WILEY | AMERICAN JOURNAL OF PRIMATOLOGY

Distinctiveness enhances long-term event memory in non-human primates, irrespective of reinforcement

Amy Lewis[1,2,3] | Josep Call[1,2] | Dorthe Berntsen[3]

[1] School of Psychology and Neuroscience, University of St Andrews, St Mary's Quad, St Andrews, Fife, UK

[2] Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[3] Center on Autobiographical Memory Research, Århus C, Denmark

Correspondence
Amy Lewis, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103, Germany.
Email: amy_lewis@eva.mpg.de

Non-human primates are capable of recalling events that occurred as long as 3 years ago, and are able to distinguish between similar events; akin to human memory. In humans, distinctiveness enhances memory for events, however, it is unknown whether the same occurs in non-human primates. As such, we tested three great ape species on their ability to remember an event that varied in distinctiveness. Across three experiments, apes witnessed a baiting event in which one of three identical containers was baited with food. After a delay of 2 weeks, we tested their memory for the location of the baited container. Apes failed to recall the baited container when the event was undistinctive (Experiment 1), but were successful when it was distinctive (Experiment 2), although performance was equally good in a less-distinctive condition. A third experiment (Experiment 3) confirmed that distinctiveness, independent of reinforcement, was a consistent predictor of performance. These findings suggest that distinctiveness may enhance memory for events in non-human primates in the same way as in humans, and provides further evidence of basic similarities between the ways apes and humans remember past events.

KEYWORDS
binding, distinctiveness, event memory, long-term memory, primates

1 | INTRODUCTION

Humans remember past events on a regular basis. Such episodic memories serve important social and instrumental functions (e.g., Pillemer, 2003). Until recently, most research on memory of non-human primates (hereafter primates) has focused on short term memory (Beran, Beran, & Menzel, 2005; Fujita & Matsuzawa, 1990; Hoffman & Beran, 2006; Inoue & Matsuzawa, 2007; MacDonald & Agnes, 1999; Menzel, 1973; Mishkin & Delacour, 1975; Robbins & Bush, 1973; Rodriguez, Zurcher, Bartlett, Nathanielsz, & Nijland, 2011), with primate episodic memory research coming into fruition over the past decade (Dekleva, Dufour, de Vries, Spruijt, & Sterck, 2011; Hoffman, Beran, & Washburn, 2009; Martin-Ordas, Haun, Colmenares, & Call, 2010; Menzel, 1999; Noser & Byrne, 2015; Schwartz & Evans, 2001; Schwartz, Colon, Sanchez, Rodriguez, & Evans, 2002; Schwartz, Hoffman, & Evans, 2005). However, comparative studies on episodic memory have been hampered by the definition of the phenomenon (Tulving, 1972, 2001), in terms of the recollection of personal past events involving autonoetic consciousness; self awareness that the event happened in one's own personal past. Since such awareness is hard, if not impossible, to

test in animals, researchers have turned to other more objective operationalizations (see Clayton, Griffiths, et al., 2001; Crystal, 2009; Dere, Kart-Teke, Huston, & De Souza Silva, 2006; Templer & Hampton, 2013 for reviews).

Despite the progress being made here, there is still controversy over what "counts" as episodic memory (Basile, 2015; Suddendorf, 2007; Suddendorf & Busby, 2003), due in part to the many stringent, as well as changing, criteria that arise from Tulving's (1972, 1983, 1984, 1985, 2002, 2005) definitions. In an attempt to overcome some of these conceptual problems, Rubin and Umanath (2015) recently proposed an alternative conceptualization for memory for events, which removes some of the restrictive criteria imposed by the consciousness based conception of episodic memory, and enables researchers to have simpler and more measureable criteria that can also be applied to non-human animals. Rubin and Umanath (2015) refer to memory for events as "event memory," which is defined as "the mental construction of a scene, real or imagined, for the past or the future" (p.1). Unlike episodic memory, autonoetic consciousness is not required. The only criteria required is the construction of a scene from an egocentric vantage point. As such, event memory involves fewer requirements than episodic memory, but still involves the process of

remembering an event or scene, as opposed to remembering solely spatial information or knowledge.

Scene construction is defined as the mental generation of a scene or event, which is achieved by binding multiple informational elements into a coherent and spatially organized representation (Hassabis & Maguire, 2007; Lind, Williams, Bowler, & Peel, 2014; Raffard, D'Argembeau, Bayard, Boulenger, & Van der Linden, 2010; Rubin & Umanath, 2015). As such, to show that one's recall is of an event memory, one needs to show evidence of scene construction, that is, the binding of information in a spatial context (hereafter contextual binding). Such contextual binding is thought to be an essential characteristic of episodic memory (Chalfonte & Johnson, 1996; Moscovitch, 1994; Raj & Bell, 2010), and it has even been argued that impairments in episodic memory, such as source memory failure, are a result of difficulties with binding stimuli or reconstructing the bound information at retrieval (Schacter & Addis, 2007; Schacter, Norman, & Koutstaal, 1998). Additionally, Rubin and Umanath (2015) refer to evidence that the hippocampus is not merely responsible for spatial memory in animals but is also involved in contextual binding. For instance, damage to the hippocampus can leave spatial memory intact but lacking in detail (Winocur, Moscovitch, Fogel, Rosenbaum, & Sekeres, 2005). As such, they argue that the function of the hippocampus in animals shares some properties with human episodic memory, and goes beyond spatial processing. Consequently, if an animal has an intact hippocampus it would likely be capable of contextual binding and event memory.

Evidence of contextual binding has already been shown in primates, corvids and rats (Clayton, Yu, et al., 2001; Crystal & Alford, 2014; Crystal & Smith, 2014; Crystal, Alford, Zhou, & Hohmann, 2013; Martin-Ordas, Berntsen, & Call, 2013; Panoz-Brown et al., 2016). For instance, Martin-Ordas et al. (2013) showed that when exposed to various contextual information, apes were able to recall the location of a tool 3 years after they had witnessed it being hidden. In order to remember where the tool was hidden the apes had to bind the relevant contextual features together and ignore a number of irrelevant associative links, such as other tasks with the same experimenter, other experiments involving tool use, other tests in the same location and so forth. In this case, only by binding the relevant contextual cues were the apes able to distinguish between events that shared many of the same contextual features, and subsequently, were able to correctly recall the event in which a tool was hidden. Furthermore, in a second experiment, apes were able to distinguish between two very similar tool hiding events in order to successfully recall the location of a tool, thus providing additional evidence of binding. Similarly, Crystal and Smith (2014) showed that rats were able to find food in a maze under conditions that required them to bind multiple disparate features, related to location, activity, and spatial cues, in order to successfully search at the relevant place. Such studies show contextual binding in action, and provide some evidence for event memory in animals.

In humans, the ability to remember an event is dependent upon the interaction between encoding and retrieval. Tulving (1974) described remembering as the product of both encoding and retrieval; "we remember an event if it has left behind a trace *and* if something reminds us of it" (p.74).

Furthermore, not all retrieval cues are equally effective. The encoding specificity principle (Tulving & Thomson, 1973) states that a retrieval cue is only effective in so far that it was encoded with the memory trace.

The effectiveness of the retrieval cue also depends on the number of memory traces to which it is associated; referred to as cue overload (Watkins & Watkins, 1975). The more traces the cue is associated with the less likely that the cue will generate the target memory to be recalled. Subsequently, the more distinctive the cue is the less likely it will be overloaded. Distinctiveness is defined by (Hunt & Worthen, 2006) as difference in the context of similarity, meaning that distinctive cues share fewer features with other cues that are either in the immediate context, referred to as primary distinctiveness, or that are stored in memory, referred to as secondary distinctiveness (Eysenck, Cermak, & Craik, 1979; Hunt & Worthen, 2006; Schmidt, 1991). A cue which shares fewer commonalities with other memory traces is less likely to become overloaded. From these two theories we can predict that successful recall of an event will be maximized when the memory trace and retrieval cue match (encoding specificity), and when the retrieval cue is distinct from other memory traces (Nairne, 2002, 2007). These mechanisms also operate when retrieval is spontaneous and thus requires little effort (Berntsen, Staugaard, & Sorensen, 2013).

As with retrieval, encoding can be enhanced depending upon the type of information to be remembered. In particular, distinctive information captures attentional resources, resulting in better encoding, regardless of reinforcement (Hunt & Worthen, 2006; Jenkins & Postman, 1948; Schmidt, 1991). Likewise, emotion captures attentional resources in a similar manner, leading to greater memory for emotional material (Cahill & McGaugh, 1995; Kensinger, 2004), often at the detriment to peripheral information (Burke, Heuer, & Reisberg, 1992; Easterbrook, 1959; Kensinger, 2009; Nashiro & Mather, 2011; Schmidt, 2007).

In animal research, encoding and retrieval processes have mainly been investigated in rodents and birds (see Shettleworth, 2010), with a few studies investigating the role of distinctiveness, where it has been found that distinctive items are recalled better than non-distinctive items (Reed & Richards, 1996; Roberts, 1980; Zentall, Hogan, Edwards, & Hearst, 1980). With regards to primate research only a handful of studies exist that examine encoding and retrieval processes. It has been shown that memory performance is good when the information to be encoded is relevant (Martin-Ordas, Atance, & Call, 2014) and distinctive (Beran, 2011; Martin-Ordas et al., 2013 experiment 2; Mendes & Call, 2014), and that emotion enhances recognition memory for pictures (Kano, Tanaka, & Tomonaga, 2008), possibly due to better encoding as a result of increased attention to emotional material (Kano & Tomonaga, 2010). Furthermore, Kano and Hirata (2015) showed that apes are able to encode and retrieve information embedded in a distinctive event. Here, apes watched a film of an actor dressed in a King Kong suit preforming an aggressive act. The following day, when watching the same film again, the apes were able to predict what would happen next through use of anticipatory looks; that is, they looked at the location in which King Kong would appear before he appeared. Thus, the apes retrieved the information previously encoded in anticipation of what was coming next.

As these primate studies have either investigated distinctiveness over very short retention intervals (i.e., Beran, 2011; Kano et al., 2008;

Martin-Ordas et al., 2014), or have not provided a control condition in which a distinctive cue is absent (i.e., Kano & Hirata, 2015; Martin-Ordas et al., 2013), we still know very little about the role of distinctiveness in long term event memory. As such, the aim of the current study was to investigate the effect of distinctiveness on long term memory for simple events in great apes.

We originally began with one experiment in mind, however, additional experiments were needed to clarify the results we obtained. For ease of reading and clarity, we present the baseline Experiment first (Experiment 1), so that the reader can see the progression of a standard procedure to a distinctive procedure. The original chronological order of the Experiments was Experiment 2, Experiment 1, Experiment 3 (see Table 1 for an overview of each Experiment). We refer to Rubin and Umanath's (2015) definition of event memory, in which evidence of contextual binding is indicative of recall of a memory of an event. We also consider an alternative memory account, associative spatial memory, in which memory performance may be a result of learning to associate a particular spatial location with a food reward. We contrast these two explanations, since the use of associative learning is a concern that is often raised when researching episodic memory in animals (see Zentall, 2006). We predict that distinctiveness will enhance memory only in the case of contextual binding. That is, distinctiveness will only enhance memory recall if the distinctive feature(s) are bound to the target location. In the case of associative learning, we predict that only reinforcement of the target location will improve recall. In the present experiments we use the term distinctiveness to refer to secondary distinctiveness (rather than primary distinctiveness), which refers to the presence of an unusual feature(s) in comparison to features in stored memory (Eysenck et al., 1979; Hunt & Worthen, 2006; Schmidt, 1991).

2 | EXPERIMENT 1: BASELINE

The aim of this experiment was to establish a baseline level of memory performance by using a standard and undistinctive baiting procedure. We presented the apes with a platform task in which one of three containers was baited. Previous research using a similar experimental task has shown that apes can recall the location of a baited container after 24 hr (Martin-Ordas & Call, 2011), but it is unknown if they can recall for longer periods in this type of task. As such, we chose to use a 2-week delay period, replicating the delay used by Martin-Ordas et al. (2013) who showed good recall for a distinctive hiding event after 2 weeks. However, we expected performance to be poorer in this task, as the platform task was not distinctive.

Additionally, we manipulated whether the experimenter identification (ID) at encoding and retrieval was matched (the same person) or non-matched (different people) and whether the apes were reinforced or not at encoding. This manipulation aimed to help distinguish between a contextual binding account and associative learning account. If the apes' performance is explained by event memory, then contextual binding would predict that performance in conditions in which the experimenter ID is matching will be better than conditions in which it is non-matching; if the apes bind the baited container's location to the contextual features present at encoding, then the more of these contextual features that are present at retrieval the more likely the correct memory is to be recalled (in line with encoding specificity theory). If performance is explained by associative learning, we would predict performance in conditions in which the apes are rewarded at encoding should be better than those which are not rewarded.

3 | METHODS

This research adhered to the American Society of Primatologists principles for the ethical treatment of primates, and was ethically approved by an internal committee at the Max Planck Institute for Evolutionary Anthropology and the University of St Andrews. Animal husbandry and research complies with the "EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria," the "EEP Bonobo Husbandry Manual," the "WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums," and the "Guidelines for the Treatment of Animals in Behavioral Research and

TABLE 1 Variables included in each of the three experiments

Experiment	Condition	No. subjects	Distinctive baiting procedure	Large food amount	Non-reinforced	Matching experimenter	Mask
1	Reinforced matching	10				✓	
	Non-reinforced matching	9			✓	✓	
	Reinforced non-matching	9					
	Non-reinforced non-matching	9			✓		
2	Mask	15	✓	✓		✓	✓
	No-mask	15	✓	✓		✓	
3	Reinforced	14		✓		✓	
	Non-reinforced	15		✓	✓	✓	

Empty cells indicate that the variable in question was not included.

Teaching" of the Association for the Study of Animal Behavior (ASAB). The research was collected during July 2015–February 2016 at the Wolfgang Kohler Primate Research Center at Leipzig Zoo (Leipzig, Germany).

3.1 | Subjects

Thirty-seven apes participated in this experiment (see Table 2); 24 chimpanzees (*Pan troglodytes;* mean age = 24 years), seven bonobos (*Pan paniscus*; mean age 14) and six orangutans (*Pongo abelii;* mean age = 19). None of the apes were food or water deprived, and all received a healthy and balanced diet during the testing period.

3.2 | Apparatus

Three opaque red containers (length = 7 cm, width = 10 cm, height = 10 cm) were positioned on a sliding platform roughly 16 cm apart. The sliding platform was positioned in-front of a Plexiglas panel frame with three circular holes, which allowed the subjects to point at the desired container and for the experimenter to pass the food reward through (see Figure 1). A plastic occluder was placed on top of the sliding platform, the experimenter baited the container behind the occluder ensuring the subject could not see which container was baited; this is a common procedure for baiting containers.

3.3 | Design

Apes were allocated to one of two exposure conditions; reinforced (R) or non-reinforced (NR) and one of two test conditions; matching experimenter (M), or non-matching experimenter (NM); a 2 × 2 between subjects' design. Conditions were balanced in terms of age, gender and species as much as possible, this was to minimize any potential effect these variables may have on performance.

3.4 | Procedure

3.4.1 | Exposure phase

The experimenter (E) sat facing the subject behind the sliding platform. On the platform were the three red opaque containers, one to the left, center and right, respectively, roughly equal distance apart. E covered the containers with the occluder so that the subject could no longer see the containers nor E's hands. E then baited one of the containers with one piece of banana (here-after, the baited container). The occluder was then removed, and E lifted the baited container to reveal its contents. The container was then placed back over the food, and the two empty containers were simultaneously lifted and replaced. E then pushed the platform toward the subject and waited for them to make a choice. The outcome of the choice differed depending on the condition:

Reinforced
If the subject chose the correct container, the food was revealed and given to the subject. The contents of the empty containers were then shown to the subject.

TABLE 2 Species, age (at time of Experiment 1), sex, and tasks participated in by subject

Subject	Species	Age (years)	Sex	Tasks participated in
Fimi	Bonobo	7	Female	1,2,3
Gemena	Bonobo	9	Female	1,2,3
Luiza	Bonobo	10	Female	1,2,3
Lexi	Bonobo	15	Female	1,2,3
Yasa	Bonobo	17	Female	1,2,3
Kuno	Bonobo	19	Male	1,3
Jasango	Bonobo	24	Male	1,2,3
Joey	Bonobo	32	Male	2,3
Bangolo	Chimpanzee	7	Male	1
Kara	Chimpanzee	10	Female	1,2
Lobo	Chimpanzee	11	Male	1,2,3
Kofi	Chimpanzee	11	Male	1
Tai	Chimpanzee	12	Female	1,2,3
Kisha	Chimpanzee	12	Female	1
Lome	Chimpanzee	13	Male	1,2,3
Alex	Chimpanzee	14	Male	1,2,3
Alexandra	Chimpanzee	15	Female	1,2,3
Annett	Chimpanzee	15	Female	1,2
Bambari	Chimpanzee	16	Female	1
Swela	Chimpanzee	20	Female	1
Frodo	Chimpanzee	21	Male	1,2,3
Sandra	Chimpanzee	22	Female	1,2,3
Jahaga	Chimpanzee	22	Female	1,2,3
Hope	Chimpanzee	26	Female	1
Daza	Chimpanzee	29	Female	2,3
Dorien	Chimpanzee	34	Female	1,2,3
Natascha	Chimpanzee	35	Female	1,3
Riet	Chimpanzee	37	Female	1,2,3
Corrie	Chimpanzee	38	Female	1,2,3
Ulla	Chimpanzee	38	Female	2
Fraukje	Chimpanzee	39	Female	1,2,3
Robert	Chimpanzee	39	Male	1,2,3
Frederike	Chimpanzee	41	Female	1,2,3
Jeudi	Chimpanzee	49	Female	1,2,3
Suaq	Orangutan	6	Male	1,3
Raja	Orangutan	11	Female	1,2,3
Pini	Orangutan	17	Female	1,2,3
Padana	Orangutan	19	Female	1,2,3
Dokana	Orangutan	26	Female	1,2
Bimbo	Orangutan	34	Male	1,3

Non reinforced
If the subject chose the correct container, the food was revealed but was not given to the subject and was thrown away into an opaque bucket. The apes could see the bucket and the throwing of the food into the bucket. The contents of the empty containers were then shown to the subject.

FIGURE 1 Set-up of the apparatus in Experiment 2. In Experiments 1 and 3 the tray on which the containers are on was not used (only the sliding platform that the tray is on) and an occluder was used

Each subject received two trials on the same day, with one additional trial if an incorrect choice was made. Two incorrect choices led to the subject being dropped from the study. This was to ensure that the apes understood what was required of them (to point to the baited container), and that they were paying attention and not simply picking the correct one by chance. The position of the baited container was the same in each trial and was counterbalanced between subjects.

3.4.2 | Test phase

The test took place 2 weeks later (13–15 days). The experimenter ID differed depending on the condition:

Matching

The experimenter ID was the same as at exposure.

Non-matching

The experimenter ID was different to that at exposure.

The procedure then followed the exposure procedure, except now E did not reveal the location of the baited container before the subject made a choice. Additionally, if the subject made a correct choice they received the food regardless of which exposure condition they were in. Subjects only received one trial.

3.5 | Data analysis

A correct response was defined as choosing the baited container. As there were three containers, chance was set to 0.33. We were interested in whether performance was above chance in each condition, we analyzed this for each condition separately using two tailed binomial tests. Alpha level was set to 0.05 and all analysis was conducted using R studio version 0.98.109 (as was the case for all subsequent experiments).

4 | RESULTS

All subjects required only two trials during the exposure phase, except for Daza and Ulla who failed three and were subsequently dropped from the experiment.

Binomial tests revealed that performance was not above chance in any of the conditions (Figure 2); reinforced matching (binomial test: $N = 10$, $p = 0.31$), non-reinforced matching (binomial test: $N = 9$, $p = 0.73$), reinforced non-matching (binomial test: $N = 9$, $p = 0.73$) non-reinforced non-matching (binomial test: $N = 9$, $p = 0.73$). As performance was numerically better in the reinforced matching compared to the other three conditions (in which performance was identical), we ran an additional analysis to compare performance between the reinforced matching and the remaining three conditions pooled together. A fisher exact test revealed no significant difference ($df = 1$, $p = 0.13$), indicating that performance was not significantly better in this condition.

5 | DISCUSSION

Subjects failed to recall the location of the baited container after 2 weeks. Performance did not differ in any of the conditions, suggesting that reinforcement and contextual binding had little to no effect on memory performance. However, it is important to note that contextual binding may not have had an effect here due to the nature of the baiting event, that is, the event was designed to be undistinctive. The cue that we chose to manipulate was the experimenter ID. As the apes are tested by numerous experimenters, and often multiple times per day, it may be that this particular cue is overloaded. As such, the experimenter may not have been an effective cue in triggering a specific, single episode at retrieval. Additionally, the other relevant cues may also have been overloaded; the location has been used for many other tasks (e.g., Call, 2006), platform tasks have been done many other times (e.g., Call, 2004), and similar containers have been used in other tasks (e.g., Call, 2006), thus, even if contextual binding took place, there was nothing distinctive about the bound representation to lead to the recall of this specific baiting event. This is consistent with Eysenck's theory of distinctiveness (Eysenck et al., 1979), in which "performance is assumed to depend far more on
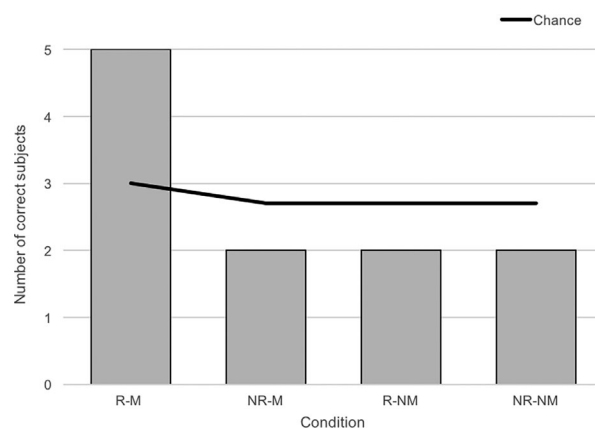

FIGURE 2 Number of correct subjects by condition. R-M, reinforced matching; NR-M, non-reinforced matching; R-NM, reinforced non-matching; NR-NM, non-reinforced non-matching. Chance shows number of subjects that would be correct if performing at chance

distinctive than non-distinctive overlap" (p.94). As such, the failure to recall the baited location is not necessarily a result of a failure of contextual binding, but rather a lack of distinct or diagnostic information in the bound representation to retrieve a specific memory, resulting in the recall of a "gist" like memory (Schacter & Addis, 2007; Schacter et al., 1998).

With regards to the associative account, it may be that the reinforcement was not great enough to influence performance. As the apes only received one piece of banana per trial, and only two trials during the exposure phase, this may not have been a large enough reinforcement to learn the association between the food and the spatial location of the container after a long delay. During training, when a delay period was not implemented, the apes were successful at choosing the correct container (except for two subjects who were not included in the analysis), thus they were able to learn where the food was, but failed to recall the information after a long delay.

6 | EXPERIMENT 2: DISTINCTIVENESS

Experiment 1 revealed that the apes failed to remember the location of the baited container after 2 weeks, as such the aim of this experiment was to improve memory performance by making the event more distinctive. This was achieved by baiting the container outside the testing room and by increasing the amount of banana. Both manipulations are very rare, if not completely novel, in our lab for this type of task, and thus are distinctive in comparison to standard baiting tasks.

Additionally, we further investigated the impact of distinctiveness by including a surprising feature in one condition and not in another; a facial mask worn by the experimenter depicting the face of the apes' keeper. Four different masks were used, one for each species. The masks were made using high quality head-shots of four of the keepers; a bonobo keeper, an orangutan keeper, and two chimpanzee keepers (the chimpanzees were housed in two separate groups and thus had separate keepers). Previous research has shown that apes are capable of recognizing human faces in the form of 2D photographic images (Martin-Malivel & Okada, 2007; Sliwa, Duhamel, Pascalis, & Wirth, 2011; Tomonaga, 1999). Thus, a photographic mask depicting the keepers face should be recognizable to the apes. The apes only saw the mask of their own keeper; for example, bonobos only saw the mask of the bonobo keeper. We chose to use masks of the keepers for two reasons. Firstly, we wanted to surprise the apes. The apes are very familiar with their keepers and thus should be surprised when they see the keeper's face on the body of a person that is not their keeper. Furthermore, it is likely they will also recognise the keeper by sound in addition to sight (e.g., see Martinez & Matsuzawa, 2009), thus, the configuration of the keeper's facial features with the body and voice of another experimenter should be surprising. Secondly, although we wanted to surprise the apes, we did not want to frighten them. Using faces of familiar keepers should not be frightening to the apes.

If the apes' performance is explained by event memory, then contextual binding would predict better memory recall in this experiment as opposed to Experiment 1, and better recall performance in the more distinctive mask condition than the non-mask condition. Likewise, if the apes' performance is due to associative learning this would also predict better performance in this experiment as opposed to Experiment 1; this is because the food reward (amount of banana) is larger, thus strengthening the reinforcement. However, this account would predict no difference between the mask and no-mask condition, as the reinforcement value does not differ.

7 | METHODS

7.1 | Subjects

The same subjects from Experiment 1 participated here, with the exception of Kuno, Swela, Natascha, Bimbo, and the addition of Joey, Daza, Ulla, Robert, Frederike, resulting in a total of 30 apes (see Table 2); 19 chimpanzees (mean age = 26.8), four orangutans (mean age = 18), and seven bonobos (mean age = 16).

7.2 | Apparatus

The apparatus and set-up was the same as Experiment 1, except the red opaque containers were replaced with blue opaque containers, measuring the same dimensions (see Figure 1). The reason we replaced the containers was to minimize proactive interference (Anderson & Neely, 1996). Additionally, a tray was included on which the containers were placed (see Figure 1), and a cardboard laminated mask was present for half of the subjects. There were four masks, depicting a color photograph of each keeper associated with each species (with two keepers for the chimpanzees). Each species only saw the mask of their keeper. The mask covered the entire face of the experimenter, except for the eyes.

7.3 | Design

The apes were allocated to one of two conditions; mask (two orang-utans, four bonobos and nine chimpanzees, age range 10–41 years, mean 22 years) no-mask (three bonobos, two orang-utans, ten chimpanzees, age range 7–49 years, mean 23 years).

7.4 | Procedure

7.4.1 | Exposure phase

Mask condition

The three blue containers were positioned on the tray, one to the left, one to the center, and one to the right. Half a sliced banana was placed under one of the containers outside of the testing room and out of sight of the subject. The experimenter (E), wearing the mask of the keeper, entered the testing room carrying the tray and placed it onto the sliding platform. E, sat facing the subject behind the sliding platform, called the subject's name and made eye contact with them (ensuring the subject looked at the mask). E then lifted up the baited container so that the banana was visible, and replaced it again once the subject had seen it. E then simultaneously lifted up the remaining two

containers, and replaced them once the subject had seen that there was no banana there.

E then pushed the sliding platform toward the subject and waited for them to make a choice (by pointing/reaching through one of the holes). If the subject chose the baited container (correct choice) they received the banana, and the two empty containers were lifted to show the subject that they were empty. If the subject chose one of the empty containers, the container was lifted, then the remaining two containers were lifted to reveal their contents. No banana was received in this case. Each subject received two trials; if an incorrect choice was made, they received one additional trial. If the subject chose incorrectly in two trials, they were dropped from the experiment. The position of the baited container was the same in each trial and was different to Experiment 1 (to minimize interference). The location of the baited container was counterbalanced between subjects.

No-mask condition

The no-mask condition was identical to the mask condition, except that E did not wear a mask of the keeper.

7.4.2 | Test phase

The test took place 2 weeks (13–17 days) later. Following the same procedure as before, and in the same testing room, E baited one of the containers (the same one previously baited) and the subject made a choice. Crucially, E did not reveal the location of the banana to the subject before they made a choice. Subjects from the mask condition saw E wearing the same mask as they saw previously. Subjects from the no-mask condition saw E wearing no mask. All subjects received only one trial.

7.5 | Data analysis

The data were analyzed in the same way as Experiment 1. In addition, to see if performance was better than in Experiment 1, we compared overall performance in Experiment 1 to overall performance in Experiment 2 using a two (response) by two (Experiment) Fisher exact test.

8 | RESULTS

All subjects required only two trials during the exposure. As we were interested in whether the apes remembered the baited container significantly above chance, we compared the number of correct choices per condition to chance (exact binomial, two tailed). Both the mask (binomial test: $N = 15$, $p = 0.05$) and no-mask condition (binomial test: $N = 15$, $p < 0.001$) were significantly above chance, and were not different to each other (Fisher exact test: $df = 1$, $p = 0.4$) (see Figure 3). Thus, subjects in both conditions were able to correctly recall the baited location from 2 weeks previously, with neither condition showing better performance than the other. Additionally, performance was better than Experiment 1 (Fisher exact test: $df = 1$ $p = 0.004$).
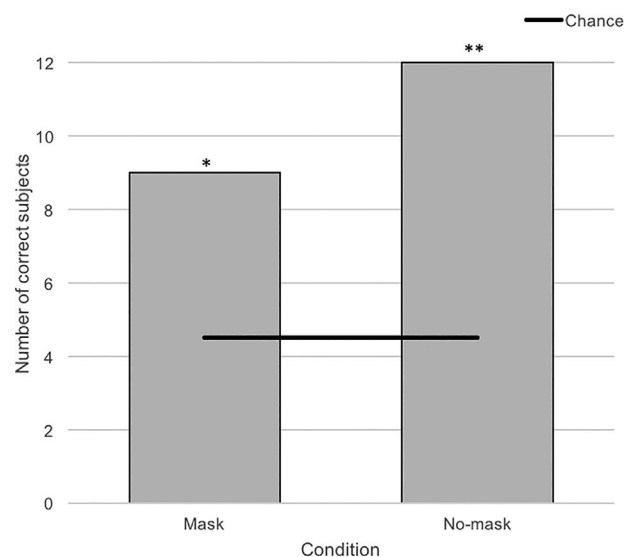

FIGURE 3 Number of correct subjects by condition, chance shows number of subjects that would be correct if performing at chance. * = 0.05. ** = <0.001

9 | DISCUSSION

The results indicate that subjects were able to recall the location of the baited container after a delay of 2 weeks. Additionally, performance was extremely high across conditions. This was somewhat surprising given the difficulty of the task; the apes had to distinguish this task from many similar tasks (e.g., Call, 2004), to distinguish these containers from other similar containers (e.g., Call, 2006), and also to recall the exact location of the baited container in an array in which the containers were extremely close together (see Figure 1). These findings add to existing evidence that apes are capable of remembering past encounters over long time intervals (e.g., Martin-Ordas et al., 2013).

The better performance in comparison to Experiment 1 supports both contextual binding and associative learning. With regards to contextual binding, none of the cues were distinctive in Experiment 1 (the task, experimenter, location and baiting procedure were common to many other tasks), even the loss of small amount of food upon a correct choice had occurred before to the same apes (e.g., Uher & Call, 2008; Vlamings, Uher, & Call, 2006), making it difficult to distinguish between similar memories even when bound (Schacter & Addis, 2007; Schacter et al., 1998). Conversely, in the current experiment, the baiting procedure and food amount were distinctive in both conditions, and when bound to the other features (e.g., experimenter, room, baited container) may have led to a distinctive, un-overloaded (i.e., Rubin, 1995; Watkins & Watkins, 1975) and highly specific (i.e., encoding specificity) cue at retrieval, facilitating successful recall. This interpretation would be consistent with the findings from Martin-Ordas et al. (2013). In the case of the associative learning, the better performance can be explained by the larger reinforcement (larger food reward) strengthening the association between the baited container's location and the presence of a food reward.

Performance between the two conditions did not differ, which is supportive of the associative learning account, given that reinforcement value was the same in both conditions. However, it is not in support of contextual binding, in which performance should have been better in the mask condition; the more distinctive features that are bound the more unique and specific the retrieval cue becomes, and thus, the more effective it is at recalling the correct memory. However, there are multiple reasons why this may not have been the case. Firstly, as performance was high in both conditions, it may be that any potential enhancement of an additional distinctive feature was not seen, although this seems unlikely as performance was better (but not significantly) in the no-mask condition. Secondly, the mask was intended to elicit surprise, and indeed, a number of individuals produced a physical reaction to the mask (prolonged looking, wariness, aggression). In both the human and animal literature emotion enhances memory, however, the effect seems to be a focal one; memory for the emotional material is enhanced at the cost of peripheral material (Burke et al., 1992; Easterbrook, 1959; Kensinger, 2009; Schmidt & Saari, 2007). In this case the mask may have captured attention, resulting in less attentional resources to encode other information, such as the experimenter, the location and the baited container. Similarly, the same effect has been found for distinctive material, that is, that distinctive items are recalled at the expense of peripheral non-distinctive items (Ellis, Detterman, Runcie, McCarver, & Craig, 1971; Schulz, 1971); (but see Schmidt, 1985).

10 | EXPERIMENT 3: REINFORCEMENT AND DISTINCTIVENESS

Performance was better in Experiment 2 compared with Experiment 1. However, it is less clear whether the better performance can be attributed to the larger reinforcement (associative learning) or by distinctiveness (contextual binding). As such, Experiment 3 aimed to distinguish between the two accounts. First, to investigate whether distinctiveness could account for the better memory performance, we kept the food amount the same as in Experiment 2, but changed the baiting procedure to the traditional method used in Experiment 1. Thus, the difference between Experiment 2 and Experiment 3 became one of distinctiveness, in which Experiment 3 was less distinctive due to the use of a standard baiting procedure and the large amount of food no-longer being distinctive. The large food amount was no longer distinctive because it occurred in Experiment 2, and thus the apes now had experience of receiving large food amounts in this type of task. To assess whether reinforcement influenced performance, we included a reinforced and non-reinforced condition (as with Experiment 1). Therefore, if the performance from Experiment 2 was a result of the larger food amount (reinforcement) we should see poorer performance in Experiment 3 in the non-reinforced compared with the reinforced condition. In short, Experiment 3 differed from Experiment 2 in terms of being less distinctive and included a non-reinforced condition. It remained the same in terms of the amount of food used.

If the apes use contextual binding then performance in both conditions should be poorer than in Experiment 2, due to a lack of distinctive cues. If the apes use associative learning, then performance in the reinforced condition should be comparable to Experiment 2 (as the reinforcement value is the same), and better than the non-reinforced condition.

11 | METHODS

11.1 | Subjects

All subjects from Experiment 2 took part in this experiment, with the exception of Kara, Annett, Ulla, Riet and Dokana. In addition, four extra apes took part (Bimbo, Suaq, Natascha and Kuno), resulting in 29 apes (see Table 2); 16 chimpanzees (mean age = 27.1 years), eight bonobos (mean age = 20), and five orangutans (mean age = 17).

11.2 | Apparatus

The same apparatus from Experiment 1 was used in this experiment, except that the blue containers were replaced with green ones (length = 13 cm, width = 7 cm, height = 6 cm) to minimize potential interference from the previous studies.

11.3 | Design

Apes were allocated to one of two exposure conditions; reinforced (R) or non-reinforced (NR). In most cases, subjects were assigned to the opposite condition they received in Experiment 1; that is, reinforced to non-reinforced. Conditions were balanced in terms of age, gender and species as much as possible.

11.4 | Procedure

11.4.1 | Exposure phase

The procedure was identical to the exposure procedure from Experiment 1, with the exception that the amount of banana under the baited container was larger (half a banana); the same amount as in Experiment 2. The position of the baited container was the same in each trial, but different from the previous two experiments.

11.4.2 | Test phase

The test took place 2 weeks (13–14 days) later. The procedure was the same as the exposure procedure, except that E did not reveal the location of the baited container before the subject made a choice. Additionally, if the subject made a correct choice they received the food regardless of which exposure condition they were in. Subjects only received one trial.

11.5 | Data analysis

The data were analyzed in the same way as the previous two Experiments. Additionally, we compared whether performance in the R condition was the same as performance in Experiment 2 (conditions

from Experiment 2 were pooled due to not being statistically different) using a 2 (Experiment 2, R) by 2 (response) Fisher exact test. We also compared performance in the NR condition to Experiment 2; 2 (Experiment 2, NR) by 2 (response) Fisher exact text.

12 | RESULTS

All subjects required only two trials during the exposure procedure, except for Frederike who required three. Performance was above chance in the NR condition (binomial test: $N = 15$, $p = 0.05$) but not in the R condition (binomial test: $N = 14$, $p = 0.78$), thus, subjects remembered the baited location in the NR but not the R condition (see Figure 4). With regards to performance between this Experiment and Experiment 2, performance in the R condition was worse (Fisher exact test: $df = 1$, $p = 0.05$) and not significantly different in the NR condition (Fisher exact test: $df = 1$, $p = 0.52$).

13 | DISCUSSION

Apes only successfully recalled the location of the baited container when they were not reinforced during the initial exposure phase. This is surprising as it goes against any law of reinforcement, strongly contradicting an associative learning account.

With regards to contextual binding, such results appear to be un-supportive. However, it may be that our original prediction was misguided; as with baiting the container outside the testing room, "throwing" away a large amount of food is not a common occurrence, and is therefore distinctive (different in comparison to the standard procedure). The crucial difference between the throwing away of food in Experiment 1 and this experiment is the amount of food that was thrown away. As the apes rarely receive such large food amounts, it is highly unlikely they have experienced such a large amount being thrown away. In contrast, they have had

FIGURE 4 Number of correct subjects by condition, chance shows number of subjects that would be correct if performing at chance. * = 0.05

experience of small amounts being discarded, such as in reverse contingency tasks (Uher & Call, 2008; Vlamings et al., 2006). Thus, even though we did not intend to include a distinctive feature to the event, the act of throwing away a large amount of food may have been distinctive, resulting in enhanced performance. Indeed, the finding that performance in this condition was comparable to performance in Experiment 2 suggests that distinctiveness may be the common explanatory variable.

Such a finding is consistent with distinctiveness effects in human memory, in which distinctiveness enhances memory regardless of reinforcement (Guitart-Masip, Bunzeck, Stephan, Dolan, & Duzel, 2010; Hunt & Worthen, 2006). Furthermore, research with primates suggests that a novel stimulus attracts attention even when it is associated with a negative outcome (Foley, Jangraw, Peck, & Gottlieb, 2014), which is consistent with our finding that a novel event leads to memory enhancement even when the event is negative. In the human literature, this effect is referred to as an "attention magnet" (Laney, Campbell, Heuer, & Reisberg, 2004), in which negatively arousing stimuli capture attention and subsequently are remembered very well.

However, it could be argued that the difference between the conditions is simply a result of whether food was received or not at encoding. We believe this is not the case for two reasons. Firstly, if we explain the performance by the giving or not giving of food before the test, then the results from Experiment 2 and Experiment 3 should differ; they should perform above chance when they did not receive food (as we see here in the NR condition), but not when they receive the food, this is not what we see in Experiment 2. Secondly, performance in the NR condition of Experiment 1 was at chance, whereas in this experiment it was above chance. Therefore, the common explanatory variable cannot be the receiving or not receiving of food at encoding.

An alternative explanation for the good performance in the NR condition here could be the role of experience. At the time of this experiment the apes had already been tested on two very similar tasks (i.e., Experiments 1 and 2), both with a 2-week retention period. As such, the apes may have anticipated that they would be tested on the location of the baited container. However, if this were the case then performance in the R condition should also be good, yet here they perform at chance. Furthermore, if the apes are simply learning that they will be tested after a delay, performance should be as good, if not better than, the first experiment they received (Experiment 2), which is not the case for the R condition.

The finding that performance in the R condition was poorer than in Experiment 2 is supportive of contextual binding. The R condition had no distinctive features; although the large food amount was distinctive in Experiment 2, here it was no longer distinctive due to the very fact it had recently occurred in Experiment 2. That is, a large food amount was no longer novel to the apes due to past experience of large food amounts in this type of task. Thus, just like Experiment 1, contextual binding may not have led to successful recall due to lack of distinct information in the bound representation, resulting in "gist" like memory rather than recall of the specific event (Schacter & Addis, 2007; Schacter
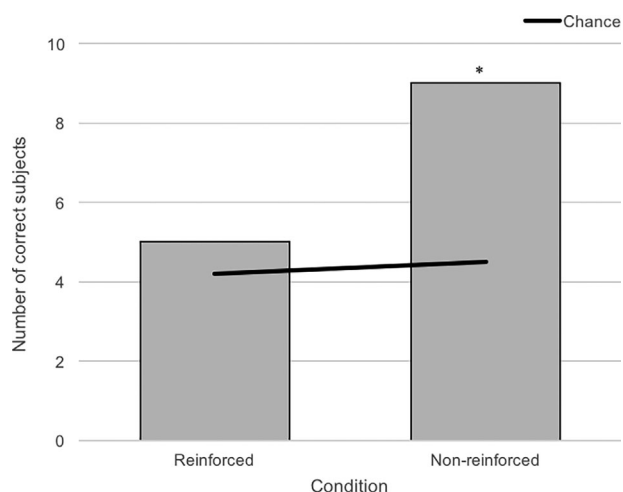
et al., 1998). In contrast, this finding contradicts associative learning, in which performance should increase as reinforcement value increases; here the condition with the high reward (R condition) was at chance, whereas the condition with no reward (NR) was above chance. Additionally, performance in the R condition was poorer than in Experiment 2, even though the reinforcement amount was identical. Such results strongly contradict an associative memory account.

14 | GENERAL DISCUSSION

The purpose of this study was to investigate the influence of distinctiveness on long-term event memory in great apes. In order to address the common concern that animals may use associative learning to recall information, we generated differing predictions based on two accounts; event memory, as shown by contextual binding, and associative learning.

Experiment 1 used a standard baiting procedure in which the apes were rewarded with a regular amount of food for a correct choice. This baseline experiment allowed for us to assess whether apes could recall an event that occurred only twice after a 2-week delay, using a standard and undistinctive procedure. Additionally, we assessed whether performance could be hindered or enhanced from this baseline by manipulating reinforcement and by matching contextual features at encoding and retrieval. The results indicated that the apes failed to remember the location of the baited container in any of the conditions, suggesting that neither associative learning nor contextual binding had an effect on memory performance. However, the poor performance could be explained by both the cues being overloaded and undistinctive, resulting in binding having no beneficial effect, and by the reinforcement value being too small for associative learning to occur and be retained over a 2-week delay.

An alternative explanation could be that the apes simply did not assume that the same container would be baited after a 2-week delay. As the apes are tested on many similar tasks, which are often unrelated to one another, the apes' experimental history may predispose them to assume that tasks separated in time are not related to one another. However, we believe this is not the case for two reasons. Firstly, the apes successfully assumed that food was in the same location in Experiments 2 and 3, as shown by selecting the correct container above chance. Secondly, previous research from our lab using a similar design has shown that apes can successfully select the location of a container baited 24 hr previously (Martin-Ordas & Call, 2011). Instead, we believe that the lack of any distinctive diagnostic cues made it very difficult for the apes to distinguish between one platform baiting experiment and another. That is to say, the apes did not fail to assume they should look in the location in which the food was hidden last, rather, that they did not have enough distinctive diagnostic information to correctly recall where it was hidden last.

In Experiment 2, we showed that by making elements of the event distinctive and by increasing the reinforcement value (larger amount of food), performance could be greatly enhanced. However, it was unclear as to whether distinctiveness (contextual binding) or reinforcement

(associative learning) accounted for the improved performance. Experiment 3 aimed to distinguish between the two accounts. We found that by using the standard baiting procedure (removing distinctiveness) and using a large food reward (high reinforcement), performance was at chance, contradicting associative learning. When the apes were not reinforced for a correct choice and a large amount of food was thrown away (a distinctive event), performance was again comparable to Experiment 2, providing support for contextual binding and strongly contradicting associative learning.

The results from Experiment 3 show that memory performance was enhanced for distinctive events, irrespective of reinforcement, thus showing commonalities with human memory (Hunt & Worthen, 2006). Such a finding is consistent with contextual binding; by binding distinct and specific features to the baited container's location, the apes could distinguish between other highly similar baiting events. The more distinctive the event, the more unique this bound representation became, and thus, the more likely the correct memory was recalled. In contrast, associative learning would not make use of distinctive material in the same way, indeed, associative learning would only improve as the strength of the association increases, which here was manipulated by increasing the amount of food that was baited in the location.

One could argue that a contextual binding account would predict enhanced performance in conditions in which encoding and retrieval cues are highly matched (i.e., encoding specificity), contradicting our findings in Experiment 1. However, this ignores the importance of the cue-overload theory, in which a cue is only effective if it is not associated to many memory traces (Watkins & Watkins, 1975). In Experiment 1, all the cues were common and undistinctive, and thus highly overloaded. Even when bound, the combination of cues was still not distinct and specific enough to generate a specific memory (e.g., see Eysenck et al., 1979), and more likely to result in the recall of a gist memory (e.g., Schacter & Addis, 2007; Schacter et al., 1998). Thus, when taking account of both the encoding specificity and cue overload theories, a contextual binding account is consistent with the results from all three experiments.

Although our findings are more consistent with a distinctiveness effect, as opposed to associative learning by reinforcement, we acknowledge that we cannot rule out other alternative explanations. The distinctiveness account does not always directly follow from our data, for instance, a distinctiveness account would predict enhanced performance for the mask condition in Experiment 2, and better performance in the matching condition compared to the non-matching condition of Experiment 1. However, we believe that when accounting for other well-known memory conceptions, such as cue-overload in Experiment 1 and attention magnets in Experiment 2, our data remain consistent with a distinctiveness account. Thus, although there may be other viable explanations, we favor a distinctiveness account.

In addition to the findings on distinctiveness and contextual binding, surprise may also have had an effect in Experiments 2 and 3. In Experiment 2, the element of surprise may have led to attention being focused on the surprising element (the mask) and consequently drawn away from the peripheral elements, including baiting of the container. This focusing of attention at the detriment to peripheral information occurs in human memory (Burke et al., 1992;

Easterbrook, 1959; Kensinger, 2009; Schmidt, 2007) and shares parallels with divided attention which has been shown in rodents (Zentall, 1985). With regards to Experiment 3, the throwing away of a large amount of food upon a correct choice may also have been surprising due to its unexpectedness. But here, and unlike the mask in Experiment 2, the location of the baited container is the focal point, as it is the baited container from which the food is thrown away. Thus, the location of the baited container may benefit from additional attention and thus be remembered to a greater extent than containers with no surprising element. Indeed, this result is consistent with the von-Restorff effect (von Restorff, 1933), in which an item that is different (isolated) from a series of similar items is remembered better than other items. In this situation, the surprising container is remembered better than the non-surprising containers. However, as we did not collect data on emotional responses, such as surprise, we can only speculate on this.

According to Rubin and Umanath (2015) definition of event memory, a memory of a past event requires mentally reconstructing a scene, with scene construction defined as the ability to bind various informational features into a coherently organized spatial representation (Hassabis & Maguire, 2007; Lind et al., 2014; Raffard et al., 2010; Rubin & Umanath, 2015). The reconstruction of a scene can occur voluntary or involuntary and can be of a single episode or multiple events. Our results are consistent with this; the apes were able to successfully recall the spatial location of one of three identical containers only when distinctive features were present, suggesting that these distinctive features were bound to the specific spatial location of the container. Although are findings are consistent with binding, we acknowledge that mechanisms other than binding may have been at work, and as such further research is needed to clarify these underlying mechanisms. Performance was not predicted by the amount of reinforcement (food reward), and thus strongly contradicts an associative learning account.

15 | SUMMARY

Our results suggest that great apes can bind distinctive information to spatial locations in order to distinguish between very similar events, providing evidence of event memory in apes (as defined by Rubin & Umanath, 2015). These results add to the growing literature on contextual binding in animals (Clayton, Yu, et al., 2001; Crystal & Smith, 2014; Crystal et al., 2013; Martin-Ordas et al., 2013), and show parallels with human memory, in which distinctiveness enhances memory for events independent of reinforcement (Hunt & Worthen, 2006).

REFERENCES

Anderson, M. C., & Neely, J. H. (1996). Interference and inhibition in memory retrieval. In E. L. Bjork, & R. A. Bjork (Eds.), *Handbook of perception and cognition* (pp. 237–313). San Diego: Academic Press.

Basile, B. M. (2015). Rats remind us what actually counts in episodic memory research. *Frontiers in Psychology*, 6, 75.

Beran, M. J. (2011). Chimpanzees (*Pan troglodytes*) show the isolation effect during serial list recognition memory tests. *Animal Cognition*, 14(5), 637–645.

Beran, M. J., Beran, M. M., & Menzel, C. R. (2005). Spatial memory and monitoring of hidden items through spatial displacements by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 119(1), 14–22.

Berntsen, D., Staugaard, S. R., & Sorensen, L. M. (2013). Why am I remembering this now? Predicting the occurrence of involuntary (spontaneous) episodic memories. *Journal of Experimental Psychology: General*, 142(2), 426–444.

Burke, A., Heuer, F., & Reisberg, D. (1992). Remembering emotional events. *Memory & Cognition*, 20(3), 227–290.

Cahill, L., & McGaugh, J. L. (1995). A novel demonstration of enhanced memory associated with emotional arousal. *Consciousness and Cognition*, 4(4), 410–421.

Call, J. (2004). Inferences about the location of food in the great apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla*, and *Pongo pygmaeus*). *Journal of Comparative Psychology*, 118(2), 232–241.

Call, J. (2006). Inferences by exclusion in the great apes: The effect of age and species. *Animal Cognition*, 9(4), 393–403.

Chalfonte, B., & Johnson, M. (1996). Feature memory and binding in young and older adults. *Memory & Cognition*, 24(4), 403–416.

Clayton, N. S., Griffiths, D. P., Emery, N. J., & Dickinson, A. (2001). Elements of episodic-like memory in animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 356, 1483–1491.

Clayton, N. S., Yu, K. S., & Dickinson, A. (2001). Scrub jays (*Aphelocoma coerulescens*) form integrated memories of the multiple features of caching episodes. *Journal of Experimental Psychology Animal Behavior Processes*, 27(1), 17–29.

Crystal, J. D. (2009). Elements of episodic-like memory in animal models. *Behavioral Processes*, 80(3), 269–277.

Crystal, J. D., & Alford, W. T. (2014). Validation of a rodent model of source memory. *Biology Letters*, 10(3), 20140064.

Crystal, J. D., Alford, W. T., Zhou, W., & Hohmann, A. G. (2013). Source memory in the rat. *Current Biology*, 23(5), 387–391.

Crystal, J. D., & Smith, A. E. (2014). Binding of episodic memories in the rat. *Current Biology*, 24(24), 2957–2961.

Dekleva, M., Dufour, V., de Vries, H., Spruijt, B. M., & Sterck, E. H. (2011). Chimpanzees (*Pan troglodytes*) fail a what-where-when task but find rewards by using a location-based association strategy. *PLoS ONE*, 6(2), e16593.

Dere, E., Kart-Teke, E., Huston, J. P., & De Souza Silva, M. A. (2006). The case for episodic memory in animals. *Neuroscience & Biobehavioral Reviews*, 30(8), 1206–1224.

Easterbrook, J. A. (1959). The effect of emotion on cue utilization and the organization of behavior. *Psychological Review*, 66, 183–201.

Ellis, N. R., Detterman, D. K., Runcie, D., McCarver, R. B., & Craig, E. M. (1971). Amnesic effects in short-term memory. *Journal of Experimental Psychology*, 89(2), 357–361.

Eysenck, M., Cermak, L. S., & Craik, F. I. M. (1979). Depth, elaboration, and distinctiveness. *Levels of processing in human memory* (pp. 89–118). Hillsdale, NJ: Erlbaum.

Foley, N. C., Jangraw, D. C., Peck, C., & Gottlieb, J. (2014). Novelty enhances visual salience independently of reward in the parietal lobe. *Journal of Neuroscience*, 34(23), 7947–7957.

Fujita, K., & Matsuzawa, T. (1990). Delayed figure reconstruction by a chimpanzee (Pan troglodytes) and humans (Homo sapiens). Journal of Comparative Psychology, 104(4), 345–351.

Guitart-Masip, M., Bunzeck, N., Stephan, K. E., Dolan, R. J., & Duzel, E. (2010). Contextual novelty changes reward representations in the striatum. Journal of Neuroscience, 30(5), 1721–1726.

Hassabis, D., & Maguire, E. A. (2007). Deconstructing episodic memory with construction. Trends in Cognitive Sciences, 11(7), 299–306.

Hoffman, M. L., & Beran, M. J. (2006). Chimpanzees (Pan troglodytes) remember the location of a hidden food item after altering their orientation to a spatial array. Jouranl of Comparative Psychology, 120(4), 389–393.

Hoffman, M. L., Beran, M. J., & Washburn, D. A. (2009). Memory for "what", "where", and "when" information in rhesus monkeys (Macaca mulatta). Journal of Experimental Psychology: Animal Behavioral Processes, 35(2), 143–152.

Hunt, R. R., & Worthen, J. B. (2006). Distinctiveness and memory. USA: Oxford University Press.

Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. Current Biology, 17(23), R1004–R1005.

Jenkins, W. O., & Postman, L. (1948). Isolation and spread of effect in serial learning. American Journal of Psychology, 61, 214–221.

Kano, F., & Hirata, S. (2015). Great apes make anticipatory looks based on long-term memory of single events. Current Biology, 25(19), 2513–2517.

Kano, F., Tanaka, M., & Tomonaga, M. (2008). Enhanced recognition of emotional stimuli in the chimpanzee (Pan troglodytes). Animal Cognition, 11(3), 517–524.

Kano, F., & Tomonaga, M. (2010). Attention to emotional scenes including whole-body expressions in chimpanzees (Pan troglodytes). Journal of Comparative Psychology, 124(3), 287–294.

Kensinger, E. A. (2004). Remembering emotional experiences: The contribution of valence and arousal. Annual Review of Neuroscience, 15(4), 241–251.

Kensinger, E. A. (2009). Remembering the details: Effects of emotion. Emotion Review, 1(2), 99–113.

Laney, C., Campbell, H. V., Heuer, F., & Reisberg, D. (2004). Memory for thematically arousing events. Memory and Cognition, 32(7), 1149–1159.

Lind, S. E., Williams, D. M., Bowler, D. M., & Peel, A. (2014). Episodic memory and episodic future thinking impairments in high-functioning autism spectrum disorder: An underlying difficulty with scene construction or self-projection? Neuropsychology, 28(1), 55–67.

MacDonald, S. E., & Agnes, M. M. (1999). Orangutan (Pongo pygmaeus abelii) spatial memory and behavior in a foraging task. Journal of Comparative Psychology, 113(2), 213–217.

Martin-Malivel, J., & Okada, K. (2007). Human and chimpanzee face recognition in chimpanzees (Pan troglodytes): Role of exposure and impact on categorical perception. Behavioral Neuroscience, 121(6), 1145–1155.

Martin-Ordas, G., Atance, C. M., & Call, J. (2014). Remembering in tool-use tasks in children and apes: The role of the information at encoding. Memory, 22(1), 129–144.

Martin-Ordas, G., Berntsen, D., & Call, J. (2013). Memory for distant past events in chimpanzees and orangutans. Current Biology, 23(15), 1438–1441.

Martin-Ordas, G., & Call, J. (2011). Memory processing in great apes: The effect of time and sleep. Biology Letters, 7(6), 829–832.

Martin-Ordas, G., Haun, D., Colmenares, F., & Call, J. (2010). Keeping track of time: Evidence for episodic-like memory in great apes. Animal Cognition, 13(2), 331–340.

Martinez, L., & Matsuzawa, T. (2009). Auditory-visual intermodal matching based on individual recognition in a chimpanzee (Pan troglodytes). Animal Cognition, 12(Suppl 1), S71–S85.

Mendes, N., & Call, J. (2014). Chimpanzees form long-term memories for food locations after limited exposure. American Journal of Primatology, 76(5), 485–495.

Menzel, C. R. (1999). Unprompted recall and reporting of hidden objects by a chimpanzee (Pan troglodytes) after extended delays. Journal of Comparative Psychology, 113(4), 426–434.

Menzel, E. W. (1973). Chimpanzee spatial memory organization. Science, 182(4115), 943–945.

Mishkin, M., & Delacour, J. (1975). An analysis of short-term visual memory in the monkey. Journal of Experimental Psychology: Animal Behavior Processes, 1(4), 326–334.

Moscovitch, M., (1994). Memory and working with memory: Evaluation of a component process model and comparisons with other models. In D. L. Schacter, & E. Tulving (Eds.), Memory systems (pp. 269–310). Cambridge, MA: MIT Press.

Nairne, J. S. (2002). The myth of the encoding-retrieval match. Memory, 10(5–6), 389–395.

Nairne, J. S. (2007). The foundations of remembering: Essays in honor of Henry L. Roediger, III. New York, NY, US: Psychology Press.

Nashiro, K., & Mather, M. (2011). How arousal affects younger and older adults' memory binding. Experimental Aging Research, 37(1), 108–128.

Noser, R., & Byrne, R. W. (2015). Wild chacma baboons (Papio ursinus) remember single foraging episodes. Animal Cognition, 18(4), 921–929.

Panoz-Brown, D., Corbin, H. E., Dalecki, S. J., Gentry, M., Brotheridge, S., Sluka, C. M., . . . Crystal, J. D. (2016). Rats remember items in context using episodic memory. Current Biology, 26(20), 2821–2826.

Pillemer, D. (2003). Directive functions of autobiographical memory: The guiding power of the specific episode. Memory, 11(2), 193–202.

Raffard, S., D'Argembeau, A., Bayard, S., Boulenger, J. P., & Van der Linden, M. (2010). Scene construction in schizophrenia. Neuropsychology, 24(5), 608–615.

Raj, V., & Bell, M. A. (2010). Cognitive processes supporting episodic memory formation in childhood: The role of source memory, binding, and executive functioning. Developmental Review, 30(4), 384–402.

Reed, P., & Richards, A. (1996). The von restorff effect in rats (Rattus norvegicus). Journal of Comparative Psychology, 110(2), 193–198.

Robbins, D., & Bush, C. T. (1973). Memory in great apes. Journal of Experimental Psychology General, 97(3), 344–348.

Roberts, W. A. (1980). Distribution of trials and intertrial retention in delayed matching to sample with pigeons. Journal of Experimental Psychology: Animal Behavior Processes, 6(3), 217–237.

Rodriguez, J. S., Zurcher, N. R., Bartlett, T. Q., Nathanielsz, P. W., & Nijland, M. J. (2011). CANTAB delayed matching to sample task performance in juvenile baboons. Journal of Neuroscience Methods, 196(2), 258–263.

Rubin, D. C. (1995). Memory in oral traditions. The cognitive psychology of epic, ballads, and counting-out rhymes. New York: Oxford University Press.

Rubin, D. C., & Umanath, S. (2015). Event memory: A theory of memory for laboratory, autobiographical, and fictional events. Psychological Review, 122(1), 1–23.

Schacter, D. L., & Addis, D. R. (2007). The cognitive neuroscience of constructive memory: Remembering the past and imagining the future. Philosophical Transactions of the Royal Society of London B Biological Sciences, 362(1481), 773–786.

Schacter, D. L., Norman, K. A., & Koutstaal, W. (1998). The cognitive neuroscience of constructive memory. Annual Review of Psychology, 49, 289–318.

Schmidt, S. R. (1985). Encoding and retrieval processes in the memory for conceptually distinctive events. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *11*(3), 565–578.

Schmidt , S. R. (1991). Can we have a distinctive theory of memory? *Memory & Cognition*, *19*(6), 523–542.

Schmidt, S. R. (2007). Unscrambling the effects of emotion and distinctiveness on memory. *The foundations of remembering: Essays in honor of Henry L Roediger, III* (pp. 141–158). New York, NY, US: Psychology Press, xi.

Schmidt, S. R., & Saari, B. (2007). The emotional memory effect: Differential processing or item distinctiveness? *Memory & Cognition*, *35*(8), 1905–1916.

Schulz, L. (1971). Effects of high-priority events on recall and recognition of other events. *Journal of Verbal Learning and Verbal Behaviour*, *10*, 322–330.

Schwartz, B. L., Colon, M. R., Sanchez, I. C., Rodriguez, I. A., & Evans, S. (2002). Single-trial learning of "What" and "Who" information in a gorilla (*Gorilla gorilla gorilla*): Implications for episodic memory. *Animal Cognition*, *5*(2), 85–90.

Schwartz, B. L., & Evans, S. (2001). Episodic memory in primates. *American Journal of Primatology*, *55*(2), 71–85.

Schwartz, B. L., Hoffman, M. L., & Evans, S. (2005). Episodic-like memory in a gorilla: A review and new findings. *Learning and Motivation*, *36*(2), 226–244.

Shettleworth, S. (2010). *Cognition, evolution and behavior*. New York: Oxford University Press.

Sliwa, J., Duhamel, J. R., Pascalis, O., & Wirth, S. (2011). Spontaneous voice-face identity matching by rhesus monkeys for familiar conspecifics and humans. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(4), 1735–1740.

Suddendorf, T. (2007). The evolution of foresight: What is mental time travel, and is it unique to humans. *Journal of Behavioral and Brain Science*, *30*, 299–313.

Suddendorf, T., & Busby, J. (2003). Mental time travel in animals? *Trends in Cognitive Sciences*, *7*(9), 391–396.

Templer, V. L., & Hampton, R. R. (2013). Episodic memory in nonhuman animals. *Current Biology*, *23*(17), R801–R806.

Tomonaga, M. (1999). Inversion effect of perception of human faces in a chimpanzee. *Primates*, *40*(3), 417–438.

Tulving, E., (1972). Episodic and semantic memory. In E. T. W. Donaldson (Ed.), *Organization of memory* (pp. 381–402). New York: Academic Press.

Tulving, E. (1974). Cue-dependent forgetting. *American Scientist*, *62*(1), 74–82.

Tulving, E. (1983). *Elements of episodic memory*. Oxford, England: Clarendon Press.

Tulving, E. (1984). Précis of elements of episodic memory. *Behavioral and Brain Sciences*, *7*, 223–268.

Tulving, E. (1985). How many memory systems are there? *American Psychologist*, *40*(4), 385–398.

Tulving, E. (2001). *Chronesthesia: awareness of subjective time. The age of the frontal lobes* (pp. 311–325). New York: Oxford University Press.

Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, *53*, 1–25.

Tulving, E., (2005). Episodic memory and autonoesis: Uniquely human? In H. S. Terrace, & J. Metcalfe (Eds.), *The missing link in cognition: Origins of self-reflective consciousness* (pp. 3–56). Oxford: Oxford University Press.

Tulving, E., & Thomson, D. (1973). Encoding specify and retrieval processes. *Psychological Review*, *80*(5), 352–373.

Uher, J., & Call, J. (2008). How the great apes (*Pan troglodytes*, *Pongo pygmaeus*, *Pan paniscus*, *Gorilla gorilla*) perform on the reversed reward contingency task II: Transfer to new quantities, long-term retention, and the impact of quantity ratios. *Jouranl of Comparative Psychology*, *122*(2), 204–212.

Vlamings, P. H., Uher, J., & Call, J. (2006). How the great apes (*Pan troglodytes*, *Pongo pygmaeus*, *Pan paniscus*, and *Gorilla gorilla*) perform on the reversed contingency task: The effects of food quantity and food visibility. *Journal of Experimental Psychology: Animal Behavioural Processes*, *32*(1), 60–70.

von Restorff, H. (1933). Über die Wirkung von Bereichsbildungen im Spurenfeld. *Psychologische Forschung*, *18*, 299–342.

Watkins, O. C., & Watkins, M. J. (1975). Buildup of proactive inhibition as a cue-overload effect. *Journal of Experimental Psychology: Human Learning and Memory*, *1*(4), 1–15.

Winocur, G., Moscovitch, M., Fogel, S., Rosenbaum, R. S., & Sekeres, M. (2005). Preserved spatial memory after hippocampal lesions: Effects of extensive experience in a complex environment. *Nature Neuroscience*, *8*(3), 273–275.

Zentall, T. R. (1985). Selective and divided attention in animals. *Behavioural Processes*, *69*(1), 1–15.

Zentall, T. R. (2006). Mental time travel in animals: A challenging question. *Behavioural Processes*, *72*(2), 173–183.

Zentall, T. R., Hogan, D. E., Edwards, C. A., & Hearst, E. (1980). Oddity learning in the pigeon as a function of the number of incorrect alternatives. *Journal of Experimental Psychology: Animal Behavior Processes*, *6*, 278–299.