropriate point in the future. It is well-established that people remember to execute delayed intentions (McDaniel and Einstein, 2007; Scullin et al., 2013); we "remember to remember". The hypothesis that animals form representations about the future can be explored by developing animal models of prospective memory (Crystal, 2013a).

Two predominant types of triggers may reactivate or prompt retrieval of a prospective memory; these are referred to as time- and event-based prospective memory. We will consider some everyday examples to help develop the distinctions between these two types of triggers. Time-based prospective memory involves remembering to take some action at a specified point in the future. Here, the trigger focuses on the passage of time. For example, after taking one's children to daycare in the morning, a parent is scheduled to pick up the kids at the end of the day. In this example, time of day may serve as a trigger to retrieve the memory to pick up the kids. As another example, when cooking, we need to remember to remove dinner from the oven after an approximate amount of time, say 30 min. In this example, an elapsing interval may serve as the trigger to retrieve the memory to empty the oven. Importantly, memory is likely involved in these two scenarios; for example, it is unlikely that the parent is actively processing (e.g., rehearsing) the plan to pick up the kids at all times throughout the day.

Event-based prospective memory involves remembering to perform an action when an event occurs. Here, the trigger to retrieve a prospective memory is the occurrence of a specific event in the environment. For example, you might plan to share some news about some interesting new data with a colleague when you see her next. In this example, the occurrence of an event (seeing your colleague) may serve as a trigger to retrieve the memory to discuss the new data. Again, it is unlikely that active processing occurs continuously.

Both time- and event-based prospective memory have been intensively investigated in laboratory and natural settings with people (Kliegel et al., 2008). In the next section, we outline recent progress in the development of animal models of prospective memory. A comparative perspective on prospective memory may serve two goals. The first goal is to explore the evolution of prospective memory. It has been suggested that future-oriented representations may be unique to humans (Roberts, 2002; Suddendorf and Corballis, 1997; Tulving, 2001, 2005). Alternatively, prospective memory, or its precursors, may be evolutionarily quite old. According to this later view, it may be possible to model fundamental aspects of human cognition in animals. This later view is compatible with the second goal of a comparative perspective on prospective memory. Animal models of prospective memory may be used to explore the biological mechanisms of cognition. Indeed, recent advances in our understanding of memory at cellular, molecular, and genetic levels of analysis may open the door to gaining a deeper understanding of human memory and disorders of human memory (Crystal and Glanzman, 2013).

An influential theme in prospective memory research in the human literature focuses on the observation that remembering to act in the future has a *cost* on ongoing performance (Kliegel et al., 2001; Marsh and Hicks, 1998; Smith, 2003). The notion of cost shares some history with research on divided attention (e.g., Craik et al., 1996). An influential area of research in studies of animal memory focuses on documenting the use of a prospective memory code (in contrast to a retrospective memory code); these two codes differ in terms of the item to be remembered, namely a previously presented stimulus in retrospective coding and a to-be-selected future stimulus or response in prospective coding. A familiar everyday example is a to-do list (prospective coding) vs. a list of things already completed (retrospective coding). A number of studies have documented that animals use prospective codes (Cook et al., 1985; DiGian and Zentall, 2007; Gipson et al., 2008; Kametani and Kesner, 1989; Kesner, 1989; Kliegel et al., 2001; Roitblat, 1980; Zentall, 2010; Zentall et al., 1990); these approaches tap into prospection by identifying the content of the animal's memory representation as the to-be-remembered stimulus or response. It is worth noting that in prospective coding (as in retrospective coding), the animal is hypothesized to maintain a memory code throughout the retention interval delay. In contrast, in prospective memory, the memory representation about the future is first activated, then it is inactivated, and finally it is reactive at a later time point. Inactivation and reactivation processes are not required in prospective coding, unlike prospective memory (Crystal, 2013b).

2. Animal models of prospective memory

This section will sketch recent progress in the development of animal models of prospective memory. We consider two animal models, one using rats and the other using non-human primates.

2.1. A rodent model of prospective memory

We recently developed a rodent model of prospective memory. A central problem that any new animal model of a cognitive ability must address is how to begin to investigate an animal's internal representations. This problem is acute for prospective memory because the human literature focuses on intentions (i.e., a delayed intention to act in the future). Of course, it is not possible to directly observe an animal's (or another person's) putative intentions. Thus, the approach here is to consider what functional changes in behavior would be expected to occur if an animal has a prospective memory. Accordingly, we drew on one theme from the human literature that focuses on the observation that remembering to act in the future has a cost on ongoing performance (Brewer et al., 2011; Marsh and Hicks, 1998; Marsh et al., 2006; Marsh et al., 2003; Marsh et al., 2002; Smith, 2003). The key insight is that actively maintaining an intention to act in the future potently depletes attentional resources; because retrieving a prospective memory is expected to reduce attentional resources that would otherwise be allocated to other activities, it may be possible to determine if an animal is currently retrieving (or failing to retrieve) its memory by monitoring performance in a sensitive ongoing task. Thus, we proposed that ongoing task performance is expected to be impaired when the animal actively maintains an intention to act. By contrast, we may be able to identify other occasions when an intention to act