RESEARCH ARTICLE

Chimpanzees Form Long-Term Memories for Food Locations After Limited Exposure

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Remembering the location of fruiting trees for extended periods of time has been hypothesized to play a major role in the evolution of primate cognition. Such ability would be especially useful when paired with a fast learning mechanism capable of consolidating long-term memory after minimal exposure. We investigated whether chimpanzees (*Pan troglodytes*) can remember different food locations after minimal exposure (i.e., 1–2 trials) both after 24 hr and after 3-month. We released pairs of chimpanzees in their indoor enclosure (the enclosure of group A measured $430\,m^2$ and group B's measured $175\,m^2$) and tested them for four consecutive days (Baseline, Test, Retest, and Post-test). During the Test and Retest food was hidden in the same location whereas no food was hidden during the Baseline and Post-test days (control trials). Subjects were tested with four different locations and assessed for their retention after 24 hr and 3-month since the initial food discovery. Results revealed that chimpanzees accurately remembered the locations in which they found the food after one or two exposures to them, and both after 24 hr and a 3-month retention interval. Am. J. Primatol. 76:485–495, 2014. © 2014 Wiley Periodicals, Inc.

Key words: long-term memory; limited exposure; retention interval; chimpanzees

INTRODUCTION

Many primate species need to remember food sources to forage efficiently and several studies have documented the use of spatial memory in wild populations [i.e., Garber & Paciulli, 1997; Janmaat et al., 2006; Janson, 1998; Noser & Byrne, 2007]. Although field primatologists have suggested that nonhuman primates are capable of remembering the location of multiple food sources after long periods of time [see e.g., Boesch & Boesch-Achermann, 2000; MacKinnon, 1974; Milton, 1988], there are few empirical studies that have assessed the long-term (longer than 24 hr) spatial memory in nonhuman primates in a foraging context. This contrasts with work that has been done in corvids. For example, Clark's nutcrackers (*Nucifraga columbiana*) can cache around 30,000 seeds, over a large area, and recover them up to 6 months later [Balda & Kamil, 1992]. Similarly, Pinyon jays (*Gymnorhinus cyanocephalus*) can remember where they cached thousands of seeds from 4 to 7 months later [Balda, 2002]. The cognitive/sensory mechanisms suggested to account for this ability in corvids include the use of landmarks [Bennett, 1993; Bossema, 1979; Kamil & Jones, 1997; Vander Wall, 1982] and their geometric relationships [Kamil & Jones, 1997], but also sensory

mechanisms such as the use of feature information of objects nearby landmarks [Kelly, 2010], orientation by the sun [Wiltschko & Balda, 1989], self-motion cues [Gibson & Wilks, 2008], and potentially inertial and magnetic cues [Kelly et al., 2010]. For a review see Kamil & Balda [1990] and Gould and colleagues [2010]. According to Milton's work on howler and spider monkeys [Milton, 1988, p. 287], "once the location of a particular food tree is known, it becomes a dependable seasonal resource in terms of its location for the lifetime of a primate." Milton's statement not only implies that primates have long-lasting memories, but also that a single exposure to a

food location is enough for it to be remembered. Such a theoretical assumption seems to be based on the complex spatial and temporal ecological conditions that primates face when living in tropical forests. In tropical forests, highly nutritious food resources (e.g., fruits, flowers, and young leaves) follow an irregular distribution in space and time [Chapman et al., 1999; Milton, 1981]. Given that highly nutritious food resources are perishable items, to optimize foraging success (i.e., maximizing the income of energy per unit of time spent foraging [MacArthur & Pianka, 1966; Stephens & Krebs, 1986]) primates need to know not only the shortest route to a feeding location but also which food is located where as well as its fruiting state [Milton, 1981, 2000]. This latter cognitive ability has been linked with human episodic memory (i.e., the ability to remember *what* the event was in one's own past, and *where* and *when* that specific event took place) [Babb & Crystal, 2005; Clayton & Dickinson, 1998, 1999; Clayton et al., 2003; Martin-Ordas et al., 2010; Mulcahy & Call, 2006; Schwartz & Evans, 2001; but see Tulving, 1983; Suddendorf & Corballis, 1997 for a different opinion about the existence of "episodic memory" in nonhuman animals]. However, to our knowledge, Milton's statement has not yet been tested. That is, the interaction between very minimal exposure (1–2 trials) to food locations and memory for those locations after long periods of time (longer than 24 hr) has yet to be investigated.

Several experimental studies though, both in captivity and in the wild, have investigated whether nonhuman primates accurately remember food locations after a brief learning experience (consisting of either discovering a food source or witnessing an experimenter placing food in a certain location) and over short periods of time, usually up to 24 hr [e.g., capuchin monkeys: Garber & Paciulli, 1997; marmosets: MacDonald et al., 1994; Menzel & Juno, 1985; pigtail macaques: Unbehagen et al., 2006; squirrel monkeys: Roberts et al., 1993; tamarins: Garber & Dolins, 1996; Dolins, 2009; vervet monkeys: Cramer & Gallistel, 1997; gorillas: MacDonald, 1994; orangutans: MacDonald & Agnes, 1999; Scheumann & Call, 2006; chimpanzees and monkeys: Tinklepaugh, 1932; bonobos, chimpanzees, and orangutans: Martin-Ordas & Call, 2011; chimpanzee: Menzel, 1973; lexigram-competent chimpanzee: Menzel, 1999]. However, there is a lack of consensus on the temporal criteria for defining long-term memory. For instance, Schwartz et al. [2002] considered a delay of 5–10 min sufficient to refer to long-term memory. Accordingly, the studies conducted by MacDonald and colleagues [Gibeault & MacDonald, 2000; MacDonald & Agnes, 1999] represent cases of long-term memory for object locations after single-trial learning exposure. For instance, MacDonald & Agnes [1999] investigated orangutans' (*Pongo pygmaeus abelii*) spatial memory using an open-field design of the radial arm maze task. In one of the tasks, a so-called win-stay task, subjects could explore eight food locations and deplete the baited ones (four out of eight). After a delay of 5–10 min, during which the experimenter re-baited the locations out-of-sight of the subjects, the orangutans' ability to return to the previously baited locations was assessed. Results showed that two out of three orangutans were accurate at returning to the previously depleted food locations (above chance level) after single-trial learning exposure to them even up to 10 min later.

Although these results convincingly show that several primates can remember multiple locations for periods of time ranging between minutes and hours, some authors would not consider them as cases of long-term memory. For instance, Bailey et al. [1996] consider long-term memory a period ranging from days to the lifetime of an animal. Surprisingly, there is very little research done demonstrating that nonhuman primates can retain information of food locations after long periods of time (i.e., longer than 24 hr) after 1–2 exposures to them. Menzel & Juno [1982] investigated long-term memory for artificial food places (i.e., objects added to the subjects' environment) in marmosets (*Saguinus fuscicollis*) after an average of 3 weeks, but after subjects had received three trials of exposure to those places. Moreover, Menzel [1999] investigated long-term memory for hidden items in the lexigram-competent chimpanzee Panzee. After Panzee witnessed the hiding of either food or non-food items in a patch of forest (to which she had no physical access), she attracted the caregiver's attention, pressed the lexigram corresponding to the hidden object, and pointed in the direction that the object was hidden until the caregiver retrieved it. Panzee could accurately remember the location and the kinds of objects hidden in such a situation after a forced retention interval of at least 16 hr in 10 trials [Menzel, 1999; see also Menzel, 2010 for an informative overview of the studies conducted with Panzee]. The few other studies that have investigated long-term memory have used non-spatial information after repeated exposure to items [Beran et al., 2000; Patterson & Tzeng, 1979].

The goal of this study was to document long-term memory in chimpanzees for spatial locations in a foraging context. We tested pairs of chimpanzees in their enclosure for four consecutive days (a so-called block). During the first day, no hiding location of food was baited; during two subsequent days, the same hiding location was baited; and on the last day no baiting took place. Each pair of chimpanzees received a total of four blocks with a different hiding location in each of them. If chimpanzees remembered where they found food 24 hr earlier, we predicted that they should return and inspect those hiding locations and do this faster than on a day in which no location had previously been baited. In Experiment 2, the same

pairs of chimpanzees were re-tested after a minimum delay of 3-month. During the first day, all subjects were released together in the enclosure (a procedure that occurs under normal circumstances); no hiding location was baited and the experimenter was not present at the observation platform. During the three subsequent days, the chimpanzees were released with their former partner, an atypical situation for the subjects but the same experimental situation as 3-month before and the experimenter was present at the observation platform. However, only during the third day was a former hiding location baited. If chimpanzees remembered where they found food 3-month earlier, we predicted that they should inspect those hiding locations where they had found food before.

METHODS

Experiment 1: Single–Trial Learning and 24-hr Retention Interval

The purpose of Experiment 1 was to investigate if chimpanzees accurately remember the hiding locations of food after one or two exposures to each and a 24-hr retention interval. For each of the hiding locations, chimpanzees initially discovered the food by chance and during the two subsequent days their memory for that same hiding location was assessed. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates and followed the institutional guidelines and laws for animal research in Germany.

Subjects

Twelve chimpanzees, belonging to two different groups (groups A and B), participated in the present study. All chimpanzees were socially housed at the Wolfgang Koehler Primate Research Center, Leipzig zoo. There were eight chimpanzees (six females and two males) in group A and four chimpanzees (three females and one male) in group B. The average age of males was 10 years and 9 months, and the average age of females was 16 years and 10 months. The experiment took place in the indoor enclosure (henceforth enclosure) of each group of chimpanzees. The enclosure of group A measured $430\,m^2$ and group B's measured $175\,m^2$.

Procedure

Prior to testing, the experimenter (E) chose four "hiding food locations" (henceforth "locations") inside the enclosures of each of the chimpanzee groups. The locations were created by various existing elements inside the enclosure (e.g., rocks, plants, enrichment boxes, and logs). They were chosen based on four criteria: (1) subjects must never have encountered food in these locations in the past; (2) hidden food

should not be visible from the entrance of the enclosure, nor from other locations; (3) subjects were required to come within $1\,m$. of the locations in order to discover the food; and (4) locations should be distributed throughout the enclosure (the minimum distance between locations was approximately 4 and $3\,m$ in group A and B, respectively).

Before the start of each trial, E scattered the chimpanzees' regular morning food (consisting of vegetables and apples, which were far less attractive than the hidden food—three bananas) throughout the entire enclosure. This procedure was invisible to the chimpanzees. Once in the enclosure, all subjects had visual access to E (who stood at the observation platform) from their enclosure.

Pairs of chimpanzees were released into the enclosure in order to increase their motivation to retrieve food as fast as possible via competition. Based on prior knowledge, pairs were established between subjects who would tolerate one another. Only one pair of subjects was tested per day and each pair received four blocks (one for each location). Each block consisted of four trials with one trial per day, and on average 2 days in between blocks. Trials lasted $20\,min$ and were always administered in the following order:

Baseline. None of the locations were baited.
Test. The E baited one location with a bunch of three bananas. If none of the subjects had discovered the bananas after $15\,min$, E "helped" them discover them by throwing pellets towards the banana location.
Retest. Same as in the test trial except that if the chimpanzees did not find the bananas, the E refrained from helping them to discover the baited location.
Post-test. Same as the baseline trial.

Predictions

If chimpanzees were capable of remembering where they had found food after a delay of 24 hr, they should preferentially visit those locations. Moreover, the latency to inspect those locations should decrease from Test to Retest. However, we predicted the latency to inspect locations in the Post-test to stabilize. We assumed that the presence of a partner stimulated competition for the baited location. Thus, during the Retest subjects should be as fast as possible to get to the baited location and they should continue doing so in the Post-test.

Coding and Analysis

Audio recordings were used during the first two blocks of chimpanzee group B, and video recordings were used from the third block onwards (group B was the first group tested). Initially audio recording was

thought to be the best method to collect data, however because the pairs were very active video recording was used instead. While using audio recording E generated the following type of data: (1) the subject who discovered the bananas (during Test and Retest); (2) the subject who inspected the location during Post-test (in which no baiting took place); and (3) the latency it took the subject to find the bananas (during Test and Retest) and to start inspecting the location (during Post-test). All blocks in chimpanzee group A were video recorded. The data scored from the audio/videotapes were the aforementioned three variables. An inspection was operationally defined as a subject being within a 2 m range of a location and visually and/or manually searching that location.

In order to investigate subjects' accuracy at returning to the previously baited location within a block (i.e., the specific location of a specific block), analyses were performed on the following two dependent variables:

Match/mismatch

We scored a match when a subject inspected and found food in a location and 24 hr later returned to that same location. Thus, if a subject inspected a location during the Test (day 2) and also both during the Retest (day 3) and the Post-test (day 4), we scored two matches. One first match due to the subject returning to the same location (during the Retest) where she had found food 24 hr earlier and a second match for returning to that same location (during the Post-test) 24 hr after having had his/her 2nd exposure to the bananas at that location. Conversely, if the subject had found food in a location during the Test but did not return to that same location during the Re-test but went back during the Post-test, we scored two mismatches (one in the Retest relative to Test and one in the Post-test relative to the Retest). Given that subjects received a total of four locations (one location per block) they could perform a total of eight matches (i.e., 1 match in the Retest relative to the Test and 1 match in the Post-test relative to the Retest, for each of the four locations). This means that potential matches and mismatches to locations in which the subject has been rewarded during previous block(s) were not taken into account. We computed the number of matches and mismatches that each subject produced in each location (i.e., per each block) and this was summed and afterwards averaged across all the subjects. Since matches and mismatches required the prior experience of finding the baited location, these were only determined for the Retest and for the Post-test trials.

Latency

We scored the time (in sec) a subject took to start inspecting a specific location (i.e., the location of a block) from the moment she/he was released into the enclosure. This means that latency analyses were only conducted when matches occurred. Because not all subjects performed one match, the initial sample size of $N = 12$ subjects decreased to $N = 7$ subjects for matches in the Retest relative to Test (across the four blocks), and to $N = 8$ subjects for matches in the Post-test relative to Retest (across the four blocks) for this particular analysis. In case a subject inspected location(s) from previous block(s) the latency of those inspections were not taken into account.

To assess inter-observer reliability a second coder scored a random sample of 20% of the filmed trials. Inter-observer reliability was good for inspections at locations (subject within a 2 m range of a location and visually and/or manually searching it; Cohen's $k = 0.677$) and perfect for latency of inspections when both coders agreed on the occurrence of an inspection (*Pearson* correlation $r = 1.000$, $P < 0.001$, $N = 23$). Non-parametric tests were used in all analyses. Due to the small samples, exact tests were always computed [Mundry & Fischer, 1998; Siegel & Castellan, 1988]. Since some of our predictions were directional, statistical tests were one-tailed unless stated otherwise.

RESULTS

Since the size of the enclosure was much larger in the chimpanzee group A than B, we tested whether the overall number of matches and mismatches within Retest and Post-test across the four blocks, as well as for latency of inspections at locations, differed between groups. There was a tendency for a difference between both groups of chimpanzees regarding mismatches in the Post-test (Mann–Whitney U-test: $U = 6$, $N_{chimp\_group\_A} = 8$, $N_{chimp\_group\_B} = 4$, $P = 0.095$) and a significant difference in latency of inspections at the locations during the Post-test (*Mann–Whitney* U-test: $U = 0$, $N_{chimp\_group\_A} = 5$, $N_{chimp\_group\_B} = 3$, $P = 0.036$). However, those differences became non-significant after correcting for multiple comparisons [Haccou & Meelis, 1992]. More specifically, no significant differences were found for matches and mismatches (*Fisher's omnibus* test: $\chi^2 = 10.69$, df = 8, $P = 0.22$) or for inspection latencies ($\chi^2 = 11.25$, df = 8, $P = 0.18$). Data were therefore collapsed across both groups of chimpanzees in subsequent analyses.

Matches and Mismatches

Figure 1 presents the frequency of matches and mismatches that occurred in the Retest (relative to Test trials) and in the Post-test (relative to Retest trials) for each of the tested subjects. Matches in the Retest (i.e., inspecting a location during the Retest trial after having found food on that same location 24 hr earlier) were significantly more common than mismatches (Wilcoxon signed-ranks test: $T^+ = 52$, $N = 11$, $P = 0.047$). Although the pattern of matches
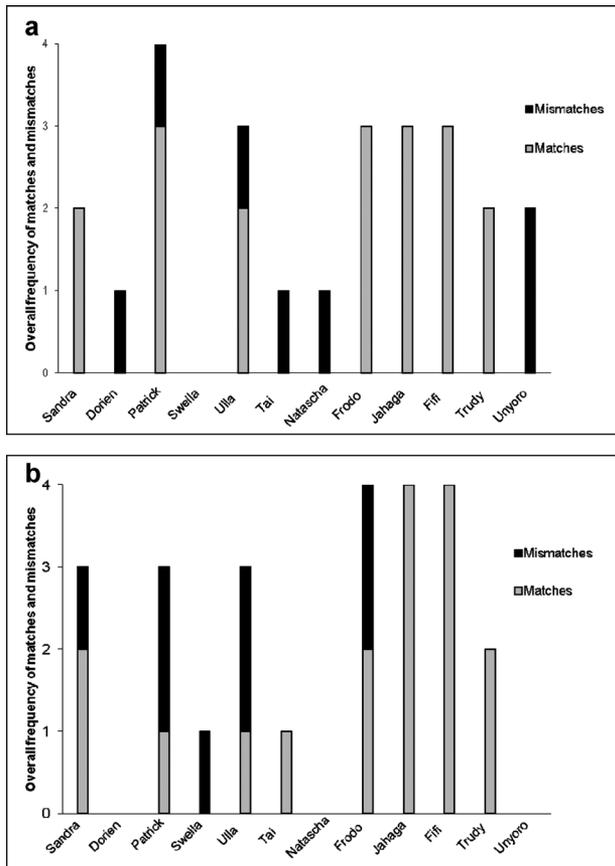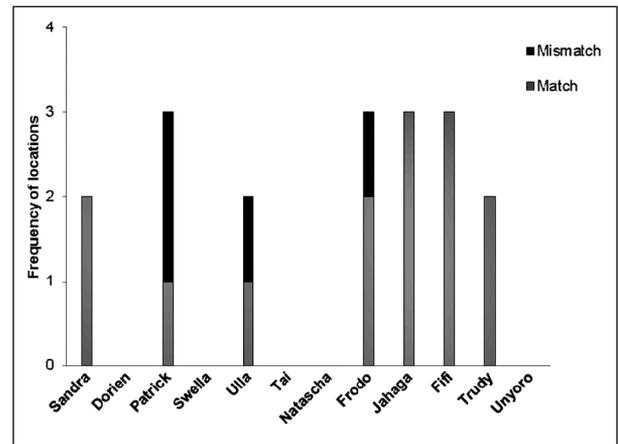
Fig. 2. Frequency of locations where each subject produced a match (i.e., inspected the location of the corresponding block—represented by the light grey bars) or a mismatch (i.e., failed to inspect the location of the corresponding block—represented by the dark bars) during the Post-test trial and after having had two exposures (i.e., during the Test and Retest trials) to the baited location. Note that subjects received a total of four locations (one location per block).

Fig. 1. Overall number of matches (light grey bars) and mismatches (dark bars) performed by each of the 12 subjects across the 4 blocks in the Retest trials (relative to Test trials) (Test_Retest) (**a**), and the Post-test trials (relative to Retest trials) (Retest_Post-test) (**b**). Four was the maximum number of matches or mismatches that a subject could accumulate in the Retest trials (Test_Post-test) as well as in the Post-test trials (ReTest_Post-test) across the 4 trial blocks.

and mismatches in the Post-test (i.e., inspecting and/or failing to inspect a location, respectively, after having found food on that same location 24 hr earlier) was similar to that found in the Retest (Retest: 1.50 matches vs. 0.58 mismatches; Post-test: 1.42 matches vs. 0.67 mismatches), matches were not significantly higher than mismatches ($T^+ = 27$, $N = 8$, $P = 0.133$). Moreover, during the Baseline no subject inspected a location of the corresponding block, a location that was baited 24 hr later (during the Test).

The total number of matches during the Retest (relative to Test trials) as well as during the Post-test (relative to Retest trials) did not differ significantly among the four blocks (Retest, *Friedman*'s test: $F = 6.500$, $N = 12$, df $= 3$, $P = 0.093$, Post-test, $F = 1.571$, $N = 12$, df $= 3$, $P = 0.839$), thus suggesting that subjects were not learning to respond to the problem over time.

Figure 2 depicts the frequency of locations that each subject inspected and/or failed to inspect during the Post-test trial after having had two

exposures (during the corresponding Test and Retest trials) to the same baited location. Inspections in the Post-test trial after subjects had retrieved food during Test and Retest were significantly more common than no inspections ($T^+ = 19.5$, $N = 6$, $P = 0.047$).

Five subjects (Dorien, Patrick, Ulla, Tai, and Natascha) inspected one location each and one subject (Unyoro) inspected two locations during Test trials but none of these subjects returned (i.e., inspected) to those same locations during the corresponding Post-test trial.

Latency

Only those subjects who performed at least one match in the Retest (relative to Test trials) or in the Post-test (relative to Retest trials) across the four blocks were included in the analyses. In other words, across the four blocks only those subjects that inspected at least one location 24 hr after having found food on that same location were taken into account. Across the four blocks, seven subjects performed at least two matches in the Retest (i.e., inspected at least two locations 24 hr after having found food in each of them), and eight subjects performed at least one match in the Post-test (i.e., inspected at least one location 24 hr after having found food in the same location). Subjects were significantly faster to inspect the location during the Retest (mean $= 57$ sec) compared to the Test (mean $= 219$ sec) (Wilcoxon test: $T^+ = 28$, $N = 7$, $P = 0.008$; Fig. 3) but equally fast to inspect the location in the Post-test (mean $= 47$ sec) as in the Retest (mean $= 99$ sec) ($T^+ = 23$, $N = 7$, $P = 0.156$, two-tailed; Fig. 3).
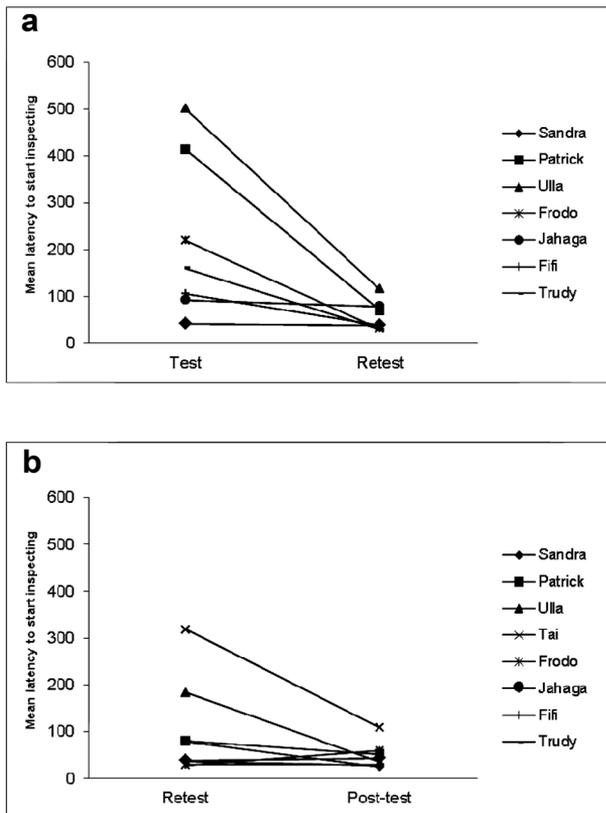
a

b

Fig. 3. Mean latency (sec) to start inspecting locations between Test and Retest trials (**a**) and between Retest and Post-test trials (**b**) when matches occurred for each subject. (a) Values are based on matches that occurred in the Retest (relative to Test trials) and (b) values are based on matches that occurred in the Post-test (relative to Retest trials).

Focusing on those subjects who were rewarded at least once in two different locations ($N = 9$) revealed that latency to inspect was quite irregular over the course of the four blocks during the Test trials (M 1st block $= 202.43 \pm SE$ 51.99; M 2nd block $= 70.63 \pm SE$ 16.6; M 3rd block $= 549.8 \pm SE$ 153.24; M 4th block $= 268.8 \pm SE$ 130.57), thus showing that subjects did not learn the problem through experience.

DISCUSSION

Chimpanzees inspected feeding sites more often and faster in the Retest (compared to the Test) at those locations where they had been rewarded 24 hr earlier. Moreover, their pattern of inspections in the Post-test and the comparable latencies with the Retest ruled out the possibility that the subjects were using olfactory cues to locate the baited location. The lack of a significant difference in the total number of matches during Retest (relative to Test trials) and Post-test (relative to Retest trials) across the four blocks, the irregular latencies observed across blocks during

the test trials and the use of new baiting locations in each new block of trials suggest that chimpanzees were not gradually learning to respond to the problem over consecutive blocks of trials but suggests that chimpanzees remembered previously rewarded locations beginning with the first block of trials. Nevertheless, it is conceivable that chimpanzees used certain cues provided by the experimental set-up (e.g., presence of the experimenter in the observation tower and being released into the enclosure in pairs) to know when to inspect the locations where they had found food 24 hr earlier. However, upon detecting those cues, chimpanzees still had to recall which specific locations they should visit.

These results are consistent with the data from other studies showing that a single exposure is sufficient to encode the location of a food source and remember it until the next day [Garber & Paciulli, 1997; Martin-Ordas & Call, 2011; Menzel, 1999]. In the next experiment we investigated whether chimpanzees would also be able to remember food locations after a minimum retention interval of 3-month.

METHODS

Experiment 2: 3-Month Retention Interval

The purpose of Experiment 2 was to investigate whether chimpanzees could remember the location(s) where they found food during Experiment 1 after a minimum retention interval of 3-month. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates and followed the institutional guidelines and laws for animal research in Germany.

Subjects

The same subjects were tested as in Experiment 1. Subjects were paired with the same partner with whom they had been paired 3-month before, with one exception. When the present experiment took place one member of a pair (Trudi) was injured and was unable to walk properly so that she provided no data when paired with her former partner. Therefore, Trudy was re-tested alone later once her condition had improved.

Procedure

Testing was conducted by the same E as in Experiment 1 in one block of four trials. Before the start of each trial E scattered the chimpanzees' regular morning food throughout the whole enclosure. In all trials subjects had visual access to E standing on the observation platform, except in the Baseline All. Only one pair of subjects was tested per day and each pair always received a single block. The

block consisted of four trials with one trial per day. Trials were 20 min long, and were always administered in the following order:

Baseline All. All chimpanzees, belonging to the same group, were released into their enclosure. E was not present at the observation platform, instead there were four cameras, each focusing on the four former locations. This condition simulated a regular day in the chimpanzees' daily routine.

Baseline Pair. Same as Baseline in Experiment 1.

Test. Same as in Experiment 1. Note that only one location previously used during Experiment 1 and randomly picked by E was baited with a bunch of three bananas.

Post-test. Same as in Experiment 1.

During the 3-month retention interval chimpanzees spent most of their morning time in the indoor enclosure where Experiments 1 and 2 took place.

Predictions

If chimpanzees were capable of remembering where they had found food 3-month earlier, they should re-visit those locations (and do it faster) when paired with the same partner and seeing E standing on the observation platform compared to a baseline period in which those elements were absent. More specifically, we predicted that subjects would perform more inspections and do so faster during the Baseline Pair than during the Baseline All trial (which simulates a regular day in the chimpanzees' daily routine). Once they had inspected the locations in the Baseline Pair and were re-presented with the same elements the next day, we anticipated that they would re-inspect those locations despite the fact that they had not encounter food the day before.

Coding and Analysis

All trials were videotaped and the following variables were scored from video tapes: (1) which formerly rewarded location(s) (from Experiment 1) was inspected by which subject(s); (2) which subject found the baited location during the Test trial; and (3) the latency of inspections to formerly rewarded locations (from Experiment 1). As in Experiment 1, an inspection was operationally defined as a subject being within a 2 m range of a location and visually and/or manually searching that location. To assess inter-observer reliability a second coder scored a random sample of 31% of the trials. Inter-observer reliability was good for inspections at locations (*Cohen's* $k = 0.6619$) and perfect for latency when both coders agreed on the occurrence of an inspection (*Pearson* correlation $r = 1.000$, $P < 0.000$, $N = 10$).

In order to investigate subjects' long-term memory for formerly rewarded location(s), analyses were performed on the following two dependent variables:

Inspections. Since not all subjects in Experiment 1 were rewarded at the same amount of locations and they could be responding to any of the four locations where they have found food 3-month earlier, we could not use the matches/mismatches measure used in Experiment 1. Instead, we calculated the percentage of inspections that they performed during the current experiment out of the number of locations that they had discovered in Experiment 1. Only those locations where the subject had found food 3-month earlier (regardless of whether the subjects had received 1 or 2 exposures to a particular location, i.e,. performed a match) were considered for data analysis. For example, if a subject had found the bananas at each of the four different locations in Experiment 1 and 3-month later inspected only two of those locations, the percentage of inspections would be 50% for this particular subject. However, a subject who had discovered the bananas in three locations during Experiment 1 and 3-month later inspected only one of those locations had a percentage of inspections of 33.33%. All cases in which a subject might have witnessed his/her partner recovering the food were not included in the analyses.

Latency. We scored the time (in sec) a subject took to start inspecting a formerly rewarded location from the moment she/he was released into the enclosure.

Non-parametric exact tests were used in all analyses. Due to the directional nature of our predictions, statistical tests were one-tailed for comparison of subjects' performance between Baseline All and Baseline Pair trial and two-tailed for every other comparison.

RESULTS

There was no evidence that the two chimpanzee groups differed in the percentage of inspections to previously rewarded locations across the four trials (*Mann–Whitney U*-test, all $U \geq 8.500$, $N_{chimp\_group\_A} = 8$, $N_{chimp\_group\_B} = 4$, smallest $P = 0.214$), or their latency to inspect those locations (all $U \geq 13.000$, $N_{chimp\_group\_A} = 8$, $N_{chimp\_group\_B} = 4$, smallest $P = 0.683$). As in Experiment 1, data were therefore collapsed across both groups of chimpanzees.

Inspections

The percentage of inspections significantly differed across trials (*Friedman*'s test: $F = 12.485$, $N = 12$, df $= 3$, $P = 0.003$, Fig. 4). Subjects inspected formerly rewarded locations significantly more often in the Baseline Pair (26.4%) compared to the Baseline All trial (2.1%) (Wilcoxon signed-ranks test: $T^+ = 28$,
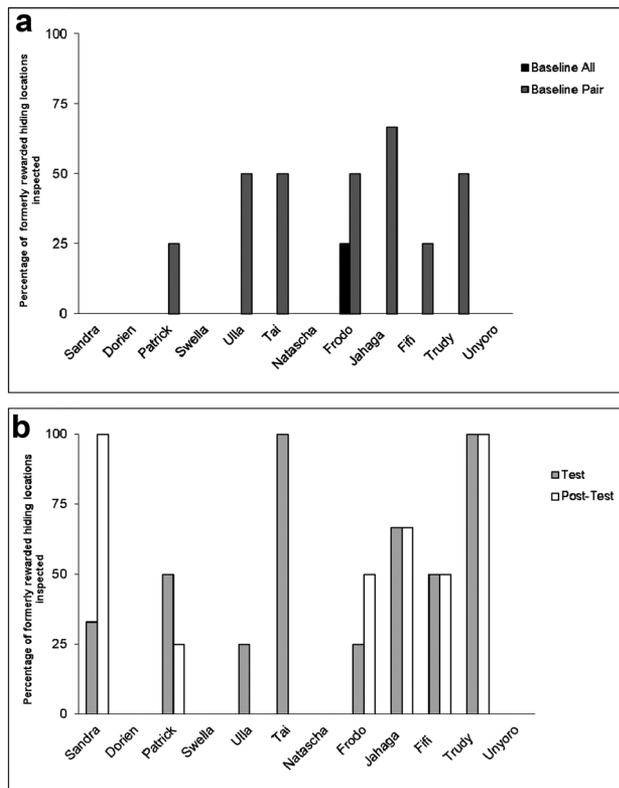
Fig. 4. Percentage of previously rewarded locations (i.e., those where subjects had found food 3 months earlier) by each subject across the Baseline All, Baseline Pair (**a**), Test, and Post-test (**b**). Four out of 12 subjects (i.e., Dorien, Swella, Natascha, and Unyoro) never inspected any location where they found food in the past in any of the four trials (Baseline All, Baseline Pair, Test, and Post-test). The maximum percentage of inspections to previously rewarded locations per trial and per subject was 100%.

$N = 7$, $P = 0.008$). In contrast, subjects inspected previously rewarded locations equally often in the Baseline Pair compared to the Test trials (37.5%) ($T^+ = 23$, $N = 7$, $P = 0.188$) and Post-test trial (32.6%) ($T^+ = 9$, $N = 5$, $P = 0.813$) as well as during the Post-test compared to the Test trials ($T^+ = 9$, $N = 5$, $P = 0.813$).

Latency

Latencies to inspect food locations significantly differed across conditions (Friedman's test, $F = 9.716$, $N = 12$, df $= 3$, $P = 0.014$; Fig. 5). Subjects were significantly faster to start inspecting former locations in the Baseline Pair (mean $= 687$ sec) compared to the Baseline All trial (mean $= 1,137$ sec) (Wilcoxon signed-ranks test: $T^+ = 21$, $N = 6$, $P = 0.016$). In contrast, there was no significant difference between the latencies in the Baseline Pair compared to the Test (mean $= 630$ sec) ($T^+ = 16$, $N = 7$, $P = 0.813$) and Post-test trials (mean $= 737$ sec) ($T^+ = 15$, $N = 7$, $P = 0.938$), as well as during the Post-test compared to the Test trials ($T^+ = 14$, $N = 7$, $P = 1.000$).
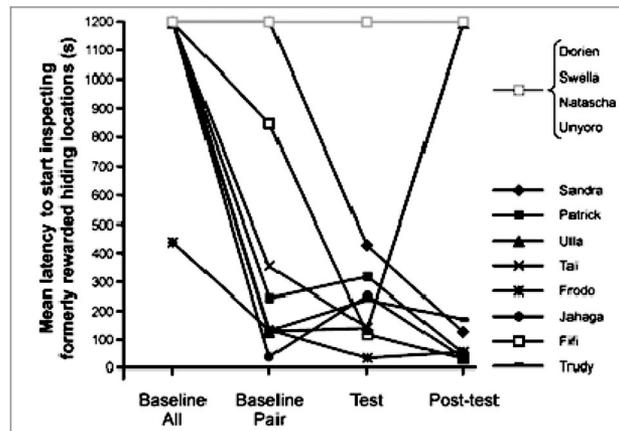

Fig. 5. Mean latency (sec) to start inspecting formerly rewarded locations by each subject. For subjects who did not inspect any formerly rewarded location (Dorien, Swella, Natascha, and Unyoro; represented by a grey line) the latency was set to 1,200 sec, that is the total duration of a trial. In the Baseline All none of the subjects, except Frodo, inspected a formerly rewarded location, thus the latency was set to 1,200 sec.

DISCUSSION

Chimpanzees inspected formerly rewarded locations significantly more and at greater speed when presented the same experimental set-up as 3-month earlier (during Baseline Pair): that is (1) being released with the same partner (from Experiment 1), and (2) seeing E on the observation platform. This means that subjects remembered formerly rewarded locations even without finding food in one of those locations for the past 3-month. During this retention interval, subjects' potential re-checking of the formerly rewarded locations was not assessed, except during the Baseline All trial (which simulated a regular day in the chimpanzees' routine). Therefore, it remains unclear whether subjects used rehearsal to help them recall the location of the hidden food. However, note that if they had continued to inspect the locations during the time between the two test periods, they would have learned that food was not there anymore, and consequently, they should not have visited previously rewarded locations during the Baseline Pair compared to the Baseline All trial. Additionally, this result ruled out olfaction as a potential explanation because there was no food in Baseline Pair. Interestingly, chimpanzees continued to inspect in the Test despite the fact that they had not found food in the previous trial, once again suggesting that memory of the food found 3-month earlier played a role in their responses.

GENERAL DISCUSSION

The results from the two experiments demonstrate that chimpanzees can remember the locations where they had previously found food up to 3-month

earlier. They also can do so after limited exposure to each of these locations.

During Experiment 1, pairs of chimpanzees received a maximum of two-trial learning exposures to each of the four locations. Subjects initially found the baited location by chance (during Test). During the two subsequent trials (Retest and Post-test) their memory for that specific location was assessed. The results from this experiment corroborate other findings showing that primates can remember the location of food rewards after a brief exposure to them and after a 24-hr retention interval [bonobos, chimpanzees, and orangutans: Martin-Ordas & Call, 2011; lexigram-competent chimpanzee: Menzel, 1999] However, Martin-Ordas & Call [2011] used a less ecologically valid experimental setting as compared with the one adopted here. That is, they used a narrow (70 cm × 35 cm) spatial distribution of the locations to be remembered as compared with the more naturalistic approach taken in this study in which the chimpanzees' indoor enclosures have been used. Despite the size difference between the two enclosures (the enclosure of group A measured $430\,m^2$ and group B's measured $175\,m^2$) we did not find any significant differences in the latencies to approach locations between both groups of chimpanzees. Other studies have claimed to have investigated spatial memory in primates after a brief exposure to food locations and over long periods of time [see Garber & Paciulli, 1997; MacDonald, 1994]. Although the retention intervals applied in such studies ranged from 24 to 48 hr, the information retrieval by the subjects was not entirely based on a single trial. That is, in MacDonald [1994] the gorillas (*Gorilla gorilla gorilla*) had experience with all the baited locations (i.e., plastic containers) over a 5-day period prior to the beginning of the experimental phase. Similarly, in Garber & Paciulli [1997] wild capuchin monkeys (*Cebus capucinus*) also received a pre-baiting period during which all the feeding sites (i.e., platforms) were baited twice daily over a period of 3 days prior to the experimental phase. Although the use of such a pre-baiting period, which functioned as a habituation phase to the new locations, is a valid procedure, that period might have enhanced the salience of the hiding locations and therefore facilitated the recovery of the information. In our study we selected locations in the subjects' enclosure that had never been used before as food hiding locations.

In Experiment 2 we tested the same pairs of chimpanzees after a minimum retention interval of 3-month. As soon as subjects faced the same setup as before, they inspected those locations in which they had found food in the past, and at greater speed than during a regular day. These findings suggest that chimpanzees used the cues provided by the experimental set-up (i.e,. being released in pairs with the same partner and seeing the experimenter on the observation platform) as a trigger to inspect the

locations where they had found food in the past. Note that the lack of searches in the Baseline All period (except for one subject) gives further credence to the idea that the cues were responsible for triggering the searches. However, chimpanzees still had to encode and remember which locations they should visit upon detecting the cues signaling the potential presence of food. Thus, the results of this study can be construed as a case of cued recall since the chimpanzees recalled food locations for at least 3 months that were (associated and) triggered by the presence of certain cues of the experimental set-up. The main cues associated with food locations in the present study can be considered social since they consisted of a partner with whom they were released into the enclosure and the experimenter standing on the observation platform. Currently, we cannot determine which of these two cues (or its combination) was more important for chimpanzees. Moreover, it is also unclear whether such social cues were more powerful in triggering memories compared to non-social cues also present in the enclosure (e.g., logs, vegetation). Future studies will be needed to determine the relative importance of each type of cue in triggering the memories about the food locations.

It is conceivable that subjects learned throughout the four blocks that certain cues (e.g., being released into the enclosure in pairs) were associated with the presence of food in particular locations. However, they would still have to remember the correct locations where they had found food previously. Furthermore, recall that in Experiment 1 the target location changed in every block of four trials and there was no evidence of learning across blocks (i.e., no decrease in latency to inspect locations was found in the Test trials across the four blocks and no significant difference in the total number of matches across the four blocks). Although one could argue that odor cues emanating from the bananas may have been used by the subjects to find the baited locations, two arguments make this possibility unlikely. First, if odor cues had guided subjects' searches, they should have inspected the baited locations in the Test just as quickly as they did in the Retest of Experiment 1. Second, subjects should not have inspected any locations in the Baseline Pair of Experiment 2 because no bananas were present in the enclosure during that time.

Being able to remember food locations over periods longer than 24 hr and after only limited exposure to them is an ecologically relevant cognitive ability for primates living in tropical forests in which the occurrence of highly nutritious food resources (e.g., fruits, flowers, and young leaves) is patchy and follows an irregular distribution in space and time [Milton, 1981]. Therefore, we find the lack of captive studies addressing long-term memory for food locations after a short exposure to them surprising (but see [Martin-Ordas & Call, 2011; Menzel, 1999,

2010]). The research studies which are thematically closer to this question have investigated memory for non-spatial information over extended periods of time [e.g., Beran et al., 2000; Patterson & Tzeng, 1979]. For example, Beran et al. [2000] reported that a female chimpanzee was able to remember the association between lexigrams and words after a period of 20 years during which she was not re-exposed to the lexigrams. However, until the chimpanzee could learn the correct associations many trials had to be administered.

In sum, these results corroborate and extend findings from other studies on spatial memory in primates by combining one to two exposures to each of the four food locations with retention intervals ranging from 24 hr up to 3-month. Future research should compare the subjects' inspections of test locations to other control locations in order to better differentiate between effects of memory and cued search activity in the subjects' performances. Moreover, one other important direction for future research will be to test other primate species, using the same experimental design applied in the current study, in order to provide insights about the evolution of spatial memory capabilities in primates. The reported results also suggest that food-hoarding animals, corvids in particular, do not seem to be the only animals with such extraordinary spatial memory capability. Perhaps corvids, great apes, and other primates have evolved the same ability independently, by way of convergent evolution [Emery & Clayton, 2004]. Nevertheless, comparative studies between corvids and other primate taxa are needed before more definitive claims can be made.

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