Published in final edited form as:

Behav Processes. 2015 March ; 0: 88–99. doi:10.1016/j.beproc.2014.07.016.

Prospective memory: A comparative perspective

Jonathon D. Crystal^{1,*} and A. George Wilson²

¹Department of Psychological & Brain Sciences, Indiana University

²Virginia Tech Carilion School of Medicine and Research Institute

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.

Keywords

prospective memory; time-based prospective memory; event-based prospective memory; animal models; primate; rodent

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 nonhumans are capable of forming representations of the future and whether newly developed paradigms sufficiently demonstrate this capability (Corballis 2013; Crystal 2012; Crystal 2013b; Eacott and Easton 2012; Roberts 2002; Roberts 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

© 2014 Elsevier B.V. All rights reserved.

*Correspondence Jonathon D. Crystal, Department of Psychological & Brain Sciences, Indiana University, 1101 E 10TH ST, Bloomington, IN 47405-7007 USA, jcrystal@indiana.edu, Phone: 812-856-2246, FAX: 812-855-4691.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

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 minutes. 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-based 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 potentially 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 is temporarily stored in memory by documenting non-impaired ongoing cognitive performance. We expect that retrieving a memory to act requires attentional resources, which would interfere with fully allocating attentional resources toward the ongoing task (which also requires attentional resources).

To prompt a plan for the future, we used the opportunity to obtain a relatively large meal. To obtain access to the meal, the rats were required to break a photobeam in a food trough, but the photobeam was only effective when the meal was available (i.e., at other times, photobeam breaks did not produce access to food). Prior to the availability of the meal, the rats were engaged in an ongoing task. Our ongoing task assessed time-perception performance. Rats judged the duration of briefly presented gaps between very brief pulses of noise. Although the rats were rewarded for correct choices in the time-perception task, the amount of food was much smaller than that available during the meal. Further, the time-perception task was discontinued when the meal started. We used this general approach to develop models of time-based and event-based prospective memory.

2.1.1 Time-based prospective memory in rats—In our time-based prospective memory approach, the meal was available at a fixed point in time, namely 90 minutes after the start of a daily session. Time-based prospective memory was suggested by impaired performance in the ongoing task immediately before the meal relative to an earlier – unimpaired – time point when the prospective memory was likely inactive (Wilson and Crystal 2012). The impairment was selective for rats that received the meal after 90 minutes, whereas no comparable impairment was observed in a different group of rats that never received meals. Because ongoing task performance was constant across early and late time points when a representation of the meal was absent, our findings suggest that the representation of the approaching meal produced the impairment in the rats that had the opportunity to learn to anticipate the meal. We independently verified that the rats indeed learned to anticipate the meal by documenting that these rats showed a prominent increase in food-trough approach behaviors (which was absent in the rats that never received meals).

We proposed that the decline in performance was produced by prospective memory. Our hypothesis is that rats form a representation of the future meal but inactivated the representation when the meal was only available at a distant future time point (i.e., inactivate early in the session). Because the representation was inactivated, we expected that ongoing task performance would be high, which is what we observed. By contrast, as the expectation of the meal grew, we propose that more attentional resources were recruited to maintain the representation of the forthcoming meal. Thus we expected that ongoing task performance would be relatively low at the late time point, which was also observed. To support the representational account, a number of alternative explanations were ruled out (for details see Section 2.1.3 and Wilson and Crystal 2012).

In another experiment (Wilson et al. 2013), we provided two cues that could serve as triggers, namely the passage of time (90 minutes) and the occurrence of an event (brief tone pulses were presented between time-discrimination trials); the tone was also continuously presented throughout the entire meal. The tones occurred between trials in the last 10 minutes before the meal but not at earlier time points in the daily sessions. Thus, an animal could use the passage of time (as in our earlier experiment in which no external event provided additional information), the occurrence of the tone pulses (which signaled that the meal was near), or both. Performance in the ongoing task was disrupted by the recent presentation of the tones relative to an earlier time point when this event had not yet occurred (Figure 1A). In addition, the rats inspected the food trough increasingly during this

time point (Figure 1B). However, they also timed the arrival of the event and/or the meal (note the large increase in response rate prior to the meal). Thus, although the rats likely used the event, they also appeared to use time.

When the meal occurred at a predictable time, the rats anticipated the arrival of the meal and showed a corresponding decline in ongoing task performance; the deleterious effect of anticipating the time of the meal provides evidence for time-based prospective memory in both experiments. Therefore, the addition of an event, without some additional steps to preclude timing of the meal, was not sufficient to document strong control by the event.

2.1.2 Event-based prospective memory in rats—To promote the use of event rather than time, we increased the validity of the event by scheduling the event (and the meal) to occur after a variable amount of time. The meal occurred 35- or 260-minutes after the start of daily sessions; only one meal occurred per day at one of these two times. Again the tone-pulse events occurred between trials in the last 10 minutes before the meal. Thus, the event provided information that the meal would be available soon. An event-based prospective memory account predicts that performance would be disrupted after the event relative to other time points when the event had not yet occurred.

Figure 2 shows a number of conditions in which we observed that performance in the ongoing task was severely disrupted after the event relative to other times in the absence of the event. Disruption occurred immediately prior to the early and late meals relative to an earlier time point without the event (Figures 2A and 2B, respectively). As expected, the rats inspected the food trough primarily during the event (Figure 2D). Because the event sometimes occurred early and late, we were able to compare the effects of the presence and absence of the event while examining an equivalent time point (namely the early time at which the event sometimes occurred). In these conditions, which preclude the use of time as a cue to predict meal availability, we observed that the event severely disrupted ongoing task performance (Figure 2C).

Next, we conducted a number of manipulations that put time and event in conflict by presenting the event at a novel time. In one case, we omitted the meal and presented the event at an intermediate time point, that is at a time when the meal would not be expected and when the event had never previously been presented. When the event occurred at a novel time, performance in the ongoing task was severely disrupted after the event (Figure 3A), despite the fact that the rats had never before experienced the meal (or expressed impaired performance) at this time during training.

A central question in developing an animal model of prospective memory is evaluating the viability of alternative explanations. An important non-prospective hypothesis is the proposal that the animal continually maintains an active representation. According to this alternative hypothesis, the animal has learned a fixed sequence of anticipation or that the meal occurs late if not early. This is a non-prospective memory hypothesis because the animal may form a representation of a future event and actively maintain it throughout. In contrast, the event-based prospective memory hypothesis requires evidence that the animal can specifically inactivate and subsequently reactivate the memory representation. Therefore,

in the absence of a meal, we conducted an additional test in which the event not only occurred in a novel temporal context but also occurred on three occasions within the same day. If rats are capable of repeatedly activating and inactivating the memory representation in an on-demand fashion, then they should show impaired ongoing-task performance selectively to the recent presentation of the event. Moreover, high levels of ongoing-task performance should recover after the warning event is terminated. By contrast, impairments would not be selective to the event when the event is presented repeatedly if the impairments are based on a learned, fixed sequence. Figure 4A shows ongoing-task performance in three zones during which the event was absent (unfilled bars) and three zones during which the event was present (filled bars). When the event was presented at three novel times, performance in the ongoing task was severely disrupted by the event (filled bars) with excellent performance at other times (unfilled bars). As expected, the rats learned that the event signaled the availability of the meal, as shown by the increase in food-trough responses (Figure 3B and Figure 4B) when the event occurred at novel times. To support a representational account of event-based prospective memory, a number of other alternative explanations were ruled out (for details see Section 2.1.3 and Wilson et al. 2013).

2.1.3 Isolating prospective-memory by ruling out alternative explanations—

The proposal that rats have prospective memory hinges on the implausibility of alternative explanations that do not assume prospective memory. Below we consider a range of alternative explanations. For each we outline how the alternative could potentially produce putative prospective-memory performance. Next, for each we outline an empirical test of the alternative explanation. Because each of the alternative explanations is ruled out by data, we argue that the prospective memory proposal is strengthened.

2.1.3.1 Response competition: Response competition is a major non-prospective-memory explanation of putative prospective-memory performance. According to this proposal, the deleterious effect on ongoing performance occurs because the occurrence of food-trough responses directly competes with, or interferes with the successful performance of, the ongoing task. This is a plausible alternative explanation because it is possible that when the animal is doing food-trough responses, it is unable to complete some key aspect of the ongoing task. More broadly, food-trough responses might interfere with any of a range of components of the ongoing task, such as processing auditory stimuli, forming a temporal judgment, or selecting or pressing levers. If any one of these components was directly impaired by response competition, the observed decline in ongoing task performance could be explained without the need to propose prospective memory.

The response competition hypothesis proposes that food-trough responses cause the impairment in ongoing task performance. Consequently, response competition predicts a *negative* correlation between the number of food-trough responses and accuracy in the ongoing task. For example, when many food-trough responses occur, ongoing task performance is predicted to be low. Similarly, when few food-trough responses occur, ongoing task performance is predicted to be high. We measured the correlation between food-trough responses and ongoing task performance and found that the correlation was zero, contrary to the response-competition hypothesis. In our initial experiment (Wilson and

Crystal 2012), the correlation was -0.006 ± 0.061 (mean $\pm$ SEM). In our more recent work (Wilson et al. 2013), the correlation was 0.028 ± 0.212 .

2.1.3.2 Reduced motivation: Reduced motivation to perform the ongoing task is a major non-prospective memory explanation of putative prospective memory performance. According to this proposal, the deleterious effect on ongoing performance occurs because food rewards for the ongoing task are ineffective when the meal is anticipated. This is a plausible alternative explanation because it is possible that the motivational value of a small piece of food in the ongoing task is substantially diminished when a large meal, consisting of hundreds of pieces of food, is anticipated. It is well-established that animals experience changes in motivation in anticipation of a substantial future shift in reward value (e.g., Flaherty and Checke 1982).

The reduced-motivation hypothesis (i.e., negative anticipatory contrast) proposes that diminished motivation causes the impairment in ongoing task performance. Consequently, reduced motivation predicts that the latency to make a short/long classification response would increase when the meal is expected to occur. Analysis of latencies to make classification responses do not support the reduced-motivation hypothesis. In our initial experiment (Wilson and Crystal 2012), latencies immediately prior to the meal did not differ from an earlier time point. In our more recent work (Wilson et al. 2013), the rats pressed the lever faster prior to the meal than at other times, an observation opposite to that predicted by anticipatory negative contrast.

2.1.3.3 Other hypotheses: The response-competition and reduced-motivation hypotheses are the major alternative explanations for putative prospective-memory performance. Other hypotheses that may be offered tend to get resolved through the same routes used in the response-competition and reduced-motivation hypotheses. For example, satiety or fatigue make similar predictions to reduced-motivation (i.e., perhaps the rats are satiated or fatigued late in the session, which could produce a decline in ongoing task performance). Satiety and fatigue are ruled out because latencies to make classification responses do not decrease when the meal is expected (Wilson and Crystal 2012; Wilson et al. 2013). Moreover, in our more recent work (Wilson et al. 2013) the dissociation of time and event directly rules out satiety and fatigue hypothesis. We showed that impaired performance occurs at time points when we predicted that the rat would retrieve a prospective memory. The range of time points include early and late meals, as well as a number of novel times. This range of time points shows that the impairment can occur at any time in an on-demand fashion. By contrast, satiety and fatigue can only handle monotonic development of impaired ongoing task performance.

Another potential hypothesis focuses on stimulus-response learning¹. In stimulus-response learning, a connection between a stimulus and a response is stamped in when the response is rewarded in the presence of the stimulus. Consequently, the subject learns to perform the response in selected stimulus situations. Because stimulus-response learning is widespread (Colwill 1993; Henson et al. 2014), one might wonder what role it plays in our model of

¹We thank an anonymous reviewer for suggesting this idea.

prospective memory. In fact, the *event* in event-based prospective memory, in our approach, is a tone, which certainly can serve the role of a stimulus in stimulus-response learning. Indeed, stimulus-response learning may support the robust anticipation at the food trough that we have documented in our approach. However, it is important to note that we have not suggested that anticipation at the food trough alone is a sufficient basis to propose prospective memory. Instead, we have pointed to food-trough anticipation only as confirmation that the animal anticipates the meal; there is extensive evidence that rats represent outcomes of their responses (e.g., Colwill 1993), which would correspond to the meal in this case, although we have not used outcome devaluation to test this proposal in our preparation. Importantly, the evidence for prospective memory comes from the observed deleterious effect on ongoing task performance at time points when we predict that the animal anticipates the meal. Thus, the combination of deleterious effect on ongoing task performance and anticipation of the meal are both needed to make the case for prospective memory, but the key finding is the decline in ongoing task performance. As discussed in this section, a number of alternative explanations for the deleterious effect on ongoing task performance have been ruled out. Aside from the alternative hypotheses described above, it is not apparent how stimulus-response learning can produce an impairment in ongoing-task performance.

We have reviewed the major non-prospective memory alternative hypotheses. Of course, it is possible that some other hypothesis will be proposed, which would then need to be tested against data. However, aside from the approaches and hypotheses described above, it is not apparent how the impairment in ongoing task performance can be explained without proposing prospective memory.

2.1.4 Summary—Accurate ongoing task performance was disrupted when the meal was expected (near the time of the meal or after the event occurred in time- and event-based models, respectively), with excellent performance at other times. In the data presented above, ongoing task performance was excellent (91%) before the event occurred, whereas it dropped dramatically (below 70%) when the event had recently been presented. We propose that the rat forms a representation of the future action (obtaining the meal) when a meal is forthcoming but delayed, it subsequently deactivates the representation (producing relatively superior performance), and finally it reactivates the representation (producing a decline in performance). In a number of tests with the meal withheld, the rats activated, inactivated, and reactivated the representation in an event-based, on-demand fashion.

2.2 Prospective memory in non-human primates

Michael Beran and colleagues have developed a number of models of prospective memory using non-human primates. We will review the development of computerized tasks, performance in a language trained chimpanzee, and comparisons with human children.

2.2.1 Prospective memory using computerized tasks—Beran and colleagues (Beran, Evans, et al. 2012) tested monkeys in a matching-to-sample task. The initial screen displayed a central item and four additional items in the periphery, one of which matched the central item. Next, the peripheral items were replaced by black squares, and the required

response was to move a cursor to the previously matching item. After the monkeys readily learned to complete the matching task, Beran and colleagues inserted a psychomotor tracking task before the monkeys had the opportunity to complete the matching task. Although tracking decreased the chance that the monkeys were continually rehearsing or visually fixating upon the matching item, the monkeys nonetheless demonstrated successful matching. In a further refinement, the monkeys received substantially more food for doing the tracking task. Despite the substantially reduced motivation, at the start of each trial, to remember the future response, the monkeys continued to succeed in the matching task.

In another experiment, Evans and Beran (2012) tested the ability of rhesus and capuchin monkeys using two concurrent computerized tasks. The monkeys were trained to remember to make a prospective-memory response (touch a stripped icon) if they had recently observed a prospective-memory cue (a flashing rectangle) on the computer monitor. At other times, the monkeys were engaged in a learning-set task, which required remembering the identity of a to-be-selected icon (e.g., happy face vs. start). On some occasions, the prospective-memory cue was embedded in the learning set task by interleaving the cues. Critically, when the prospective-memory cue was presented, the monkeys needed to remember to initiate the prospective-memory response after a brief delay; the prospective-memory response could not be produced earlier because the experimenters controlled the delay between presentation of the cue and the opportunity to respond. Because the two tasks were embedded, engaging in the learning-set task may have prevented the monkeys from actively processing the prospective memory cue/response during a delay. The monkeys remember to select the prospective-memory response when reward for doing so was available. Moreover, some monkeys self-initiated the prospective memory response before the target icon appeared on the computer monitor. The monkeys presumably acted on their intention to make the response without the aid of an icon to remind them to do so.

2.2.2 Prospective memory in a language trained chimpanzee—In yet another study, Beran and colleagues (Beran, Perdue, et al. 2012) used a language trained chimpanzee (Panzee). Panzee had received extensive earlier training that allowed her to exchange lexigram tokens for real-world referents, such as various food items. Panzee was given two interleaved foraging opportunities, one of which involved food that was scattered in an outdoor enclosure, and the other which involved exchanging tokens for inaccessible food items located indoors. Prior to beginning to forage, Panzee selected between two food items in her indoor area (40 M&Ms vs. one of apple, banana, bread, sweet potato etc.). After Panzee made a choice, the experimenter immediately placed the non-selected item into an opaque container and placed the container just outside her enclosure. Next, the experimenter distributed the M&Ms in the outdoor enclosure. The outdoor enclosure also contained several tokens, including the food items used in the earlier choice phase. The tokens were placed face down, so Panzee needed to turn each token over to see what lexigram appeared on the face-down side. While Panzee foraged for the M&Ms, she might touch, turn over, or take a token. After up to 30-min of foraging outside, Panzee returned to the indoor enclosure, where an experimenter waited until Panzee slide a token out of her enclosure. If the token matched the content of the food item located inside the opaque container, the experimenter gave her the food item. If Panzee did not bring a token, or brought the wrong

token, she was given the opportunity to name the food item in the container by using her lexigram keyboard, which was mounted on the enclosure wall, but she did not actually receive the food item. Thus, the only way to obtain the food item hidden in the container was to bring the appropriate token with her when returning to the indoor area. On control trials, Panzee foraged for food outside and had the same opportunities to bring tokens inside, but no additional food item was placed in the container in the indoor area.

After seeing the less-preferred food item being hidden in the container, Panzee returned with the correct token on 67% of the trials; she rarely returned with an incorrect token (10% of trials) or without any token (24%). By contrast, on control trials (when no food was placed in the container), she rarely returned a token (25% of trials); instead she mostly returned without any token (75% of trials; there was no correct token in this case). Critically, after seeing the baiting of the container, she presented the correct token on 88% of the trials in which she returned with a token, which was different from chance. Failing to exchange a token occurred significantly more often on control trials than expected by chance. She also frequently discontinued searching for tokens after turning over the correct token (71% of trials with a baited container). On trials in which she failed to bring in a token or brought an incorrect token, she successfully identified the item in the container using her lexigram keyboard on 57% of trials. She remained in the outside enclosure for about 15 minutes.

A number of lines of evidence suggest that Panzee used prospective memory to "remember to remember" to obtain the hidden food item. Panzee needed to remember the less-preferred food item, and she accurately did so on the majority of trials. This was accomplished while she engaged in a different task (foraging for the more preferred food) for about 15 minutes. It is unlikely that Panzee actively rehearsed the lexigram name of the hidden food item throughout the delay. Indeed, during the delay, Panzee sometimes engaged in other activities such as sitting outdoors, grooming, etc. before retrieving the token and exchanging. Beran and colleagues (Beran, Perdue, et al. 2012) did not report performance as a function of trials; thus, it is not known if Panzee learned to bring the token into the enclosure for subsequent exchange gradually over the course of the test trials. Learning to bring the item into the enclosure over trials could be viewed as an example of retrospective memory rather than prospective memory².

2.2.3 Prospective memory comparisons of children and chimpanzees—Perdue and colleagues (2014) used analogous tasks with 3-year old children and chimpanzees. The children and the chimpanzees were given a choice between two items (toys for the children and food items for the chimpanzees). The chosen item was immediately presented to the participant, and the non-preferred item was placed in an opaque container. Next, they were given an ongoing task (quantity judgments) to prevent rehearsal and impose a brief delay. Finally, when the ongoing task ended, the children could request the hidden item (by verbally asking for it); similarly, the chimpanzees could request the hidden item (by pointing to the container, for a non-language trained chimpanzee) or by using a lexigram keyboard (for language trained chimpanzees) when the ongoing task ended. Critically, to successfully

²We thank an anonymous reviewer for suggesting this idea.

request the hidden item, the participants needed to remember to request it at the end of the ongoing task.

Children rarely made spontaneous requests for the toy (17% of the children). By contrast, about half of the children requested the toy when given explicit prompts (e.g., "Is there anything you were supposed to remember to do?", "What's in this box?", etc.). The chimpanzees, in contrast, spontaneously directed the experimenter to the container on 89% of the trials. On control trials, with an empty container, chimpanzees rarely directed the experimenter to the container (17% of control trials). Because the item in the container could not immediately be obtained, the participants needed to remember to request it after a delay.

The initial performance of the chimpanzees was similar to that of the children's performance (only 1 of 4 chimpanzees spontaneously directed the experimenter to the container on the very first trial). Thus, it is likely that the chimpanzees gradually learned that the hidden food item was available at the end of the ongoing task if they remembered to request it. By contrast, the children were only tested once. This is perhaps an important difference between the children and chimpanzees. Critically, it is possible that the chimpanzees learned the rewarded response over trials, which can occur without prospective memory. Similarly, it is worth noting that accurately responding to the prompt "what's in this box?" may be supported by retrospective memory without prospective memory because the correct answer requires retrieval of the content of the intention without carrying out the intention at an appropriate time point³.

3. Comparative questions based on insights from prospective memory in people

In the next sections we review selected approaches from the human literature to identify targets for development using animal models of prospective memory.

3.1. The impact of prospective memory on ongoing task accuracy

Next we review a number of theoretical perspectives on the impact of prospective memory on ongoing task performance. A prospective memory task is similar to a divided attention task (McDaniel and Einstein 2007), and from this perspective, the preparatory attention and memory theory (PAM) (Smith 2003; Smith and Bayen 2004) posits that successfully completing a prospective memory requires active maintenance of a planned action. If this maintenance is interrupted (e.g., the ongoing task is too engrossing or completing the prospective memory is now deemed unimportant), prospective memory accuracy decreases (Kliegel et al. 2001; Loft et al. 2008). Moreover, ongoing task accuracy decreases regardless of whether the prospective memory cue is encountered during the task or not (Smith 2003), meaning that the deleterious effect is driven by a cognitive mechanism or strategy rather than by the presented stimuli. Indeed, a number of studies have found deleterious effects (i.e., degraded performance due to attentional resources being siphoned away from an ongoing task while maintaining an intention) due to active monitoring of the environment

³We thank an anonymous reviewer for suggesting these ideas.

for retrieval cues (Cohen et al. 2008; Einstein et al. 2003; Harrison et al. 2014; Smith 2003; Smith et al. 2007). However, other studies have found that deleterious effects are sometimes not present (e.g., Harrison et al. 2014; Kliegel et al. 2001), which has been interpreted as evidence for the proposal that the subjects were engaged in an automatic retrieval process that was not demanding of attention (i.e., monitoring the environment for retrieval cues was not needed in this case) (McDaniel and Einstein 2007).

The multiprocess theory (McDaniel and Einstein 2000) proposes that multiple factors determine whether a participant will complete a prospective memory by either 1) using a system akin to the one described in PAM theory (where deleterious effects are expected due to active monitoring), or 2) engage in automatic retrieval (where deleterious effects are not expected). Here, automatic retrieval refers to a strategy in which the subject expects the prospective memory retrieval cue to be overt; accordingly, the subject does not allocate attentional resources to actively monitor the environment for this cue. When the retrieval cue is expected to be overt, deleterious effects would not be expected as all attentional resources could be allocated to the ongoing task and prospective memory accuracy would not suffer.

According to the multiprocess theory, automatic retrieval is generally expected to be more prominent during event-based, rather than time-based, prospective memory because retrieval cues are presented in the environment (i.e., externally generated) in an event-based task and thus are not dependent on a self-generated assessment of time (which is internally generated). Moreover, automatic processing is expected to occur when the event-based retrieval cue is similar to the ongoing task (e.g., the event is the word “banana” and the ongoing task is a word/non-word classification task); this has been referred to as the difference between a focal and a non-focal cue. The term focal cue denotes that the subject needs to attend to a single facet of the stimuli to complete both the ongoing task and the prospective memory tasks. In contrast, the cue is non-focal if two distinct qualities of the stimuli must be processed (e.g., the event is the font color of a presented word and the ongoing task is a word/non-word classification judgment). Finally, automatic processing is more likely if the prospective memory is less important than successfully completing the ongoing task (Loft et al. 2008); automatic processing is especially important if the prospective memory task is based on a focal cue (Marsh et al. 2005).

Recently, a refinement of the multiprocess theory of prospective memory has been proposed. This proposal (the dynamic multiprocess framework) focuses on intentions where a very long delay (e.g., hours to weeks) occurs before the action can be completed (Scullin et al. 2013). Under these conditions, it is very unlikely that a subject could engage in continuous monitoring no matter the conditions, especially if they sleep in-between intention formation and execution, therefore the memory for the intention is believed to be recovered through automatic retrieval due to 1) the elapsing of a time limit, 2) encountering contextual cues that the individual associates with the correct time to execute the intention, or 3) random retrieval processes. According to this proposal, delayed intentions are completed by alternating between the two processes described in multiprocess theory, engaging in alternating periods of active monitoring and automatic retrieval.

Evidence that alternation between active monitoring and automatic retrieval is influenced by the demands of the task has been found in a recent fMRI study. Activity in the anterior pre-frontal cortex (PFC) was observed during an event-based prospective memory session with non-focal cues; however, when focal cues were used, activity in this region was not present (McDaniel et al. 2013). These results are consistent with the multi-process theory of prospective memory (McDaniel and Einstein 2000) because under the more difficult non-focal prospective memory task, subjects engaged a continuous monitoring process (and the anterior PFC was involved in this process), but participants' instead engaged automatic retrieval during focal cue conditions. However, during a time-based prospective memory task, where participants could select to check a physical clock to determine whether they should complete the intended action, the anterior PFC was active when participants checked the clock (Oksanen et al. 2014). The dynamic multiprocess framework (Scullin et al. 2013) proposes that when a time limit is reached, instances of automatic retrieval of the intended action occurs, and the anterior PFC appears to be implicated. While the anterior PFC appears to be involved in automatic retrieval, the timing process responsible for signaling that the time limit has been exceeded is mediated by the hippocampus (Gordon et al. 2011). Combined these results suggest that: 1) the subject engaged in both active monitoring and automatic processing to complete a prospective memory task, 2) conditions have been identified where a subject uses one of these process over the other, and 3) that new methods are needed to determine how and when subjects alternate between these two processes. Perhaps more invasive techniques (compared to fMRI) may be needed to determine when a subject switches between active monitoring and automatic retrieval, which may open opportunities for advancements in animal models of prospective memory.

3.2 Applications to animal models

A number of techniques could be used to identify the neural substrates of prospective memory. Potential measures of neuronal activity include electrophysiology, microdialysis, and voltammetry. Time- and event-based prospective memory tasks (Wilson and Crystal 2012; Wilson et al. 2013) may be used to probe neuronal activity using advanced techniques to identify network patterns (Lapish et al. 2008) in such areas as the orbitofrontal cortex, which is believed to be involved in forming abstract representations the environment (Wilson et al. 2014), and the hippocampus, which has been shown to represent the passage of time (MacDonald et al. 2011), when the rats engage in different parts of prospective memory tasks. These approaches may identify the neuronal underpinning of behaviorally silent phenomenon such as retrieval.

Likewise, it would be possible to use ablation techniques where these structures are removed to document selective impairments in prospective memory. Finally, a number of genetic modifications (knock-out, knock-in rodent models, and ontogenetic approaches) could be used to identify which neurotransmitter systems or receptor subtypes within these structures are involved in prospective memory. These approaches could have a significant impact on our understanding of prospective memory and may constrain theories of prospective memory, such as the multiprocess theory and the dynamic multiprocess framework.

3.3 Age-related prospective-memory deficits

Studying developmental changes in prospective memory across the lifespan provides an opportunity to gain insight into the mechanisms underlying prospective memory. Prospective-memory performance is characterized by an inverted U-shaped curve (Zimmermann and Meier 2006), with younger children and older adults displaying deficiencies compared to older children and younger adults, respectively. The deficiency is characterized by a failure to execute the intended action at the appropriate time; yet when subsequently asked about the delayed intention, participants in these age groups still remembered their intentions. A prospective memory task requires subjects to maintain both a retrospective component (i.e., remember what needs to be done) and a prospective component (i.e., remember when it must be done; Kvavilashvili 1987) and these two age groups frequently fail to complete the prospective component. Many studies have attempted to understand when and why these prospective memory deficits in young children and older adults occur.

3.3.1. Young children—It is currently unknown precisely how prospective memory develops in children. Several factors may contribute to the observed prospective memory deficits seen in young children compared to older children. These factors include: unlearned strategic prospective memory cue formation skills, undeveloped working memory ability, a lack of planning skills, inferior theory of mind (or the ability to infer the intentions of others), and inferior episodic future thinking abilities. Beal (1987) observed that 6–7 year olds, but not 3–4 year olds, strategically placed objects in their environment to remind themselves of actions they intended to complete in the future. Differences in inhibition have been proposed to explain the age-related difference in event-based prospective memory between 4 and 5 years old (Mahy et al. 2014). Introducing a delay between blocks in an event-based prospective memory task disrupted the performance of 4 years old, but improved the performance of 5 years because these older participants elaborated upon or rehearsed the plan they had formed to complete the intended action during the break (Mahy and Moses 2011). The prospective memory abilities of 4 and 6 year olds was found to be correlated with the score they received on a test of their theory-of-mind ability (Ford et al. 2012). Finally, in Nirgo, Brandimonte, Cicogna, and Cosenza (2013), groups of 4, 5, 6, and 7 year olds were all given a test, based on methods developed on Atance and O'Neill (2001), in which they were given a future scenario and asked to select, from a series of objects, items that would be most beneficial to them in the future scenario and then explain their selections. Across all age groups, prospective memory ability and scores on this test of future thinking ability were significantly correlated.

Because there are a number of factors that may contribute to prospective memory deficits in young children, there may be multiple pathways by which an individual can develop prospective memory. Animal models of prospective memory, specifically models that use non-human primates, could be used to further investigate whether there are multiple pathways by which prospective memory develops. Several non-human primate researchers have used phylogenetic comparative cognition (MacLean et al. 2012) and meta-analyses combined with Bayesian statistics (Amici et al. 2012) to classify the cognitive capabilities of a number of non-human primate species for the purposes of revealing what evolutionary

pressures are associated with various facets of cognition. Thus, it may be possible to identify the cognitive abilities that are necessary or sufficient to produce prospective memory. One approach would involve testing two species that are low vs. high in factors that have been attributed to low vs. high prospective memory success in younger and older children, respectively.

3.3.2 Older adults—Elderly adults are less accurate at time-based than event-based prospective memory (d'Ydewalle et al. 2001; Einstein and McDaniel 1990; Henry et al. 2004; Kvavilashvili and Fisher 2007; Shum et al. 2013). Proposed explanations for this finding include the hypothesis that time-based prospective memory tasks require a greater level of self-initiation compared to event-based prospective memory tasks (Einstein et al. 1995; Maylor 1993) and the hypothesis that time-based prospective memories inherently place greater demand on attentional resources that are diminished with age (Martin and Schumann-Hengsteler 2001).

The pattern of results are somewhat complex. In naturalistic settings older adults have been shown to have superior prospective memory abilities compared to young controls; one explanation for this finding focuses on the hypothesis that older adults are better at linking retrieval cues with objects they anticipate interacting with at a future time point (Henry et al. 2004; Kvavilashvili and Fisher 2007). In contrast, older adults show prospective memory deficits when tested in the laboratory, and it is proposed that, under these circumstances, their strategies are not effective because they are in a novel environment (Maylor 1993). This “linking strategy” is believed to be an approach that elderly subjects adopt to compensate for the loss of time-based prospective memory. However, the negative effects of age on prospective memory performance appear to be ameliorated when participants are asked to engage in planning before engaging in a prospective memory task in a novel, experimental setting (Shum et al. 2013).

Animal models could be used to gain further insight into changes in prospective memory ability due to age-related cognitive decline. Unlike experiments that use human subjects, the entire life-history of an animal subject can be controlled. Likewise the age of an animal at the time of testing can be fully controlled.

But perhaps the greatest advantage to animal models would be to test the effectiveness of pharmaceutical and behavioral therapeutic approaches aimed at curtailing age-related deficiencies. The rodent-based prospective memory task described earlier could be used to elucidate the pathological impact of age-related cognitive decline on prospective memory ability. As this task requires intact prospective memory ability in order to see a *decline* in ongoing task accuracy, the nature of the resulting *improvement* in such a task (given an impairment in prospective memory) opens opportunities to test the effectiveness of pharmacological agents. Moreover, it may be possible to independently manipulate motivational and cognitive variables by using rats of different ages and standard techniques that are expected to impact hunger.

3.4. Impact of clinical conditions on prospective memory

In a series of studies, using both experimental and naturalistic protocols, as well as through surveys, like the Prospective and Retrospective Memory Survey (Crawford et al. 2003) and the Memory for Intentions Screening Test (Woods et al. 2008), prospective memory deficits have been noted in a number of clinical conditions. These include Alzheimer's disease (Troyer and Murphy 2007), mild cognitive impairment (Blanco-Campal et al. 2009), obsessive-compulsive disorder (Cuttler and Graf 2008), attention deficit hyperactivity disorder (Altgassen et al. 2014), and various forms of substance abuse and exposure (Heffernan, Clark, et al. 2010; Heffernan and O'Neill 2013; Heffernan, O'Neill, et al. 2010; Heffernan et al. 2012; Martin et al. 2007; Terrett et al. 2014; Weinborn et al. 2013).

While many studies have catalogued that individuals in specific disease states develop prospective memory deficits, few studies have attempted to use the observed prospective memory deficits to further elucidated the nature of the neuropathology (but see Kliegel et al. 2011 as an exception). This approach is difficult when using people with clinical conditions for a number of reasons. Participants may be at different levels of disease progression. If participants are receiving treatments, different types of drug and/or doses may complicate this approach. Finally, substance abusers likely have varying histories of drug exposure, and if they are in recovery, they may have different levels of withdraw or craving.

Experiments on animals, specifically a rodent model, offer many advantages. For example, 1) the disease state could be introduced at specific ages, 2) treatments can be precisely controlled, and 3) in models of drug abuse, the animals' history can be precisely controlled.

4. Conclusions

As summarized in this review, a number of animal models of prospective memory have been developed. Rodent models of prospective memory may be especially useful for exploring the neural substrates that support prospective memory and the role of clinical conditions in disorders of prospective memory. Non-human primate models may be especially useful for studying development pathways which may impact competencies needed to support prospective memory. Finally, we believe that comparative approaches may prove useful for exploring insights and theories of prospective memory derived from the human literature. The establishment of animal models of prospective memory is at an early stage of development. We hope that these and other models will be used to understand the biological mechanisms that support prospective memory. The validation of animal models of prospective memory will create opportunities to use advances in our understanding of memory at cellular, molecular, and genetic levels of analysis to explore prospective memory in animals. These approaches may lead to new insights about the biological mechanisms that are responsible for impaired and spared aspects of cognition in preclinical models, which ultimately may be used to promote retained cognition and develop treatments for human memory disorders.

Acknowledgements

This article is in honor of the contributions of Tom Zentall to the study of comparative cognition. Supported by National Institute on Aging grant AG044530 to JDC.

References

- Altgassen M, Koch A, Kliegel M. Do Inhibitory Control Demands Affect Event-Based Prospective Memory Performance in ADHD? *Journal of attention disorders*: 1087054713518236. 2014
- Amici F, Barney B, Johnson VE, Call J, Aureli F. A modular mind? A test using individual data from seven primate species. *PloS one*. 2012; 7:e51918. [PubMed: 23284816]
- Atance CM, O'Neill DK. Episodic future thinking. *Trends in cognitive sciences*. 2001; 5:533–539. [PubMed: 11728911]
- Beal, CR. Memory for future intentions: Investigating pulses and steps. In: Gruneberg, MM.; Morris, PE.; Skyes, RN., editors. *Practical aspects of memory: Current research and issues*. Chichester, UK: Wiley; 1987.
- Beran MJ, Evans TA, Klein ED, Einstein GO. Rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*) remember future responses in a computerized task. *Journal of Experimental Psychology: Animal Behavior Processes*. 2012; 38:233–243. [PubMed: 22545901]
- Beran MJ, Perdue BM, Bramlett JL, Menzel CR, Evans TA. Prospective memory in a language-trained chimpanzee (*Pan troglodytes*). *Learning and Motivation*. 2012; 43:192–199. [PubMed: 23139433]
- Blanco-Campal A, Coen RF, Lawlor BA, Walsh JB, Burke TE. Detection of prospective memory deficits in mild cognitive impairment of suspected Alzheimer's disease etiology using a novel event-based prospective memory task. *Journal of the International Neuropsychological Society*. 2009; 15:154–159. [PubMed: 19128540]
- Brewer GA, Ball BH, Knight JB, Dewitt MR, Marsh RL. Divided attention interferes with fulfilling activity-based intentions. *Acta Psychologica*. 2011; 138:100–105. [PubMed: 21704959]
- Cohen A-L, Jaudas A, Gollwitzer PM. Number of cues influences the cost of remembering to remember. *Memory and Cognition*. 2008; 36:149–156. [PubMed: 18323071]
- Colwill RM. An associative analysis of instrumental learning. *Current Directions in Psychological Science*. 1993; 2:111–116.
- Cook RG, Brown MF, Riley DA. Flexible memory processing by rats: Use of prospective and retrospective information in the radial maze. *Journal of Experimental Psychology: Animal Behavior Processes*. 1985; 11:453–469. [PubMed: 4009126]
- Corballis MC. Mental time travel: a case for evolutionary continuity. *Trends in Cognitive Sciences*. 2013; 17:5–6. [PubMed: 23153675]
- Craik FI, Govoni R, Naveh-Benjamin M, Anderson ND. The effects of divided attention on encoding and retrieval processes in human memory. *Journal of Experimental Psychology: General*. 1996; 125:159. [PubMed: 8683192]
- Crawford JR, Smith G, Maylor EA, Della Sala S, Logie R. The Prospective and Retrospective Memory Questionnaire (PRMQ): Normative data and latent structure in a large non-clinical sample. *Memory*. 2003; 11:261–275. [PubMed: 12908675]
- Crystal JD. Prospective cognition in rats. *Learning and Motivation*. 2012; 43:181–191. [PubMed: 23180886]
- Crystal JD. Prospective memory. *Current Biology*. 2013a; 23:R750–R751. [PubMed: 24028958]
- Crystal JD. Remembering the past and planning for the future in rats. *Behavioural Processes*. 2013b; 93:39–49. [PubMed: 23219951]
- Crystal JD, Glanzman DL. A biological perspective on memory. *Current Biology*. 2013; 23:R728–R731. [PubMed: 24028954]
- Cuttler C, Graf P. Sub-clinical checking compulsions are related to impaired prospective memory independently of depression, anxiety and distractibility. *Journal of anxiety disorders*. 2008; 22:642–654. [PubMed: 17656066]
- d'Ydewalle G, Bouckaert D, Brunfaut E. Age-related differences and complexity of ongoing activities in time-and event-based prospective memory. *The American journal of psychology*. 2001
- DiGian KA, Zentall TR. Pigeons may not use dual coding in the radial maze analog task. *Journal of Experimental Psychology: Animal Behavior Processes*. 2007; 33:262–272. [PubMed: 17620025]
- Eacott MJ, Easton A. Remembering the future: The influence of past experience on future behavior. *Learning and Motivation*. 2012; 43:167–168.

- Einstein GO, McDaniel MA. Normal aging and prospective memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 1990; 16:717.
- Einstein GO, McDaniel MA, Richardson SL, Guynn MJ, Cunfer AR. Aging and prospective memory: examining the influences of self-initiated retrieval processes. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 1995; 21:996.
- Einstein GO, McDaniel MA, Williford CL, Pagan JL, Dismukes R. Forgetting of intentions in demanding situations is rapid. *Journal of Experimental Psychology: Applied*. 2003; 9:147. [PubMed: 14570509]
- Evans TA, Beran MJ. Monkeys exhibit prospective memory in a computerized task. *Cognition*. 2012; 125:131–140. [PubMed: 22883317]
- Flaherty CF, Checke S. Anticipation of incentive gain. *Animal Learning & Behavior*. 1982; 10:177–182.
- Ford RM, Driscoll T, Shum D, Macaulay CE. Executive and theory-of-mind contributions to event-based prospective memory in children: Exploring the self-projection hypothesis. *Journal of experimental child psychology*. 2012; 111:468–489. [PubMed: 22169353]
- Gipson CD, DiGian KA, Miller HC, Zentall TR. Radial maze analog for pigeons: Evidence for flexible coding strategies may result from faulty assumptions. *Learning and Motivation*. 2008; 39:285–295. [PubMed: 19884963]
- Gordon BA, Shelton JT, Bugg JM, McDaniel MA, Head D. Structural correlates of prospective memory. *Neuropsychologia*. 2011; 49:3795–3800. [PubMed: 21982698]
- Harrison TL, Mullet HG, Whiffen KN, Ousterhout H, Einstein GO. Prospective memory: Effects of divided attention on spontaneous retrieval. *Memory and Cognition*. 2014; 42:212–224. [PubMed: 24046252]
- Heffernan TM, Clark R, Bartholomew J, Ling J, Stephens S. Does binge drinking in teenagers affect their everyday prospective memory? *Drug and alcohol dependence*. 2010; 109:73–78. [PubMed: 20071106]
- Heffernan TM, O'Neill TS. Exposure to second-hand smoke damages everyday prospective memory. *Addiction*. 2013; 108:420–426. [PubMed: 22913297]
- Heffernan TM, O'Neill TS, Moss M. Smoking and everyday prospective memory: a comparison of self-report and objective methodologies. *Drug and alcohol dependence*. 2010; 112:234–238. [PubMed: 20800391]
- Heffernan TM, O'Neill TS, Moss M. Smoking-related prospective memory deficits in a real-world task. *Drug and alcohol dependence*. 2012; 120:1–6. [PubMed: 21726964]
- Henry JD, MacLeod MS, Phillips LH, Crawford JR. A meta-analytic review of prospective memory and aging. *Psychology and Aging*. 2004; 19:27–39. [PubMed: 15065929]
- Henson RN, Eckstein D, Waszak F, Frings C, Horner AJ. Stimulus- response bindings in priming. *Trends in Cognitive Sciences*. 2014; 18:376–384. [PubMed: 24768034]
- Kametani H, Kesner RP. Retrospective and prospective coding of information: Dissociation of parietal cortex and hippocampal formation. *Behavioral Neuroscience*. 1989; 103:84–89. [PubMed: 2923680]
- Kesner RP. Retrospective and prospective coding of information: role of the medial prefrontal cortex. *Experimental Brain Research*. 1989; 74:163–167. [PubMed: 2924832]
- Kliegel M, Altgassen M, Hering A, Rose NS. A process-model based approach to prospective memory impairment in Parkinson's disease. *Neuropsychologia*. 2011; 49:2166–2177. [PubMed: 21255592]
- Kliegel M, Martin M, McDaniel MA, Einstein GO. Varying the importance of a prospective memory task: Differential effects across time - and event-based prospective memory. *Memory*. 2001; 9:1–11. [PubMed: 11315657]
- Kliegel, M.; McDaniel, MA.; Einstein, GO. Prospective memory: Cognitive, neuroscience, developmental, and applied perspectives. Psychology Press; 2008.
- Kvavilashvili L. Remembering intention as a distinct form of memory. *British journal of psychology*. 1987; 78:507–518.
- Kvavilashvili L, Fisher L. Is time-based prospective remembering mediated by self-initiated rehearsals? Role of incidental cues, ongoing activity, age, and motivation. *Journal of Experimental Psychology: General*. 2007; 136:112. [PubMed: 17324087]

- Lapish CC, Durstewitz D, Chandler LJ, Seamans JK. Successful Choice Behavior Is Associated with Distinct and Coherent Network States in Anterior Cingulate Cortex. *Proceedings of the National Academy of Sciences of the United States of America*. 2008; 105:11963–11968. [PubMed: 18708525]
- Loft S, Kearney R, Remington R. Is task interference in event-based prospective memory dependent on cue presentation? *Memory and Cognition*. 2008; 36:139–148. [PubMed: 18323070]
- MacDonald CJ, Lepage KQ, Eden UT, Eichenbaum H. Hippocampal “time cells” bridge the gap in memory for discontinuous events. *Neuron*. 2011; 71:737–749. [PubMed: 21867888]
- MacLean EL, Matthews LJ, Hare BA, Nunn CL, Anderson RC, Aureli F, Brannon EM, Call J, Drea CM, Emery NJ. How does cognition evolve? Phylogenetic comparative psychology. *Animal cognition*. 2012; 15:223–238. [PubMed: 21927850]
- Mahy CEV, Moses LJ. Executive functioning and prospective memory in young children. *Cognitive Development*. 2011; 26:269–281.
- Mahy CEV, Moses LJ, Kliegel M. The impact of age, ongoing task difficulty, and cue salience on preschoolers’ prospective memory performance: The role of executive function. *Journal of experimental child psychology*. 2014
- Marsh RL, Hicks JL. Event-based prospective memory and executive control of working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 1998; 24:336.
- Marsh RL, Hicks JL, Cook GI. On the relationship between effort toward an ongoing task and cue detection in event-based prospective memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2005; 31:68.
- Marsh RL, Hicks JL, Cook GI. Task interference from prospective memories covaries with contextual associations of fulfilling them. *Memory & Cognition*. 2006; 34:1037–1045. [PubMed: 17128602]
- Marsh RL, Hicks JL, Cook GI, Hansen JS, Pallos AL. Interference to ongoing activities covaries with the characteristics of an event-based intention. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2003; 29:861.
- Marsh RL, Hicks JL, Watson V. The dynamics of intention retrieval and coordination of action in event-based prospective memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2002; 28:652.
- Martin EM, Nixon H, Pitrak DL, Weddington W, Rains NA, Nunnally G, Grbesic S, Gonzalez R, Jacobus J, Bechara A. Characteristics of prospective memory deficits in HIV-seropositive substance-dependent individuals: Preliminary observations. *Journal of Clinical and Experimental Neuropsychology*. 2007; 29:496–504. [PubMed: 17564915]
- Martin M, Schumann-Hengsteler R. How task demands influence time-based prospective memory performance in young and older adults. *International Journal of Behavioral Development*. 2001; 25:386–391.
- Maylor EA. Aging and forgetting in prospective and retrospective memory tasks. *Psychology and Aging*. 1993; 8:420. [PubMed: 8216962]
- McDaniel MA, Einstein GO. Strategic and automatic processes in prospective memory retrieval: A multiprocess framework. *Applied cognitive psychology*. 2000; 14:S127–S144.
- McDaniel, MA.; Einstein, GO. *Prospective memory: An overview and synthesis of an emerging field*. Thousand Oaks, CA: Sage Publications; 2007.
- McDaniel MA, LaMontagne P, Beck SM, Scullin MK, Braver TS. Dissociable neural routes to successful prospective memory. *Psychological science*. 2013; 24:1791–1800. [PubMed: 23907544]
- Nigro G, Brandimonte MA, Cicogna PC, Cosenza M. Episodic future thinking as a predictor of children’s prospective memory. *Journal of experimental child psychology*. 2013
- Oksanen KM, Waldum ER, McDaniel MA, Braver TS. Neural Mechanisms of Time-Based Prospective Memory: Evidence for Transient Monitoring. *PloS one*. 2014; 9:e92123. [PubMed: 24643226]
- Perdue B, Evans T, Williamson R, Gonsiorowski A, Beran M. Prospective memory in children and chimpanzees. *Animal Cognition*. 2014; 17:287–295. [PubMed: 23884791]
- Roberts, WA. *Principles of Animal Cognition*. Boston: McGraw-Hill; 1998.

- Roberts WA. Are animals stuck in time? *Psychological Bulletin*. 2002; 128:473–489. [PubMed: 12002698]
- Roberts WA. Evidence for future cognition in animals. *Learning and Motivation*. 2012; 43:169–180.
- Roitblat H. Codes and coding processes in pigeon short-term memory. *Learning & Behavior*. 1980; 8:341–351.
- Schacter DL, Addis DR. The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2007; 362:773–786.
- Schacter DL, Addis DR, Buckner RL. Remembering the past to imagine the future: the prospective brain. *Nature Reviews Neuroscience*. 2007; 8:657–661.
- Scullin MK, McDaniel MA, Shelton JT. The Dynamic Multiprocess Framework: Evidence from prospective memory with contextual variability. *Cognitive Psychology*. 2013; 67:55–71. [PubMed: 23916951]
- Shum DHK, Cahill A, Hohauser LC, O'Gorman JG, Chan RCK. Effects of aging, planning, and interruption on complex prospective memory. *Neuropsychological rehabilitation*. 2013; 23:45–63. [PubMed: 22973855]
- Smith RE. The cost of remembering to remember in event-based prospective memory: investigating the capacity demands of delayed intention performance. *Journal of Experimental Psychology-Learning Memory and Cognition*. 2003; 29:347–61.
- Smith RE, Bayen UJ. A multinomial model of event-based prospective memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2004; 30:756.
- Smith RE, Hunt RR, McVay JC, McConnell MD. The cost of event-based prospective memory: Salient target events. *Journal of Experimental Psychology-Learning Memory and Cognition*. 2007; 33:734–746.
- Suddendorf T. Mental time travel: continuities and discontinuities. *Trends in Cognitive Sciences*. 2013; 17:151–152. [PubMed: 23453751]
- Suddendorf T, Corballis MC. Mental time travel and the evolution of the human mind. *Genetic, Social, & General Psychology Monographs*. 1997; 123:133–167.
- Terrett G, McLennan SN, Henry JD, Biernacki K, Mercuri K, Curran HV, Rendell PG. Prospective memory impairment in long-term opiate users. *Psychopharmacology*. 2014:1–10.
- Troyer AK, Murphy KJ. Memory for intentions in amnesic mild cognitive impairment: Time- and event-based prospective memory. *Journal of the International Neuropsychological Society*. 2007; 13:365–369. [PubMed: 17286894]
- Tulving, E. Chronesthesia: Awareness of subjective time. In: Stuss, DT.; Knight, RC., editors. *The Age of the Frontal Lobes*. New York: Oxford University Press; 2001.
- Tulving, E. Episodic memory and autonoesis: Uniquely human?. In: Terrace, H.; Metcalfe, J., editors. *The Missing Link in Cognition: Origins of Self-Reflective Consciousness*. New York: Oxford University Press; 2005.
- Wasserman, EA.; Zentall, TR. *The Oxford Handbook of Comparative Cognition*. New York: Oxford University Press; 2012.
- Weinborn M, Moyle J, Bucks RS, Stritzke W, Leighton A, Woods SP. Time-based prospective memory predicts engagement in risk behaviors among substance users: results from clinical and nonclinical samples. *Journal of the International Neuropsychological Society*. 2013; 19:284–294. [PubMed: 23312588]
- Wilson AG, Crystal JD. Prospective memory in the rat. *Animal Cognition*. 2012; 15:349–358. [PubMed: 21922257]
- Wilson AG, Pizzo MJ, Crystal JD. Event-Based Prospective Memory in the Rat. *Current Biology*. 2013; 23:1089–1093. [PubMed: 23727093]
- Wilson RC, Takahashi YK, Schoenbaum G, Niv Y. Orbitofrontal Cortex as a Cognitive Map of Task Space. *Neuron*. 2014; 81:267–279. [PubMed: 24462094]
- Woods SP, Moran LM, Carey CL, Dawson MS, Iudicello JE, Gibson S, Grant I, Atkinson JH. Prospective memory in HIV infection: Is “remembering to remember” a unique predictor of self-reported medication management? *Archives of Clinical Neuropsychology*. 2008; 23:257–270. [PubMed: 18243645]

- Zentall TR. Animals may not be stuck in time. *Learning & Motivation*. 2005; 36:208–225.
- Zentall TR. Mental time travel in animals: A challenging question. *Behavioural Processes*. 2006; 72:173–183. [PubMed: 16466863]
- Zentall TR. Coding of stimuli by animals: Retrospection, prospection, episodic memory and future planning. *Learning and Motivation*. 2010; 41:225–240. [PubMed: 23258942]
- Zentall TR, Steirn JN, Jackson-Smith P. Memory strategies in pigeons' performance of a radial-arm-maze analog task. *Journal of Experimental Psychology: Animal Behavior Processes*. 1990; 16:358–371.
- Zimmermann TD, Meier B. The rise and decline of prospective memory performance across the lifespan. *The Quarterly Journal of Experimental Psychology*. 2006; 59:2040–2046. [PubMed: 17095485]

Highlights

- A number of animal models of prospective memory have been developed
- Rodent models are useful for exploring neural substrates and clinical conditions
- Non-human primates are useful for studying developmental pathways and competencies
- Comparative approaches are useful to explore insights and theories of human prospective memory

Figure 1.

A disruption in performance is shown by a compressed range in the psychophysical function after the event provided information that the meal could be obtained soon. (A) Anticipation of a meal reduced performance in the ongoing gap-duration task after the event relative to excellent performance at an earlier time point. Smooth curves are the best fitting functions to the mean data shown in the figure. Data are means with 1 SEM. (B) Rats anticipated the arrival of the meal, as shown by the increase in food-trough responses before the meal and the increase that occurs when the event provided information that the meal could be obtained soon. The horizontal line indicates when the event was presented during the last 10-min before the meal. The meal could be obtained beginning at 90 min by interrupting a photobeam in the food trough. The error bar is 1 SEM averaged across 90 min. Reproduced with permission from Wilson, A.G., Pizzo, M.J., & Crystal, J. D. (2013). Event-based prospective memory in the rat. *Current Biology*, 23, 1089–1093. © 2013 Elsevier Ltd.

Figure 2.

Performance in the ongoing task was severely disrupted after the event, relative to excellent performance at an earlier time point when the event had not occurred, for both early and late meals. (A–C) Anticipation of early (A) and late (B) meals severely disrupted performance in the ongoing task after the event, relative to excellent performance at an earlier time point. (C) When event and time were dissociated (using data from 25–34 min, with and without the event), performance was severely disrupted by the event. (A–C) Smooth curves are the best fitting functions to the mean data shown in the figure. Data are means with 1 SEM. (D) Rats

anticipated the arrival of the meal, as shown by the increase in food-trough responses when the event provided information that the meal could be obtained soon; the meal could be obtained early or late (beginning at 35 or 260 min, respectively), which was randomly determined on each day. Horizontal lines indicate the last 10-min before the meal when the event was presented. The error bar is 1 SEM averaged across 35 and 260 min for each curve. Reproduced with permission from Wilson, A.G., Pizzo, M.J., & Crystal, J. D. (2013). Event-based prospective memory in the rat. *Current Biology*, 23, 1089–1093. © 2013 Elsevier Ltd.

Figure 3.

Event-based prospective memory is shown by putting event and time in conflict. (A) When the event was presented at a novel time, performance in the ongoing task was severely disrupted by the event. Smooth curves are the best fitting functions to the mean data shown in the figure. Data are means with 1 SEM. (B) When the event was presented at a novel time (illustrated by the horizontal bar), rats anticipated the arrival of the meal, as shown by the increase in food-trough responses when the event provided information that the meal could be obtained soon. The error bar is 1 SEM averaged across 290 min. Reproduced with permission from Wilson, A.G., Pizzo, M.J., & Crystal, J. D. (2013). Event-based prospective memory in the rat. *Current Biology*, 23, 1089–1093. © 2013 Elsevier Ltd.

Figure 4.

Multiple, repeated presentations of the event on the same day demonstrate that rats inactivate and reactivate the memory representation in an on-demand, event-based fashion. (A) When the event was presented at three novel times, performance in the ongoing task was severely disrupted by the event (filled bars), with excellent performance shown at other times (unfilled bars). Events occurred at 70–89, 130–149, and 200–219 min. No-event data come from 11–20, 110–129, and 160–199 min. Data are means with 1 SEM. (B) When the event was presented at three novel time (illustrated by the horizontal bars), rats anticipated the arrival of the meal, as shown by the increase in food-trough responses when the event provided information that the meal could be obtained soon. The error bar is 1 SEM averaged across 290 min. Reproduced with permission from Wilson, A.G., Pizzo, M.J., & Crystal, J. D. (2013). Event-based prospective memory in the rat. *Current Biology*, 23, 1089–1093. © 2013 Elsevier Ltd.