



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

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ABSTRACT

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

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

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

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

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

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

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

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

2002; Metcalfe & Kober, 2005; Suddendorf & Busby, 2003; Suddendorf & Corballis, 2007), but there is no consensus for the relationships among these capacities.

Some of the strongest evidence for planning (and perhaps mental time travel) comes from studies with great apes. Mulcahy and Call (2006) reported that bonobos (*Pan paniscus*) and orangutans (*Pongo pygmaeus*) transported and saved tools that they could only use 1 h or 14 h later. However, this case of planning involved apes that chose tools with the baited sites visible, suggesting that those rewards or the site of those rewards motivated the planning behavior. When the apes were not given access to the baited site at the time when they had the chance to choose the correct tool, they were less likely to select the correct tool. Osvath and Osvath (2008) showed that chimpanzees and orangutans could override immediate needs by choosing a tool they could only use later rather than choosing a food they could eat now. This suggested that the apes anticipated a future opportunity to access food using the tool. However, this test did not overcome the limitation imposed by the Bischof–Köhler hypothesis as the choice of the tool may have resulted from the apes preferring the delayed food more than the immediately available food. In addition, the tool may have served as a reminder of the preferred food, and therefore the choice was still tied to options available in the present.

Some studies using similar methodologies provide evidence against the Bischof–Köhler hypothesis. For example, jays (*Aphelocoma californica*) will cache foods preferentially in locations where they have learned they will be hungry later in time (Raby, Alexis, Dickinson, & Clayton, 2007). Also, Correia, Dickinson, and Clayton (2007) reported that scrub jays would cache foods differentially even if they were pre-fed those foods to satiety, suggesting that current motivational state did not interfere with caching based on future needs. However, Bird, Roberts, Abroms, Kit, and Crupi (2003) reported that rats did not succeed in a similar cache retrieval paradigm. Thus, phylogenetic differences may exist, and there may be good reasons for these differences in performance, possibly relating to differences in biological versus psychological control over caching.

Planning future responses goes hand in hand with prospective memory. Prospective memory is the ability to remember to perform activities in the future. It reflects processes that combine forming intentions, planning future responses, retaining those intentions or plans during a delay period, and properly executing the intended or planned responses when the correct time is reached (e.g., Einstein & McDaniel, 1990, 2005; Ellis, 1996; Ellis & Freeman, 2008; Kliegel, McDaniel, & Einstein, 2000; Shallice & Burgess, 1991). Critically, execution of intended actions cannot occur immediately, and the prospective memory must be embedded within ongoing activity so as to prevent continuous rehearsal (McDaniel & Einstein, 2007). Although prospective memory is easily disrupted and fragile, humans routinely use it as a tool to aid in planning future behavior (Kliegel, Mackinlay, & Jager, 2008; Kliegel et al., 2000; McDaniel, Einstein, Graham, & Rall, 2004; Smith, 2003, 2008). Also, many instances of prospective memory in humans seem to meet the requirements of the Bischof–Köhler hypothesis (e.g., remembering to buy food at the grocery store that is not presently appealing but that will be used later in some meal preparation).

The present experiment attempted to assess planning and prospective memory in a chimpanzee named Panzee. She is a special subject for this type of research because of her unique rearing experiences. Panzee has had considerable experience in relating information about her environment to the humans around her, and she does this through use of the lexigram symbol system, which consists of geometric forms that each represent a different kind of item, including foods, objects, and individuals. From her first year of life, Panzee was immersed in a language-rich environment wherein spoken English and lexigram symbols were used consistently. This exposure resulted in Panzee's ability to comprehend speech and respond using lexigram symbols (Brakke & Savage-Rumbaugh, 1995, 1996; Rumbaugh & Washburn, 2003). Panzee still communicates using lexigrams, allowing for unique experimental opportunities. For example, in one study, Panzee watched an experimenter hide an object in the forest that surrounds her outdoor yard. To obtain that object, she had to recruit an experimentally naïve human to retrieve the object. She did this by indicating to the naïve caregiver, out of view of the object, the object's name on a lexigram keyboard, followed by gesturing that the caregiver should accompany her outdoors. Panzee then directed the person to the location of the hidden object with hand and arm gestures, and in nearly all cases guided the person to within a foot of the location (Menzel, 1999). Panzee also showed very few "false positives," that is, she rarely induced a person to search in the forest when no object had been hidden. This seems a clear case of recall memory, and perhaps even approaches the episodic memories experienced by humans. In those tests, Panzee's use of the lexigrams provides information about what she remembers seeing. We utilized this capacity in the present experiment to assess whether Panzee would remember to get a lexigram token after a delay to obtain a less-preferred item that was previously rejected in favor of a more preferred item.

Our experiment involved presenting Panzee with two food items, one of which she would choose over the other while in her indoor area. The chosen item was then spread around her outdoor yard for her to forage. Plastic lexigram tokens were distributed throughout her outdoor yard, each representing a different food item. The unchosen item was placed in a sealed, opaque container that remained indoors. Panzee had already learned that these tokens could be used to exchange for food indoors. So, the question was whether Panzee would remember the food type that she had just neglected in favor of another type when she later had exhausted her foraging for the preferred item. If she did, she should then search for and retrieve the lexigram representing that item and bring it back indoors to try to obtain the less preferred food item. Success here would suggest that although Panzee did not initially prefer that food type, she still encoded its identity. She might also have formed the intention to retrieve that food later by bringing in the correct token to match that item. This would approximate the prospective memory task of anticipating that something needed to be done later to obtain a deferred goal that was not, at the present time, the most motivating aspect of the environment but that would be motivating and relevant later. Critically, Panzee also participated in control trials that involved no additional food item indoors to confirm that Panzee

was not bringing in any type of token to request non-test food items (e.g., those still in the refrigerator) but instead was implementing the intended response of naming the indoor food.

Methods

Participant

We tested one adult (26 year old) female chimpanzee named Panzee.¹ Panzee was housed along with three other chimpanzees in a building with multiple indoor and outdoor enclosures. For testing, we limited Panzee to one indoor enclosure and an adjacent outdoor enclosure while the other chimpanzees were kept in neighboring enclosures. Panzee had 24-h access to water and was fed three daily meals consisting of fruits, vegetables, and protein sources.

As mentioned above, Panzee was language trained from an early age and used and responded to lexigram symbols in a variety of ways. Pertinent to the present study is that Panzee participated in two prior studies involving lexigram tokens similar to the ones used here. In the first study, Panzee and two other language trained chimpanzees were tested for their ability to trade tokens with conspecifics for mutual gain (Brosnan & Beran, 2009). In the second study, the same three chimpanzees were assessed for self-control through their capacity to choose lexigram tokens representing highly preferred foods over immediately available, moderately preferred foods when the tokens could only be exchanged later for the foods they represented (Beran & Evans, 2012).

Materials

The lexigram tokens used in this study were similar to those used in the prior studies mentioned above. They consisted of 7.5 cm × 7.5 cm × .5 cm white plastic tokens with a lexigram symbol affixed to one side. The lexigrams presented as tokens in this study represented the following food items: apple, banana, bread, coffee, Coca-Cola, grapes, juice, kiwi, M&Ms, orange, peach, peanuts, pear, and sweet potato. We also introduced a 25 cm × 10 cm × 10 cm opaque plastic container with lid, in which we placed the selected test food item for each trial. In the final test, we used an additional apparatus with which Panzee was highly familiar. This was a 75 cm × 30 cm × 45 cm black wooden bench with a sliding shelf on which we could provide Panzee with choice options for a particular trial (see below for more details).

Procedures

We conducted the study in 3 phases: familiarization, training, and testing. In all three phases, an experimenter showed Panzee a food item and then hid it in an opaque container. At some point in the session, Panzee had the opportunity to select an appropriate lexigram token from a set of four or more alternatives. Then, sometime later, Panzee could exchange that token for the item in the container.

Familiarization phase

The objective of the familiarization phase was to acquaint Panzee with the materials and general procedures used in the study. Because she was already familiar with two-sided lexigram tokens, she simply had to generalize her token knowledge to the one-sided tokens used here. Also, she needed to learn that the tokens could be used to request the item hidden in the container by the experimenter (and that the tokens could not be used to request other food items not involved in the test). To do this, we presented Panzee with trials in which she watched while an experimenter (hereafter E1) baited the container with a nameable food from her indoor enclosure, and then E1 gave Panzee access to an adjacent indoor enclosure containing eight face-down lexigram tokens. After a five-minute delay, a naïve experimenter (hereafter E2) entered the test area and gave Panzee the opportunity to exchange a token for the item hidden in the container.

Training phase

The purpose of the training phase was to show Panzee that the lexigram tokens could be made available in an outdoor location as well as to confirm that Panzee remembered the identity of the hidden item as well as the purpose of the tokens, from a location where the container and hidden item were out of view. Trials began similarly to the familiarization phase, with Panzee watching as E1 baited the container with a food item. E2 then gave Panzee access to an outdoor location which contained eight face-down tokens. After five minutes, another naïve experimenter (hereafter E3) entered the indoor test area and made him or herself available to exchange the hidden food item for the appropriate lexigram token.

Testing phase

In the test phase, we added critical elements to the design that allowed us to assess Panzee's capacity for prospective memory. At the beginning of each test trial, E1 presented Panzee with the choice between two nameable food items on the

¹ In addition to Panzee, we also began the study with two other language-trained chimpanzees, Sherman and Lana. However, these two did not succeed in the familiarization and training steps and thus were dropped from the study prior to conducting the formal experiment.

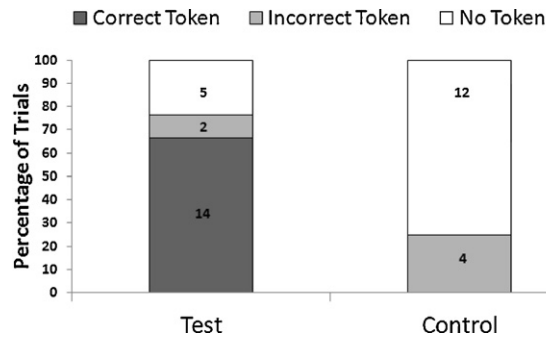


Fig. 1. Percentage of trials in which Panzee brought in the correct token, an incorrect token, or no token in each of the two conditions. The numbers in the bars represent the number of actual trials of that type.

black wooden bench mentioned above. One choice was always 40 M&Ms and the other choice was a randomly determined food item from the list given above. E1 placed whichever item Panzee *did not* choose immediately into the opaque container and then left the test area while the container remained just outside of Panzee's enclosure. Then, E2 distributed Panzee's chosen option (typically the M&Ms, which are a very highly preferred food) in the outdoor enclosure and immediately gave Panzee access to that enclosure. The outdoor enclosure also contained eight face-down tokens including those representing M&Ms and the other choice item presented at the beginning of the trial. At that time, E3 entered the indoor test area and remained there, available to exchange the hidden food item for a token if Panzee chose to return a token, and if it matched that hidden food item. Panzee was given 30 min in the outdoor enclosure, and during this time E2 recorded her behavior, including each token that Panzee touched, each that she turned over, and whether she kept a token she touched or left it on the ground. If Panzee did not return to the indoor enclosure within 30 min without any direct prompting, then she was called back indoors by E2 whether or not she had acquired a token.

E3 waited for Panzee to return indoors and slide a token out of her enclosure. Then, E3 opened the container to determine what, if anything, was in the container. Thus, E3 did not know what, if anything, was in this container until it was opened after a token was exchanged by Panzee. As before, if Panzee offered the appropriate token, then she was given the item in the container. If Panzee returned indoors without a token or the token she offered did not match what E3 found in the container, then E3 asked Panzee to use her lexigram keyboard (mounted on the enclosure wall) to indicate the contents of the container without yet showing her that item directly (i.e., it was still in the opaque container). If Panzee failed to name the item appropriately using the keyboard in either of these cases, E3 then took the food item out of the container and showed her the food item and asked her to name it. In all of the cases in which no appropriate token was brought indoors, Panzee did not receive the item in the container (even if she later named it correctly on the keyboard).

Paneez completed 21 test trials as described above as well as 16 control trials in which no item was placed in the opaque container. In the control trials, Panzee chose between the 40 M&Ms and an empty bowl. As expected, she always chose the M&Ms, leaving nothing to be put in the opaque container; however, E1 still opened and closed the container and placed it outside of her enclosure in an identical manner to the test trials. E3 was naïve to the experimental condition, so he or she responded to Panzee's token offerings, or lack of thereof, the same way in control trials as outlined above for test trials – without any knowledge of what food item, if any, was in the opaque container.

Data analysis

For each trial, we recorded whether Panzee attempted to exchange a token or not. Exchanges were defined as bringing a token into the indoor area and pushing it out of her cage toward either the experimenter or the container. For test trials, attempting to exchange a token was considered a success, and *not* exchanging a token was considered a failure. Conversely, for control trials, attempting to exchange a token was considered a failure (because the bucket was empty), and *not* exchanging a token was considered a success. We used a chi-square goodness-of-fit test to determine whether these behaviors (trading a token or *not* trading a token) were evenly distributed across control and test trials. For test trials in which Panzee exchanged a token, we used a binomial distribution to compare the actual number of correct tokens exchanged to that expected by chance ($1/8$ tokens = .125 probability of randomly selecting the correct token). We also recorded several aspects of her behavior on test trials, including how often she selected M&Ms as the item to be scattered outdoors, whether she picked up and ate the outdoor food items before turning over any tokens outdoors, whether she discontinued her investigation of the tokens once she found the correct one, and whether she brought a token inside without prompting before the 30 min had elapsed.

Results

Out of 37 total trials, Panzee attempted to exchange a token on 20 trials (16 test trials and 4 control trials; see Fig. 1). There were significantly more token exchanges made during test trials than expected by random distribution across trial type,

$\chi^2(1, N=20) = 4.40, p < .05$. Panzee did *not* exchange a token on 17 trials (12 controls and 5 test trials). This behavior occurred significantly more often during control trials than expected by random distribution across trial type, $\chi^2(1, N=17) = 5.18, p < .05$. On test trials in which Panzee exchanged a token, she presented the correct token 14 out of 16 times, which is significantly more often than predicted by chance ($p < .001$, binomial test).

On test trials ($N=21$), Panzee selected M&Ms in the initial choice from the tray 81% of the time, and always picked up and ate her chosen food items in the outdoor area before turning over tokens in the yard. In 71% of these 21 test trials, she discontinued her search for tokens as soon as she flipped over the correct token. She came in unprompted within the 30-min test period on 76% of test trials, and her average duration outdoors before returning on those trials was 12.59 min ($SD = 6.86$ min; range = 4.56–28.29 min). She came in unprompted within 30 min on 81% of the control trials, and her average duration outdoors on those trials was 18.67 min ($SD = 8.26$ min; range = 5.29–29.37 min). Thus, Panzee was outdoors for a relatively long period of time on the majority of trials and did not return to the test area immediately.

On test trials in which she failed to bring a token indoors or did not trade the *correct* token (7 out of 21 test trials), she identified correctly four out of these seven items on her lexigram keyboard when the experimenter asked “what’s in here?” while pointing at the bucket, even though she still could not see the item in the bucket.

Discussion

Panzee’s performance showed many of the hallmark features of prospective memory. First, at the time in which she chose between the two food items, she had to remember the non-chosen item, and do so in a way that would later allow her to locate the correct lexigram token to match that item. This would indicate that she anticipated what she would need to do later. Panzee was clearly motivated to some degree to receive that other food item, and she accurately remembered the name of that item on the majority of those trials. Panzee then went outdoors and engaged in a different task (foraging for the more preferred food) before she implemented retrieval of the token for the indoor food item. It was possible that Panzee could have retrieved that token immediately upon entering the outdoor yard, and this would not have been very strong evidence of prospective memory because the likelihood for continuous rehearsal would have been much greater. However, she did not do this. Instead, she went outdoors and retrieved and ate the highly preferred food items she had selected indoors, and then often spent time sitting outdoors surveying the area outside her cage, grooming, or doing other activities before retrieving the token and bringing it back indoors. Also, Panzee’s performance was impressive in that, on the majority of trials, she overturned the tokens only until she found the one that corresponded to the indoor type of food item, suggesting that she was implementing the intention to retrieve a specific token that matched that food item seen earlier in the trial. Thus, Panzee’s performance showed that she encoded the type of indoor item, then engaged in other activities for a period of time, and then spontaneously implemented the token retrieval process and the return to the indoor area to finally obtain the remaining food item.

It is important to note that Panzee could have performed well without such a heavy emphasis on prospective memory. She might have passively remembered the second (non-chosen) food item without also forming the intention to *specifically retrieve the token for that item later in time*. Then, when she was outdoors and no other food option remained there, she remembered what type of food was indoors, and then searched for the lexigram that matched that item, without ever implementing any earlier intention to do such a search. This scenario would not necessarily involve an intention to retrieve, given that the retrieval happened later. However, given that the lexigram tokens outdoors were face down and could not act as specific cues to different food names, and given that they were present throughout the trial, Panzee still needed to spontaneously encode that memory of the food item indoors. Future research with her will be needed to more closely distinguish these possibilities about what memory processes are specifically at work during this task.

Panzee’s performance also highlights that she encoded and retained information about an available food item that, at the time of encoding, was clearly not the most motivating thing in her environment (see also Menzel, 2005). Panzee chose between two foods, and it was the one she chose that she was allowed to obtain more immediately. Despite this, she remembered to later get the less preferred food item. Although these data do not refute the Bischof–Köhler hypothesis, they are informative nonetheless about Panzee’s ability to encode intended future actions that are not the most immediately motivating aspects of her world. Refuting the Bischof–Köhler hypothesis would require that, at the time of choosing between the two available food items, Panzee would have to anticipate that only later would one of those items be, in some way, valuable, whereas at the time of choice it was not valuable at all. This type of prospective memory remains to be investigated, so that a more thorough test of the Bischof–Köhler hypothesis can be given. However, the present data suggest at least that Panzee can anticipate a future need (the token matching the indoor food item) for something that she does not presently want *as much as* something else in her environment.

In some sense, these results should not be surprising. It is well established that animals make many decisions in their natural habitats about where next to travel, when to disengage from feeding in one location and move to another, and even anticipate future needs such as returning to a shelter location before it becomes too dark. However, in those cases, one can assume that the animals’ behaviors are driven by an immediate apprehension that something needs to change in the environment (e.g., location in space, density of food in the immediate area, etc.) right now, and then the animals act to bring about that change. In Panzee’s case, this was not true. In the immediate present, her higher priority goal (as inferred through her choice behavior) was to obtain one food type, which she then did by going outdoors and retrieving that food. Only

later, when that was complete, did she then implement token retrieval, and this could only be successful if she had already encoded what food item remained indoors. Thus, it seems likely that Panzee was encoding a prospective action that she did not intend to implement immediately, but only when other more pressing needs were met (e.g., getting the food outdoors, and perhaps other things such as surveying the area outdoors, etc., which she engaged in for some time after eating all of the outdoor food).

There remains the question of whether other chimpanzees, and particularly non-language trained chimpanzees, would show the same levels of performance. Of course, the use of lexigram tokens can only occur with chimpanzees that understand such symbols, but the question is instead whether symbol competency of any sort might make unique contributions to prospective memory in this species. Other areas of research have provided such evidence; for example, chimpanzees that understand numerical symbols perform better on the reverse-reward contingency task when symbols are used compared to when actual food items, or even non-edible but quantitative stimuli such as rocks are used in the discriminations (e.g., Boysen & Berntson, 1995; Boysen, Mukobi, & Berntson, 1999).

The results of the present study, along with some of the recent research with a number of other nonhuman species (e.g., Chappell & Kacelnik, 2002; Clayton et al., 2005; Correia et al., 2007; McKenzie et al., 2004; Mulcahy & Call, 2006; Osvath & Osvath, 2008; Raby et al., 2007; Wilson & Crystal, 2012; Zentall, 2006), suggest that animals may be capable of anticipating future needs, and then either acting to bring about opportunities to fulfill those needs or prospectively remembering what needs to occur later to obtain something that presently is not available or not highly motivating (also see Crystal, 2012; Eacott & Easton, 2012; Roberts, 2012). Of course, these behaviors are likely still more limited than many of the prospective memory and planning capacities of humans, who can anticipate not only certain future needs, but also hypothetical ones (e.g., fire insurance for possible loss of property), and ones that may not occur for decades (e.g., retirement income, medical needs). This long-term anticipation of real and possible future needs allows for many of the advanced planning skills seen in adult humans, but the precursors of such skills appear possible and likely in the behavior of nonhuman animals who also exhibit some evidence of future oriented processes such as planning and prospective memory.

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