

Long-Term Spatial Memory and Learning Set Formation in Captive Capuchin Monkeys (*Cebus libidinosus* = *Sapajus cay*)

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Abstract Researchers have long suspected that nonhuman primates have long-term spatial memory for locating food. However, few empirical studies have assessed spatial memory for a period longer than 1 day in nonhuman primates in a foraging context. We used a modified version of the radial maze to test long-term memory for periods of 2 days or longer in two groups of *Cebus libidinosus* = *Sapajus cay* ($N=10$; $N=6$) in captivity (environment completely human constructed) and semicaptivity (relatively natural environment with few human-made structures) at La Plata Zoo and Botanical Park, Buenos Aires, Argentina, between 2007 and 2010. The experimental design included a set of three accessible baited feeders interspersed among three nonaccessible baited feeders. We tested monkeys in one initial exposure period, four periods of long-term memory (2 days, 76 days, 76+2 days, and 4 months of delay), and one period of inversion of the experimental set location. We used the latter to analyze the monkeys' abilities to develop learning sets. Captive subjects appeared to remember sites with accessible and nonaccessible food for periods of 2 days, 76 days, and 4 months, and used learning sets to reduce relearning times when exposed to a change in the learned

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locations. Although semicaptive subjects also appeared to remember sites with accessible and nonaccessible food, their performance was less accurate. We conclude that capuchins used spatial memory to improve their foraging efficiency.

Keywords Captivity · Long-term delays · Memory consolidation · Modified radial maze · Semicaptivity · Zoos

Introduction

Researchers have long suspected that nonhuman primates have long-term spatial memory for locating food (Milton 1981, 1988), but few empirical studies have assessed spatial memory for a period longer than 1 day in a foraging context (Cunningham 2003; Janmaat and Chancellor 2010; Mendes and Call 2014). Long-term memory should be useful in environments where the location of fruit is stable over long periods, whereas medium-term memory (several days) will suffice when fruiting renewal rates are moderately rapid (1–2 days) (Corlett 2011). In the case of South American primates, the extreme diversity of plant foods in tropical forests and the patchy manner in which they are distributed in space and time could have been a major selective force in the development of long-term memory (Milton 1981, 1988). This extreme diversity offers a complex environment to frugivores (Suarez 2003) because the number of fruiting species will be high but most individual tree species (that usually fruit at the same time) have very low densities.

Although individual fruit trees have a stable location, tree species vary across time in their seasons of peak fruiting and maturation rates (Milton 1981). Spatial long-term memory in big ranging areas might not be useful for primates that feed on ephemeral fruiting trees, as their foraging environment might change too rapidly (what is fruiting today will be not fruiting in a few days). To exploit resources optimally, primates may need to combine long-term memory of fruiting trees with the ability to remember the phenological relations between those trees (the ability to learn that a set of trees of the same species will probably fruit all together; Janmaat *et al.* 2012), i.e., the ability to form learning sets. Combining these two abilities will allow primates to learn more quickly when they face the common situation where one spatially fixed set of resources is replaced by a new set of spatially fixed resources.

While memory is considered a permanent record of an experience, the process of acquiring new information and storing it as long-term memories is called consolidation of memory (Lezak 1995). Bailey *et al.* (1996) consider long-term memory as a period ranging from days to the lifetime of an animal. Several experiments in the wild and captivity have investigated different aspects of spatial memory in nonhuman primates over periods up to 24 h, and conclude that nonhuman primates remember the spatial location of resources (Dolins 2009; Garber and Dolins 1996; Garber and Pacuilli 1997; Janson 1998; MacDonald *et al.* 1994; Menzel and Juno 1985), the location of food sites depleted by the primate itself or by groupmates (Gibeault and MacDonald 2000; MacDonald 1994; MacDonald and Agnes 1999; Roberts *et al.* 1993), the spatial locations and type of food items (Scheumann and Call 2006), and the spatial locations and quantity of food in each site (Janson 1998, 2007), distinguishing between different events in which the same food items were hidden in different places at different times (Martin-Ordas and Call 2011).

To our knowledge, only three studies have tested memory of nonhuman primates for periods longer than 2 days. Cunningham (2003) tested three groups of captive white-faced saki monkeys (*Pithecia pithecia*) and a single isolated adult female for their ability to remember the locations of baited and empty sites over delays ranging from 1 to 120 days. Her results indicated that these delays did not significantly affect accuracy and that memory in saki monkeys persisted after a delay of 120 days. Janmaat and Chancellor (2010) compared the exploration of a new area by gray-cheeked mangabeys (*Lophocebus albigena johnstonii*) with ranging and foraging behavior in their old area, after a group split. Controlling for weather variables, they found that mangabeys moved longer daily travel distances, explored more area per day, and had larger group spreads in the new area compared to the old area. The increase in search enabled the monkeys to counteract their lack of knowledge of food locations in the new area, as the efficiency in finding fruit in general did not differ between the old and new areas. Finally, Mendes and Call (2014) tested pairs of chimpanzees on their ability to recall food locations after 24 h, after 4 days, and after 3 months. The chimpanzees displayed accurate recall for the locations in which they previously found food at each time interval.

Studies of short-term spatial memory often isolate subjects from their group (D'Amato and Buckiewicz 1980; Dolins 2009; Fragaszy *et al.* 2003; Ludvig *et al.* 2003; MacDonald *et al.* 1994; Platt *et al.* 1996; Poti 2000; Poti *et al.* 2005; Rosengart and Fragaszy 2003; Spinozzi *et al.* 2002; Tavares and Tomaz 2002). Although this approach has the virtue of focusing on individual-level psychological processes, it is very unlike the natural environment where the behavior evolved. Studies testing captive primate subjects in a group context are rare and none have assessed spatial memory for a period longer than 24 h (Menzel and Juno 1985: *Saguinus fuscicollis*; Gibeault and MacDonald 2000: *Gorilla gorilla gorilla*; Scheumann and Call 2006: *Pongo abelii*, *Nomascus gabriellae*).

In addition to spatial memory of feeding sites, it would be useful for fruit-eating primates to be able to form learning sets about ensembles of feeding sites, such as all the fruiting individuals of a given species, which tend to mature fruit at the same time (Milton 1981). Conventional behaviorist trial and error learning theory (Hull 1930) assumed that all learning was made on a trial and error basis, in contrast to the gestalt theory that learning was achieved suddenly or insightfully (Harlow 1949). To integrate trial and error learning and gestalt learning, Harlow (1949) proposed the theory of learning sets: when an animal learns a new type of problem, it uses trial and error in the beginning, but as experience increases, the animal replaces trial and error with an eventual insight into the situation, allowing it to redirect its behavior and learn faster in a novel situation in which a previously learned pattern could be identified. Thus trial and error learning theory and insight learning theory are merely two phases of a learning model: an initial phase and an ending phase (Harlow 1949).

We here investigated the ability of captive and semicaptive capuchins to recall the location of feeding sites across periods of days to months, and to form a learning set about the experimental design that includes both productive and nonproductive feeding sites. We define long-term memory as the ability of subjects to retain information for 2 days or longer after the stimulus was removed. We test whether capuchins show evidence of having an expectation about the experimental design after repeated exposures to the same feeding array, by reversing the positions of rewarded and nonrewarded sites. To our knowledge, there are no published studies of the ability of capuchins to form learning sets of spatial memory.

We used a quasi-experimental design that enabled us to test monkeys' ability to generate spatial memory in a fixed environment, within their normal group context. We exposed the subjects to the problem of where food is accessible and where it is not. We predicted spontaneous organization of behavior in the presence of nonsystematic training, measured as a decrease in the number of incorrect choices during search. If capuchins were able to remember locations of accessible and nonaccessible feeders for a period of 2 days, then they should progressively avoid visiting nonaccessible feeders as they spend more time interacting with the experimental design. If they were able to store this information in their long-term memory, then after periods of 76 days or 4 months without interacting with the experimental design their performance should still be significantly above that of naïve monkeys. Finally, if monkeys were capable of integrating the information about locations that they have learned (learning sets formation), then they should relearn a new spatial situation faster than they did at the beginning of the experimental procedure.

Methods

Subjects

We tested two groups of capuchin monkeys: Cage Group ($N=10$) housed in a cage constructed of concrete and wire mesh and Island Group ($N=6$) housed on an artificial island; both groups live at La Plata Zoo and Botanical Park in Buenos Aires, Argentina. We recognized all group members by distinct combinations of body size, color pattern, and facial marks. All of the adults arrived at the zoo when they were juveniles and all current juveniles were captive-born with known birth dates in the zoo's records. Cage Group was composed of three adults (≥ 6 yr old; two males, one female), six juveniles 1–5 yr old (four males, two females), and one infant. Island Group was composed of three adults (one male, two females), one male juvenile, and two infants. The subjects participated in enrichment programs with their caretakers but they had not participated in memory experiments prior to the present one.

We fed groups once a day with a complex diet consisting of vegetables, fruits, eggs, cereals, and cooked chicken pieces. Island Group also had access to naturally occurring food (arthropods, small vertebrates, and nuts). Food provided during the experiment was integrated into their normal diet to prevent subjects gaining weight.

Experimental Design and Materials

We conducted the experiment in the capuchin exhibits between 2007 and 2010. We divided the home cage (14.8 m \times 4 m) where Cage Group was housed into two indoor enclosures, A and B (each 6 m \times 4 m) separated by a sliding door, and two sleeping enclosures of 2.8 m \times 4 m, one next to enclosure A and the other next to enclosure B. Testing always took place in enclosure A, where monkeys were accustomed to receiving food. The artificial island (40 m \times 110 m) where Island Group was housed had a dense forest and various species of birds living with the monkeys.

We based our experimental design on a modified version of the designs developed by Tarou and Maple (2000) and Ludvig *et al.* (2003). This design served to encourage

monkeys to interact freely with food locations in a three-dimensional space, considering their natural foraging behavior (Sánchez Vazquez *et al.* 2011). Monkeys moved around collecting food from a set of three accessible baited feeders interspersed among three nonaccessible baited feeders, with one accessible feeder always next to one nonaccessible feeder (Fig. 1). We made feeders of polyvinyl chloride and tied them securely with a rope on a substrate. Capuchins could insert their hands into a hole on the top of the accessible feeders to extract the food item. Nonaccessible feeders had a recessed nonvisible conical plastic barrier inside that made it impossible to gain access to food (Fig. 2). The only way the subjects could check if the feeder had accessible food was by inserting their hands or looking through the hole of the feeder.

In Cage Group, we hung feeders from the wire mesh of the cage at 2-m intervals. On the island, we hung feeders from tree trunks, separated by 3–4 m. Many external landmarks (visual or olfactory cues that can be used as guides or beacons; Garber 2000) were available for the monkeys, but the feeders were identical in shape (cylindrical), size (14 cm tall and 11 cm diameter), and color (opaque white).

All the feeders had the same food inside to avoid providing olfactory differences between them, and the pieces of food were not visible. We baited feeders with cornflakes that were part of the daily diet at the zoo. We baited both accessible and nonaccessible feeders with food to force the monkeys to ignore food-associated sensory information and rely solely on memory. This situation is a more stringent test of memory ability compared to when feeders are baited or empty because monkeys needed to remember not only where to find food but also specifically where food was accessible or not. Although the grill in the inaccessible containers might have reduced air flow and thus food-associated odors, subjects had to get very close to the feeders in any case to check if they were accessible or not, and if accessible, if there was any food remaining. The fact that monkeys often visited inaccessible feeders and tried to remove the grill indicates that the subjects were aware of the presence of food inside the nonaccessible containers.

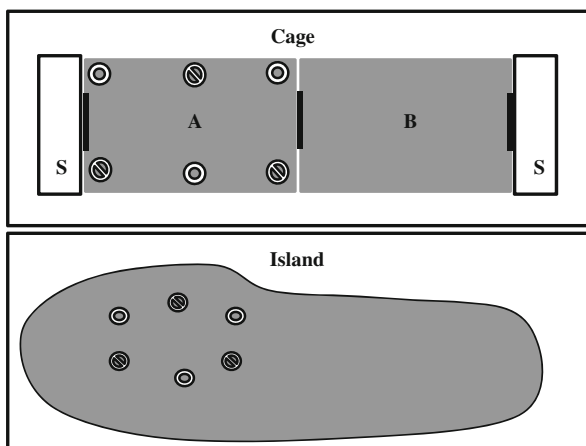


Fig. 1 Spatial location of feeders during experimental periods of long-term memory in capuchins (*Cebus libidinosus* = *Sapajus cay*) in Cage Group and Island Group at La Plata Zoo and Botanical Park, Buenos Aires, Argentina (2007–2010). Empty circles = accessible feeders; crossed circles = inaccessible feeders. A and B = enclosures; S = sleeping enclosures; black lines = doors.



Fig. 2 Accessible (left) and nonaccessible (right) feeders (from Tujague and Lahitte 2013: Experimental study of one group of *Cebus libidinosus* = *Sapajus cay* at La Plata Zoo and Botanical Park, Buenos Aires, Argentina, between 2007 and 2008).

Monkeys were food deprived for ≥ 20 h before the experiment but they had access to water *ad libitum*. Two assistants installed the experimental setup and took it out each time the experiment ended. For Cage Group, we baited all the feeders and installed them in enclosure A while the subjects were kept in enclosure B. After the baiting procedure, we lifted the sliding door and allowed the entire group to enter enclosure A. For Island Group, the installation of the previously baited feeders occurred in the presence of the subjects, as the monkeys could not be isolated. Testing occurred in the morning before the daily feeding of the subjects.

We considered each case in which the monkeys were initially exposed to the experimental design as an experimental session (Sánchez Vazquez *et al.* 2011). We defined a visit as any time a monkey reached into a feeder (accessible or not), looked inside, displayed exploratory behaviors, or retrieved food from a feeder, and we defined exploration as each time monkeys put their hands and/or feet on the feeder, pulling feeders up and down, hitting them, or trying to open the feeders with their mouths (Sánchez Vazquez *et al.* 2011).

We tested monkeys as follows:

- 1) Initial exposure period: To habituate the monkeys to the experimental environment we installed two baited accessible feeders and let the subjects interact with them until all members of a group had used a feeder to collect food. We ended the initial exposure period when each monkey had retrieved food from a feeder at least once. This was 5 days after the first interaction for Cage Group and only 1 day for Island Group. Subjects began to search the feeders as soon as they were introduced into the experimental enclosure. The location used for the two accessible feeders during this period was not the same used in the experiment so that the monkeys could not transfer any knowledge about food location to the following experimental periods.
- 2) 2-day long-term memory (2 days): This included 15 sessions of exposure to the experimental design of the six feeders described previously for Cage Group and 12 sessions for Island Group. Sessions were separated by 48 h.

- 3) 76-day long-term memory (*76 days*): After a period of 76 days without interacting with the experimental design, we installed the experimental design again in the enclosure and collected the same data as in *2 days*, but for a single session.
- 4) 2-day long-term memory after 76 days (*76+2 days*): At 48 h after the *76 days* experiment, we repeated the same scheme of successive sessions as in *2 days*. We performed 15 sessions for Cage Group and 9 for Island Group.
- 5) 4-month long-term memory (*4 months*): After a period of 4 months without interacting with the experimental design, we installed the experimental design again in the enclosure and collected the same data as in *76 days*.

The spatial position of accessible and nonaccessible feeders remained stable during periods 2–5.

- 6) Inverse experiment (*inverse*): At 48 h after the 4-month experiment we reversed the treatment (accessible or nonaccessible) of each feeder, keeping the location constant. We performed 15 experimental sessions for Cage Group and 10 sessions for Island Group. This period functioned as a transfer or control period, in which subjects were exposed to a reverse situation after training. The difference in the number of sessions for each group during experimental periods was due to climate conditions limiting access to the island.

M. P. Tujague recorded visits to accessible and nonaccessible feeders using focal animal sampling for *2 days* for Cage Group and focal group sampling for the rest of the periods for both groups (Altmann 1974). We used focal animal sampling for *2 days* for Cage Group because it was difficult to recognize all the individuals during the first experimental period. In later experiments, the observer could identify and record data on all group members concurrently. The change of sampling methods did not affect the efficiency of data collection or the comparisons between experiments because the number of visits recorded for the first experimental period was nearly the same as that obtained during the following periods. During the sessions, if monkeys removed the food from an accessible feeder it was considered a correct visit but if the monkeys reached into a nonaccessible feeder or tried to remove food from it, we considered this an incorrect visit. Each experimental session finished when at least one of the accessible feeders was empty.

Data Analysis

During each session we recorded 1) total number of correct visits and incorrect visits per subject and 2) session duration. We calculated the spatial memory performance index, modified from Ludvig *et al.* 2003 as $(\text{correct visits} - \text{incorrect visits}) / (\text{correct visits} + \text{incorrect visits})$. To ensure that choices were guided by memory and not by observing another monkey at the site, we excluded from analysis visits in which any subject reached into a feeder (accessible or not) while another individual was eating, exploring, or resting at the same feeder. However, we included cases in which a monkey visited a feeder previously (but not currently) used by another monkey. This criterion allows for the fact that imitative learning could affect the behavior of the subject after other individuals had left the baited feeder. Imitation underlies memory formation in a group context. If imitation occurs after a significant delay (≥ 24 h),

memory is also involved (Meltzoff and Moore 1994). Our aim was not to exclude social influences on learning, but to ensure that any such effect was guided by memory rather than immediate social attraction. Because such socially mediated memories must also incorporate the spatial location of the feeder, we consider them to be evidence of spatial memory. In any case, social influences on individual choice of feeders should not create a pattern indicating spatial memory when spatial memory is in fact absent.

The spatial memory performance index can take values between 1 and -1 , with values >0 implying memory consolidation, reaching a perfect use of memory when the value is 1. A value <0 indicates that subjects made more incorrect than correct visits during sessions and might reveal the operation of other processes, e.g., bias, competition between foragers, as well as durable memory during the reversal experiment. We expected four possible patterns of the performance index over time, depending on the presence or absence of long-term memory over 2 days or 4 months (Fig. 3a–d). Performance could be exact (index = 1, Fig. 3a) or inexact ($0 < \text{index} < 1$, Fig. 3b, c). In the absence of 2-day memory, the index should vary around 0, with some negative values due to sampling effects (Fig. 3d). As subjects had no information about the locations of feeders at the beginning of the experiment, we also expected the monkeys to visit both types of feeders (accessible and nonaccessible) equally for the first session, but as learning and consolidation of memory took place, we expected an increase in visits to accessible feeders, leading to higher spatial memory performance index values in later sessions.

We analyzed group performance with a generalized linear mixed model (GLMM) in R (R Development Core Team 2011) using the lmer package. We treated focal animal identity as a random effect, with session, experimental period (2 days, 76+2 days, and inverse), and subject age and sex as fixed effects. We

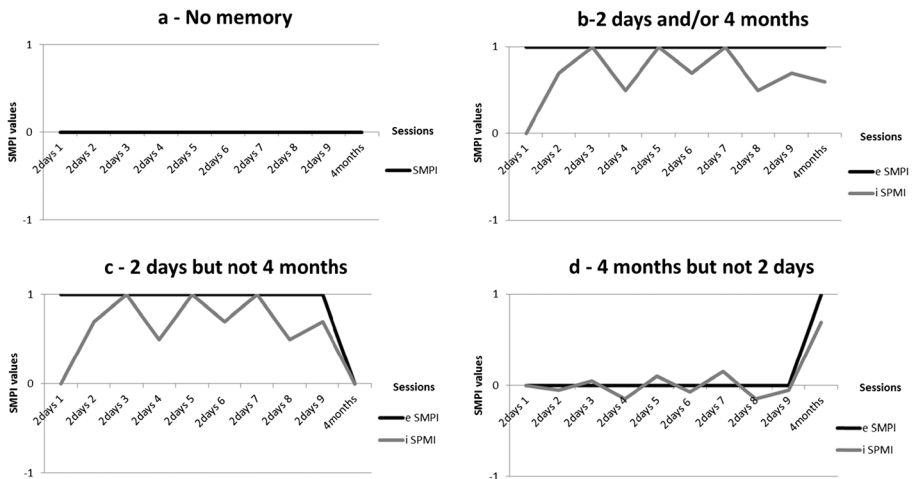


Fig. 3 Expected patterns of efficiency of *Cebus libidinosus* = *Sapajus cay* during each experimental period as a function of the presence of 2-day or 4-month long-term memory at La Plata Zoo and Botanical Park, Buenos Aires, Argentina, between 2007 and 2010. **(a)** No presence of memory. **(b)** With the presence of both long-term memories. **(c)** With 2-day but no presence of 4-month long-term memory. **(d)** With 4-month but no presence of 2-day long-term memory. Black lines represent the pattern obtained with a perfect performance ($e = \text{exact}$). Gray lines represent the pattern obtained with a nonperfect performance ($i = \text{inexact}$). 2 days = 2-day long-term memory; 4 months = 4-month long-term memory; SMPI = spatial memory performance index.

tested for sex and age effects because differences in spatial memory performance by sex and age have been reported for primates. Older individuals make significantly more spatial memory errors (Bachevalier *et al.* 1991; Moffat *et al.* 2001), and females commit significantly fewer memory errors and take significantly less time to reach criterion memory performances than males (Duff and Hampson 2001).

We chose the model with the lowest Akaike's information criterion (AIC) as the best fit model. To compare specific sessions of the same experimental period or sessions between periods we used Student's paired two samples *t*-test (controlling for subject identity) with a 0.05 level of significance. We used one-tailed Student's *t*-tests throughout because we assume that monkeys learn by interacting with the experimental design and thus should show higher spatial memory performance index over time. We calculated the effect size using Cohen's *d* (Morales Vallejo 2012; Nakagawa and Cuthill 2007) for each Student's *t*-test. Cohen (1988 in Nakagawa and Cuthill 2007) suggested conventional values as reference points to interpret *d* values: low ($d=0.2$ or lower), moderate ($d=0.5$), and high ($d=0.8$ or highest).

Ethical Note

All research reported in this article adhered to the International Primatological Society and the American Society of Primatologists Principles for the Ethical treatment of Non-human Primates and complied with the protocols approved by the Animal Care and Use Committee. It also adhered to the legal requirements of Argentina and was approved by La Plata Zoo and Botanical Park.

Results

For Cage Group, the mean duration of sessions for each experimental period was 62.46 min \pm SD 15.2 (2 days, $N=15$ sessions); 43.6 min \pm SD 10.7 (76+2 days, $N=15$ sessions); and 43.7 min \pm SD 8.7 (*inverse*, $N=15$ sessions). For Island Group, corresponding means were 43.7 min \pm SD 13.1 (2 days, $N=12$ sessions); 27.9 min \pm SD 9.3 (76+2 days, $N=9$ sessions); and 28.6 min \pm SD 6.7 (*inverse*, $N=10$ sessions).

Cage Group

The best fit model included experimental period, session, and the interaction of period*session (Electronic Supplementary Material [ESM] S1). Although mean performance index was higher in 76+2 days than 2 days, performance increased only weakly with session number within each of these two periods; in contrast, the mean performance index was lower in *inverse*, but increased markedly during the last five sessions of this experiment (Table I, Fig. 4; GLMM, interaction of period*session, $\text{Chiq} = 6.07$, $\text{df}=2$, $P=0.048$, $\text{AIC}=311.25$, N observations = 404). We found no differences between individuals of different sex (GLMM, $\text{Chiq}=0.0016$, $\text{df}=1$, $P=0.97$, $\text{AIC}=313.25$, N observations=404) or age categories (GLMM, $\text{Chiq}=1.72$, $\text{df}=1$, $P=0.19$, $\text{AIC}=311.53$, N observations=404).

Table I Mean spatial memory performance index±standard deviations (SD) and 95 % confidence intervals (CI) per session for each experimental period for Cage Group (*Cebus libidinosus* = *Sapajus cay*) at La Plata Zoo and Botanical Park, Buenos Aires, Argentina, between 2007 and 2010

Period	2 days	76+2 days	Inv.
Sessions			
1	0.43±0.48 CI: 0.06–0.8	0.57±0.17 CI: 0.43–0.7	0.1±0.17 CI: –0.02 to 0.24
2	0.12±0.56 CI: –0.3 to 0.5	0.65±0.2 CI: 0.48–0.82	0.45±0.25 CI: 0.24–0.65
3	0.4±0.3 CI: 0.18–0.52	0.58±0.19 CI: 0.43–0.73	0.23±0.28 CI: 0.02–0.45
4	0.68±0.2 CI: 0.52–0.84	0.7±0.21 CI: 0.61–0.94	0.37±0.34 CI: 0.1–0.63
5	0.34±0.43 CI: 0.007–0.67	0.56±0.3 CI: 0.3–0.82	0.41±0.21 CI: 0.24–0.57
6	0.45±0.46 CI: 0.09–0.8	0.79±0.3 CI: 0.53–1.04	0.38±0.3 CI: 0.15–0.62
7	0.33±0.06 CI: 0.61–0.35	0.75±0.26 CI: 0.55–0.95	0.76±0.36 CI: 0.48–1.04
8	0.57±0.64 CI: 1.00–0.	0.57±0.29 CI: 0.34–0.79	0.2±0.42 CI: –0.09 to 0.5
9	0.68±0.2 CI: 0.54–0.83	0.57±0.32 CI: 0.32–0.82	0.59±0.34 CI: 0.32–0.86
10	0.49±0.35 CI: 0.24–0.74	0.85±0.18 CI: 0.71–0.99	0.3±0.41 CI: –0.01 to 0.62
11	0.72±0.35 CI: 0.47–0.97	0.76±0.24 CI: 0.58–0.95	0.63±0.3 CI: 0.37–0.89
12	0.67±0.39 CI: 0.37–0.97	0.92±0.15 CI: 0.8–1.00	0.79±0.15 CI: 0.67–0.92
13	0.5±0.37 CI: 0.25–0.84	0.81±0.19 CI: 0.6–0.96	0.65±0.35 CI: 0.35–0.95
14	0.41±0.53 CI: –0.03 to 0.85	0.81±0.41 CI: 0.49–1.12	0.61±0.32 CI: 0.34–0.89
15	0.21±0.6 CI: –0.29 to 0.71	0.95±0.08 CI: 0.89–1.00	0.73±0.26 CI: 0.5–0.95

2 days and 76+2 days=first and second 2 days long-term memory period; Inv. = inverse period

The variance associated with individual identity (random effect) was 0.005, representing 3.78 % of the total variance of the performance index in the model, which suggests that undescribed differences between subjects were not important in explaining use of memory in this task for Cage Group. The first and last sessions in 2 days did not differ in mean performance index (Table II). The negative value of d (Table II) indicates that mean value of session 15 was lower than that of session 1, but both values of the index were significantly above 0, indicating memory formation. This suggests that subjects could learn and remember the positions of accessible feeders by interacting with the experimental design for less than an hour. We found significant increases in mean performance between the first and last sessions of the 76+2 days experiment, showing an increase in memory consolidation; the last session had an index value close to 1 (perfect performance). The effect size of this comparison was high (Table II). We also found significant differences in mean performance index between the first and last inverse sessions, suggesting that subjects decreased their performance relative to their near-perfect values at the end of 76+2 days, but eventually recovered it at the end of the inverse period, reaching a high index value. The effect size for this comparison was also high (Table II). Taking all of these comparisons into account, it seems that the subjects of Cage Group were able to develop a consolidated memory only in the last sessions of 76+2 days and inverse, whereas they had had lower spatial memory performance index values in the 2 days experiment.

During the 76 days experiment, all of the subjects showed high index values above 0, with a total of 87 correct visits and 27 incorrect visits. The difference between the

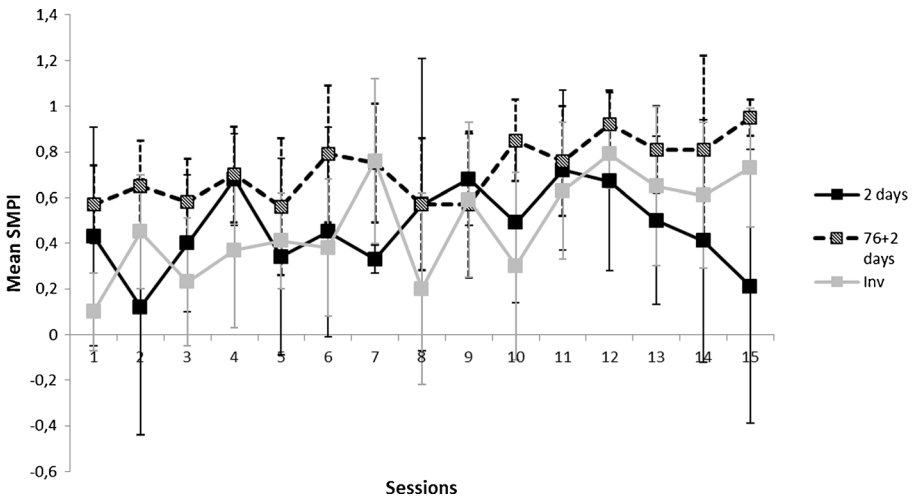


Fig. 4 Mean spatial memory performance index (SMPI)±standard deviations per session for each experimental period for Cage Group (*Cebus libidinosus* = *Sapajus cay*) at La Plata Zoo and Botanical Park, Buenos Aires, Argentina, between 2007 and 2010. 2 days and 76+2 days = first and second experimental period of 2-day long-term memory; Inv. = inverse experiment.

mean index values of the last 2 days and the 76 days sessions was not significant (Table II). Although low spatial memory performance index values during the last session of 2 days might have been an anomaly, it appears that the monkeys may have shown some consolidation of memory during the 76-day absence of experiments. Performance became more stable and higher during the 76+2 days experiment.

Table II Comparison between sessions of the same and different experimental periods for Cage Group (*Cebus libidinosus*=*Sapajus cay*) at La Plata Zoo and Botanical Park, Buenos Aires, Argentina, between 2007 and 2010

CG sessions	t-value	P-value	CI 95 %	Mean±SD	Cohen’s d and N
S1–S15 2 days	0.63	0.272	−0.4 to 0.7	S1=0.43±0.48 S15=0.21±0.60	−0.25; N=17
S1–S15 76+2 days	7.707	0.000*	−0.5 to (−0.27)	S1=0.57±0.17 S15=0.95±0.08	4.75; N=20
S1–S15 Inv.	−6.135	0.000*	−0.85 to (−0.38)	S1=0.1±0.18 S15=0.73±0.26	2.43; N=20
S15 2 days–76 days	1.828	0.054	−0.83 to 0.1	2 days=0.21±0.60 76 days=0.57±0.17	2.11; N=18
S15 76+2 days–4 months	1.983	0.0415*	−0.03 to 0.45	76+2 days=0.95±0.08 4 months=0.75±0.35	−0.57; N=20

CG=Cage Group; S1– S15=sessions; 2 days and 76+2 days=first and second 2-day long-term memory period; Inv. = inverse period; 76 days and 4 months=76-day and 4-month long-term memory period; t-value and P-value=results from Student’s paired two samples t-test; *significant using α : 0.05; CI 95 %=confidence interval for mean difference; SD=standard deviation; Cohen’s d=effect size value

Thus, the monkeys performed better the second time they were exposed to the design for consecutive sessions (see Table I and Fig. 4 for details).

During the 4 months experiment all the subjects showed performance indexes above 0 with a total of 55 correct visits and 11 incorrect visits. We found significant differences between the mean index values of the last session of the 76+2 days experiment and the sole 4 months session, although both values were very high and close to 1 (Table II). The effect size for this comparison was moderate and negative, reflecting both an almost perfect performance in the last session of the 76+2 days experiment and an apparent loss of memory of the task in the intervening 4 months (Table II).

Island Group

The best fit model for Island Group included experimental period, session, the interaction of period*session, and sex (ESM S2). Mean performance index per session within each experimental period did not increase with session number in 2 days and 76+2 days, but did in *inverse* (Table III, Fig. 5; GLMM, interaction of period*session, $\text{Chi}^2 = 8.66$, $\text{df} = 2$, $P = 0.013$, $\text{AIC} = 161.93$, N observations = 166). Females performed better on average than males across all the experimental periods (GLMM, $\text{Chi}^2 = 16.29$, $\text{df} = 1$, $P < 0.0001$). We found no significant differences between age categories (GLMM, $\text{Chi}^2 = 0.71$, $\text{df} = 1$, $P = 0.40$, $\text{AIC} = 163.22$, N observations = 166).

The variance associated with individual identity (random effect) was 0.038, representing 19.64 % of the total variance of the model. Thus, differences between subjects other than sex and age might have been important in explaining individual levels of performance. In comparison with Cage Group, Island Group had lower

Table III Mean spatial memory performance index \pm standard deviations (SD) and 95 % confidence intervals (CI) per session for each experimental period for Island Group (*Cebus libidinosus*=*Sapajus cay*) at La Plata Zoo and Botanical Park, Buenos Aires, Argentina, between 2007 and 2010

Period	2 days	76+2 days	Inv.
Sessions			
1	0.53 \pm 0.28 CI: 0.23 to 0.83	0.25 \pm 0.52 CI: -0.39 to 0.9	-0.18 \pm 0.35 CI: -0.62 to 0.25
2	0.017 \pm 0.59 CI: -0.6 to 0.63	0.12 \pm 0.24 CI: -0.18 to 0.42	0.29 \pm 0.53 CI: -0.36 to 0.95
3	0.46 \pm 0.35 CI: 0.09 to 0.84	0.28 \pm 0.28 CI: -0.07 to 0.64	0.19 \pm 0.26 CI: -0.12 to 0.51
4	0.45 \pm 0.31 CI: 0.12 to 0.79	0.32 \pm 0.28 CI: -0.02 to 0.67	0.31 \pm 0.19 CI: 0.08 to 0.5
5	0.35 \pm 0.47 CI: -0.14 to 0.84	0.28 \pm 0.59 CI: -0.45 to 1.01	0.47 \pm 0.38 CI: -0.003 to 0.94
6	0.01 \pm 0.5 CI: -0.56 to 0.59	0.1 \pm 0.39 CI: -0.39 to 0.59	0.49 \pm 0.35 CI: 0.05 to 0.92
7	0.48 \pm 0.53 CI: -0.17 to 1.14	0.2 \pm 0.24 CI: -0.08 to 0.53	0.49 \pm 0.31 CI: 0.1 to 0.8
8	0.46 \pm 0.52 CI: -0.08 to 1.00	0.52 \pm 0.37 CI: 0.05 to 0.98	0.74 \pm 0.35 CI: 0.3 to 1.12
9	0.001 \pm 0.63 CI: -0.66 to 0.66	0.24 \pm 0.49 CI: -0.37 to 0.86	0.78 \pm 0.49 CI: 0.16 to 1.3
10	0.4 \pm 0.54 CI: -0.16 to 0.97		0.3 \pm 0.41 CI: -0.2 to 0.81
11	0.47 \pm 0.3 CI: 0.15 to 0.8		
12	0.36 \pm 0.34 CI: -0.003 to 0.73		

2 days and 76+2 days=first and second 2-day long-term memory period; Inv. = inverse period

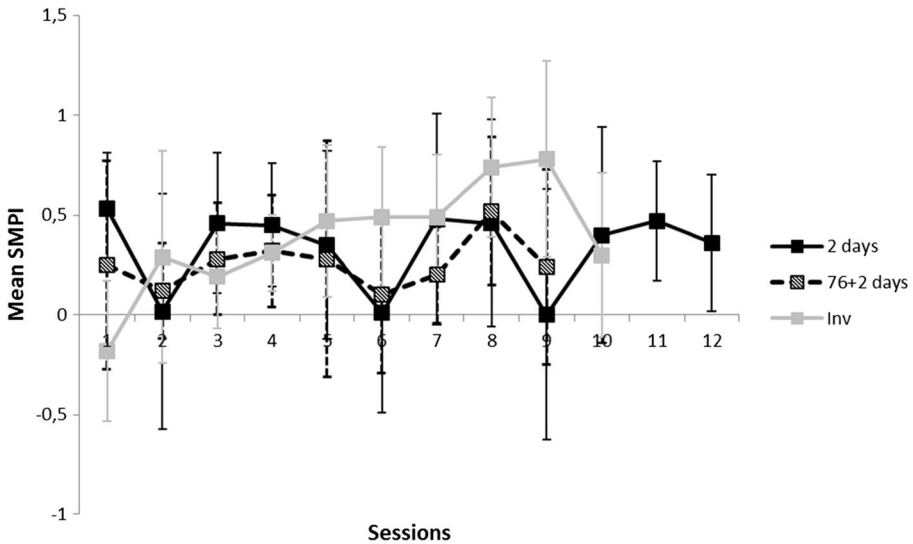


Fig. 5 Mean spatial memory performance index (SMPI)±standard deviations per session for each experimental period for Island Group (*Cebus libidinosus* = *Sapajus cay*) at La Plata Zoo and Botanical Park, Buenos Aires, Argentina, between 2007 and 2010. 2 days and 76+2 days = first and second experimental period of 2-day long-term memory; Inv. = inverse experiment.

performances and, despite showing memory formation, they did not show a clear pattern of memory consolidation. Index values fluctuated greatly in all the experimental periods and the subjects reached a value close to 1 only during the *inverse* period (Table III, Fig. 5).

We found no significant differences in mean performance index between the first and last sessions of the *2 days* experiment, and the effect size of the difference was low and negative (Table IV). We also found no significant differences in mean performance index between the first and last sessions of *76+2 days*, and the effect size was again low and negative (Table IV). As we expected, the index value in the first session of *inverse* was negative, suggesting performance below chance. Similar to Cage Group, we found significant differences in mean performance index between the first and last *inverse* sessions (the highest index values of all the experimental periods) with a high effect size (Table IV), indicating that subjects were able to consolidate memory during the inversion process.

During *76 days* some subjects showed negative values of the performance index, with a total of 43 correct visits and 33 incorrect visits. We found no significant differences between the mean index values of the last session of *2 days* and the *76 days* sessions. The effect size for this comparison was low and negative, indicating that there was little difference between the two performances (Table IV). Although both sessions had mean index values >0 , their distributions showed high variation.

For *4 months* we recorded a total of 43 correct visits and 56 incorrect visits. We found no significant differences in performance between the last session of *76+2 days* and the *4 months* session. The effect size for this comparison was moderate and negative, showing that performance had declined over the elapsed time (Table IV).

Table IV Comparison between sessions of the same and different experimental periods for Island Group (*Cebus litidinosus=Sapajus cay*) at La Plata Zoo and Botanical Park, Buenos Aires, Argentina, between 2007 and 2010

IG sessions	t-value	P value	CI 95 %	Mean±SD	Cohen's d and N
S1-S12 2 days	1.050	0.171	-0.25 to 0.59	S1=0.53±0.28 S12=0.36±0.34	-0.5; N=12
S1-S9 76+2 days	-0.52	0.480	-0.72 to 0.75	S1=0.25±.52 S9=0.24±0.49	-0.02; N=10
S1-S10 Inv.	-3.865	0.009*	-0.84 to (-0.13)	S1=-0.18±0.35 S10=0.3±0.41	1.17; N=10
S12.2 days -76 days	1.266	0.137	-0.21 to 0.58	2 days=0.36±0.34 76 days=0.22±0.37	-0.3; N=10
S9 76+2 days -4 months	0.444	0.343	-1.12 to 1.49	76+2 days=0.24±0.49 4 months=-0.05±0.46	-0.5; N=10

IG = island group; S1-S12=sessions; 2 days and 76+2 days=first and second 2-day long-term memory period; Inv. = inverse period; 76 days and 4 months=76-day and 4-month long-term memory period; t-value and P-value=results from Student's paired two samples t-test; *significant using α : 0.05; CI 95 %=confidence interval for mean difference; SD=standard deviation; Cohen's d=effect size value

In summary, these results suggest that Island Group was able to consolidate spatial memory only during the *inverse* experiment and that subjects did not demonstrate long-term memory.

Discussion

Subjects from both groups learned to find food in all experimental periods and were able to remember the location of accessible and nonaccessible feeders, although we found differences in the levels of performance within and between groups. Because each session lasted several minutes, it is not surprising that we found memory formation from the first session even in the first experiment. Only in one case was the mean performance index value below 0 (first session of the *inverse* period for Island Group), but we expected this result because we had reversed the foraging array outcomes. In Cage Group, subjects also decreased their performance to near 0 in the first session of the *inverse* period, although it was not negative.

In the 2 *days* long-term memory after the 76 *days* and *inverse* periods, we found memory consolidation that exceeded that in 2 *days* long-term memory: performance index values increased and became more stable across sessions, while variation among subjects decreased. Subjects from Island Group achieved memory consolidation only at the end of the *inverse* period. This delayed consolidation may have resulted from the strong contrast in reward contingencies caused by the reversal of the spatial design, which might have worked as a stimulus to integrate previously formed but weak spatial memories from previous stages of the experiment. Studies of reinforcement show that it is easier to notice the absence of reinforcement (in this case, food in formerly accessible feeders) after a consistent reinforcement schedule (always receive reward in the same place; Domjan 1998).

The excess of correct visits over incorrect visits in almost every test session suggests that subjects created a spatial record (map) of the situation (environmental context) and used it to search and locate food. Foraging efficiency depends on the subject's ability to discern accurate signals of the food and to remember its location in time and space (Dominy 2004). We controlled for visual and olfactory variables: accessible and nonaccessible feeders were identical externally, and all contained food (controlling for smell). In addition, individuals were not fed in the morning to ensure that they were hungry, and sessions were performed at the same time of the day. These design features suggest that the progressive increase in the performance index values for the Cage Group and the last *inverse* sessions in Island Group were not related to some process other than the consolidation of memory of rewarded and unrewarded locations in space (Ludvig *et al.* 2003).

We also found evidence that capuchins can retain spatial memories for considerably longer than 2 days. Stable memory performance has been observed in studies in which subjects were tested in their home cages, a situation generally considered less stressful to the monkeys than an experimental room (Tavares and Tomaz 2002). Cage Group subjects retained memory of feeder positions for periods of 76 days to 4 months, showing apparent memory consolidation across this long period. Studies of optimal foraging strategies predict that frequent changes in the environment should favor a short-term memory window, whereas stability should favor long-term storing of

experiences (Janmaat *et al.* 2013) and that keeping memories for too long may result in inappropriate behavior when conditions change (Shettleworth 2010). The more complex and less predictable testing situation of Island Group in comparison with Cage Group could have led to reduced long-term memory consolidation.

Extended long-term memory may make sense from an adaptive perspective. Capuchins have long lives—up to 50 yr in captivity (Weigl 2005) and *ca.* 30 yr in the wild (Janson *et al.* 2012; Nowak 1999)—and travel through the same environment throughout most of their lives. Long-term memories would be very useful to find locations of stable resources but could be not developed in environments where conditions frequently change. We suggest that these long-term memories in combination with the ability to form learning sets will give subjects an advantage in environments where food locations are stable but synchronous fruiting periods vary between tree species: when one tree from one species carries fruit, it will indicate that the whole set of trees from the same specie will probably carry fruit too.

Higher values for the inverse period compared with 2 *days* long-term memory period, and the ability to reach performance index values closer to 1 in the last sessions of the *inverse* period may indicate the existence of learning sets or “learning how to learn.” Learning sets refers to the learning of discrimination problems progressively more quickly as a function of training (Schrier 1984). In many cases what appears to be quick learning, reflecting a high level of intelligence, insight, or abstraction, may in fact be the end result of a gradual learning process, i.e., of learning set formation (Schrier and Thompson 1984). This concept may be particularly relevant to the results we obtained with Island Group: our subjects, which did not seem to improve their performance across 31 training sessions, showed a clear improvement in efficiency when they were exposed to a new situation (the *inverse* period). The marked contrast with the previous reward pattern may have increased the signal-to-noise ratio of spatial locations of obtained rewards and thus allowed individuals to perceive and consolidate a latent pattern to which they had been exposed already (Warren 1974).

The generally lower performance of Island Group relative to Cage Group may have several causes. The most likely cause is the availability to Island Group of abundant alternative foraging opportunities. These may have reduced the interest of Island Group subjects in the food reward, as suggested by the observation that Island Group individuals frequently removed cornflakes from the feeders and threw them to the ground. The more rapid removal of the food from feeders in comparison with Cage Group shortened experimental sessions (which were terminated when one or more feeders was emptied). The widespread availability of potential equally or more attractive foraging opportunities for Island Group subjects may also have weakened the incentive to form long-term memories for the accessible feeders, thus accounting for their reduced performance and lack of obvious consolidation of long-term memory. Finally, the duration of experimental periods was longer in Cage Group than in Island Group. A possible explanation for this situation could be that some subjects in Cage Group stayed near feeders, blocking access to them without feeding.

In the GLMM, differences between subjects did not account for much of the overall variation in performance index in Cage Group, but were high in Island Group, where sex also had a significant effect on performance, with females performing better than males. The differences that were observed might be attributed to features that were not measured in this study; for example, social rank is important for capuchin groups in

relation to access to food (Di Bitetti and Janson 2001; Garber and Brown 2005). Among social foragers, factors such as sensory capabilities, social dominance, and information obtained from conspecifics can account for species differences in decision making as well as in performance between groups of the same species (Bicca-Marques and Garber 2004). For Island Group, differences in the environmental context could promote differences between individuals in the attention they paid to the design. Although hierarchical differences between individuals could affect performance (Fichtner Gomes and Bicca-Marques 2012), our experimental design offered individuals enough feeding opportunities to avoid these differences: we provided a high number of feeders relative to the number of individuals and spatially separated the feeders to avoid conflicts. Food was sufficient to satiate the entire group so there were no individual differences in the opportunities to learn.

In summary, capuchins learned and remembered the spatial positions of accessible and nonaccessible feeders, helping them improve their foraging efficiency for periods of 48 hours, 76 days, and 4 months. Over longer retention intervals and during use of an inverted spatial design, the subjects demonstrated behavior consistent with learning sets to solve a problem of spatial resource modification in a shorter time.

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