



## **Individual variability in visual recognition memory of black-handed spider monkeys (*Ateles geoffroyi*)**

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Recognition memory is an ability that allows animals to respond differentially to stimuli, individuals, or situations experienced in the past and plays an important role in foraging and social behavior. We tested the ability of black-handed spider monkeys (*Ateles geoffroyi*) to remember and recognize visual stimuli that belong to 6 categories. Seven adult spider monkeys (*Ateles geoffroyi*) solved a delayed match-to-sample task where they had to touch a list of picture samples with different lengths (3, 4, and 5 pictures). After that, they waited for different retention intervals (0, 15, and 30 s), and 2 pictures were presented. The spider monkeys touched 1 of 2 pictures, signaling which was presented in the list. The results indicate effects of the retention interval, the list length, and the list position on picture recognition. Individual plots also show different strategies of the individuals used to solve the task, such as remembering the first picture in the list (primacy), remembering the last picture in the list (recency), or remembering both positions in the list; these strategies change as the retention interval increases. The results did not show better recognition for any of the picture categories. Based on these results and previous research, we recommend changes to the task and the statistical analysis for a better understanding of the underlying mechanism of recognition memory.

*Keywords:* list-length effect, primacy, recency, recognition memory, spider monkey

Recognition memory is the ability to respond differentially to stimuli, events, or other individuals experienced in the past (Clark, 2013). Recognition abilities have been explored in humans and animals using stimuli like odors and flavors (Bromley & Doty, 1995; Miranda, 2012; Reed, 2000) and auditory stimuli (Cohen et al., 2009). However, visual stimuli are used most often to assess recognition memory (Cohen et al., 2009; Tajika, 2001).

For animals, recognition memory plays an important role during different activities, like foraging (Bracis et al., 2015; Kamil & Roitblat, 1985) and social interactions (Fysh, 2018; Johnston & Edmonds, 2009). A specific type of recognition memory used during foraging called taste-recognition memory helps animals approach appropriate food items or avoid items with potential side effects (Bermúdez-Rattoni, 2004; Bermúdez-Rattoni et al., 2005; Miranda, 2012; Ruetti et al., 2014). Long-term spatial memory also plays an important role in foraging since nonhuman animals must remember the routes to feeding patches or feeding items that change seasonally (Bracis et al., 2015; Di Fiore & Suarez, 2007; Suarez et al., 2019). In social interactions, recognition memory allows animals the ability to remember different types of social interactions and the individuals involved (Fysh, 2018; Johnston & Edmonds, 2009), because animals can recognize other individuals based on idiosyncratic characteristics like scent (Feinberg et al., 2012; Palagi & Dapporto, 2006) or faces (Pascalis & Bachevalier, 1998).

Different tasks can be used to study recognition memory in experimental settings. In animals, individuals can be tested on their ability to recognize objects, locations, and the order in which stimuli were presented, among others (Barker et al., 2007). Another manipulation used in different animal species is the serial presentation of stimuli. In a task using this manipulation, a list of stimuli is presented, and, after a delay called the retention interval, the individuals complete a terminal condition using the information from the previous list. This could be a same-different task (Basile & Hampton, 2010; Matzke & Castro, 1998; Wright, 1999; Wright et al., 1985) or a delayed match-to-sample (DMS) task (Beran, 2011; Reed et al., 1991).

The same-different task and the DMS task are comprised of three parts: sampling, retention interval, and a terminal task. In the sampling condition, a series of stimuli are presented one by one. The retention interval is a delay during which the information from the sampling condition is retained until it is used. In the terminal condition of the same-different task, a stimulus from the sampling condition is presented in 50% of the trials, while in the other 50%, it is a new stimulus, and a key is presented in all of the trials. The animals should touch the stimulus if it was presented in the sampling condition, and touch the key if the stimulus was not in the sampling condition (Basile & Hampton, 2010; Matzke & Castro, 1998; Wright, 1999; Wright et al., 1985). For the terminal condition of the DMS task, a stimulus that was presented in the sampling condition is presented along with a new stimulus in 100% of the trials. The animals should touch the stimulus that was part of the sampling condition and ignore the new stimulus (Beran, 2011; Reed et al., 1991).

One of the advantages of serial presentation is the possibility of studying serial-position effects, in which stimuli at the beginning (primacy) and at the end of a list (recency) are more easily recognized (Basile & Hampton, 2010; Murdock, 1962), opening the possibility of studying how recognition is modulated by different variables like familiarity (Basile & Hampton, 2010), retention-interval length (Wright, 1999), list length (Brandt et al., 2019; Dennis et al., 2008; Gronlund & Elam, 1994; Kinnell & Dennis, 2012; Strong, 1912), and the emotional content of the stimuli (Kano et al., 2008), among others.

In primates, the studies on recognition memory have been performed on different species using the same-different task or the DMS task. The results have shown that different variables modulate recognition memory. For example, using the same-different task, an experiment with rhesus macaques (*Macaca mulata*) showed that it is easy to recognize the first and last stimuli presented in a list (primacy and recency, respectively), but younger individuals showed only recency, while adults showed primacy and recency, indicating that the serial-position effects develop throughout the individuals' lives (Matzke & Castro, 1998). The results of experiments on capuchin monkeys (*Cebus apella*) and rhesus macaques (*Macaca mulatta*) show that primacy and recency depend on the length of the retention interval. When the retention intervals were short (1-10 s), capuchin monkeys and macaques showed primacy and recency effects, but, at retention intervals of 20-30 s, primacy was stronger, and recency dissipated (Wright, 1999; Wright et al., 1985). The data from other experiments in rhesus macaques showed that primacy and recency effects depend on how frequently a picture is seen. The experiment manipulated the size of the bank of pictures used to set a list of 4 pictures and found the effect of primacy and recency when the bank of stimuli was small (6 pictures) or medium (60 pictures), but not when the bank of pictures was large (2,400 pictures; Basile & Hampton, 2010).

With the DMS task, the results from experiments with squirrel monkeys (*Samiri sciureus*) have also shown primacy and recency under different retention intervals (0.5 and 5 s). In this study, they ran a second experiment manipulating the presentation time of the stimuli (0.5 and 1 s) and stimulus list length (3 or 6 pictures). The researchers also compared the performance of the squirrel monkeys against humans. The results did not show interactions between the variables for humans or squirrel monkeys, and a higher level of accuracy and a higher effect of recency was found in humans; while primacy and recency were found in squirrel monkeys for both stimulus list lengths (Roberts & Kraemer, 1981). The data of the experiments with the squirrel monkeys also did not show a reduction in accuracy when the retention interval was longer (Roberts & Kraemer, 1981). The results of experiments with chimpanzees (*Pan troglodytes*) have shown that it is easy to recognize a picture in a list of stimuli when the picture belongs to a different category, a result called the isolation effect or von Restorff effect (Beran, 2011).

The effect of the number of stimuli in a list on recognition memory has been tested in humans and is called the list-length effect. This effect is characterized as a reduction of the capability of the individuals to recognize a stimulus when the number of stimuli presented serially (list length) increases (Gronlund & Elam, 1994; Strong, 1912). Previous studies using Bayesian analysis techniques have identified that the list-length effect can be found when the stimuli are pictures but not in tasks with a list of words (Brandt et al., 2019; Kinnell & Dennis, 2012). As we mentioned previously, this effect was not found in the performance of squirrel monkeys (Roberts & Kraemer, 1981).

In the case of black-handed spider monkeys (*Ateles geoffroyi*), different studies have shown the relevance of recognition and memory. The research has shown that recognition abilities play an important role during foraging, allowing spider monkeys to choose food items using the variations of fruit colors against the background of leaves (Riba-Hernández et al., 2004). Because fruit is the most common item in the diet of spider monkeys (González-Zamora et al., 2009), and because fruit availability changes seasonally (Castellanos & Chanin, 1996; Wallace, 2005), spider monkeys should remember food items from one season to the next to forage efficiently, and a mechanism like recognition memory could allow spider monkeys to deal with this problem.

Concerning the memory abilities of black-handed spider monkeys, current evidence comes from studies with free-ranging individuals and experiments with individuals in captivity. Black-handed spider monkeys tend to use sleeping trees and are capable of moving from those trees to feeding sites following stable routes, returning to the sleeping trees at sunset (Ramos-Fernandez et al., 2004). Previous studies have considered the use of routes as evidence of spatial memory (Valero & Byrne, 2007). Another member of the *atelidae* family, black-faced spider monkeys (*Ateles chamek*), have shown that they are capable of using different routes each season, and the routes were highly stable year after year for at least eight years (Di Fiore & Suarez, 2007).

Experimentally, the research carried out by Amici et al. (2010) using a short-term memory task called the cups task, where a reward was hidden inside one of three cups in view of the monkeys, showed that spider monkeys were very accurate at retrieving the reward when they did not have to wait. However, if the spider monkeys had to wait for a retention interval of 30 or 1,800 s to retrieve the reward, the accuracy dropped as the retention interval became greater (Amici et al., 2010). Another test carried out by our research group has shown that spider monkeys are capable of remembering the location of a reward and the amount of the reward of that location for periods as long as 24 hr (Reynoso-Cruz et al., 2020).

Despite the evidence of the memory and visual recognition capabilities of spider monkeys, their visual recognition memory has not been tested. The previous experiments indicate that this species is suitable for conducting experimental tests of memory (Amici et al., 2010; Reynoso-Cruz et al., 2020). We investigated whether spider monkeys are capable of remembering and recognizing different pictures ordered in a list and whether their recognition memory is modulated by the position of the picture in the list, list length, and retention interval.

Based on previous studies with other primate species, we hypothesized that the black-handed spider monkeys (*Ateles geoffroyi*) would be able to recognize pictures seen in the past, and their recognition ability would depend on the position of the picture in the list, modulated by the retention interval, and their precision would not be affected by the retention interval or the number of stimuli in the list. From this hypothesis, we predicted: (1) The spider monkeys would show effects of primacy and recency; (2) the retention interval would modulate the serial-position effect, and, as the length of the retention interval increased, the recency effect would dissipate, and the primacy effect would increase; (3) the precision of the spider monkeys would be the same, no matter the size of the retention interval or the length of the list of pictures to remember.

## Method

### Individuals

Seven adult black-handed spider monkeys (*Ateles geoffroyi*) participated in this experiment, 4 females (Camila, Lluvia, Mary, and Paulina) and 3 males (Brutus, Nery, and Neto). The animals have previously participated in studies of memory (Reynoso-Cruz et al., 2020), but they have not interacted previously with pictures or participated in experiments on recognition. All of the individuals were living in captivity in a reserve managed by the Instituto de Neuroetología located in the town of Catemaco, Veracruz, in the southeast of Mexico. The mean age of the individuals at the beginning of the experiment was 11.25 years old ( $SD = 3.93$ ). The spider monkeys were housed in pairs in enclosures of  $8 \times 4 \times 4$  m ( $l \times w \times h$ ). The enclosures were built with a chain-link fence that allowed the individuals to look outside, move their extremities outside their enclosure, and to interact with other monkeys that live in adjacent enclosures. The individuals were trained to stay at the fence in front of the researcher and interact with different objects. During the experiments, the individuals were separated by a barrier to work individually, and, after the daily session ended, the individuals were reunited again.

The monkeys were not physically restricted to stay in front of the researcher, and they could abandon the experiment at any moment. The monkeys were not deprived of food to do the task. We worked before their feeding time to motivate the monkeys to work for a food reward, and, after the daily session ended, the spider monkeys were fed. The diet was composed of cultivated and wild fruits, vegetables, and leaves that varied according to the season.

The enclosures of the spider monkeys were enriched with physical, nutritional, and social stimuli. The physical stimuli included branches with different textures that were arranged in different positions regularly (approximately every 30 days), swings made with tires, ropes, and ladders for climbing. The nutritional stimuli included food items from the diet presented in different shapes or forms (e.g., smoothies, popsicles, gelatin). Finally, for social enrichment, the spider monkeys were rotated from their enclosures to interact with other monkeys. The rotation took place approximately every 6 months.

### Ethics

Our procedures followed the guidelines for the care and use of mammals in neuroscience and behavioral research (National Research Council, 2003) and the ethics directives of the Psychology Department at UNAM (<http://www.psicologia.unam.mx/comite-de-etica-de-investigacion-de-la-facultad-de-psicologia/>). The experiment and the procedures were authorized by the Mexican government (SEMARNAT [09/GS-2132/05/10]).

### Materials

We used black, plastic, letter-sized cards ( $21.6 \times 27.9$  cm) as the background where the pictures were displayed. The pictures belonged to six different categories and each category contained different numbers of pictures, as Table 1 shows. The categories were fruits, tools, beverages, snacks, vegetables, and husbandry objects. These categories were taken from a previous experiment with chimpanzees (Beran, 2011), and the pictures were taken from free banks of pictures available on the internet (the pictures used in the experiment are available at [10.6084/m9.figshare.12429722](https://www.figshare.com/figure/12429722)). The pictures were color-printed at a size of  $6 \times 6$  cm ( $l \times w$ ) and laminated to protect from scratches and the elements. We used pieces of cereal as a reward (Cheerios®). The individuals had previous experience with some of the stimuli presented in the categories of fruits and vegetables, since some of the fruits pictured were part of their regular diet.

**Table 1**

*Categories Used in the Experiment*

List Size	Category	Number of Pictures
3	Fruits	15
	Tools	15
4	Beverages	20
	Snacks	20
5	Vegetables	25
	Husbandry	25

*Note.* The number of pictures was chosen to avoid the familiarity effect.

## Procedure and Experimental Design

We designed our task based on a previous experiment with chimpanzees using a DMS task (Beran, 2011) designed for a touch screen. The chimpanzees had to watch a list of pictures, and, after a retention interval, two pictures were presented, one from the list and one new, and they had to touch the picture from the list to receive a food reward (Beran, 2011). We adapted the procedure to the needs of the spider monkeys, changing the touchscreen for plastic cards and training the individuals to touch the pictures instead of watching the pictures. We used a  $3 \times 3$  factorial design with three list-lengths (3, 4, and 5) and three retention intervals (0, 15, and 30 s) as variables in the study. The design of the experiment is shown in Table 2.

**Table 2**

### *Experimental Design*

Retention Interval	List Size		
	3	4	5
0	60	80	100
15	60	80	100
30	60	80	100
Categories	Fruits / Tools	Beverages / Snacks	Vegetables / Husbandry
Total Pictures	30	40	50
Total Number of Trials	180	240	300

*Note.* 60, 80, and 100 refer to the number of trials per retention interval (20 trials per each position in the list, divided into two categories of pictures).

### *Training*

Because the task required the spider monkeys to touch lists with different numbers of pictures one by one (sample condition), wait for a retention interval, and then do a matching condition, we shaped the behaviors needed for the task following the steps (1) touch a picture, (2) touch a list of pictures, (3) matching, and (4) combine the list of pictures with the matching.

For the training, we used two pictures that belonged to the six categories used in the task (12 pictures in total). These pictures were different from the ones that we used during the experiment and were used only during training (the pictures used during the training are available at <https://doi.org/10.6084/m9.figshare.12429722.v1>).

The first step was to train the individuals to touch the pictures using two pictures attached to the center of plastic cards. The plastic cards were presented one after the other 20 cm outside the monkey's enclosure to ensure that the spider monkeys used their hands to touch them. Once the monkey touched the picture, that completed the trial, and the next picture was shown. We continued this training for six training sessions of 30 trials, one session daily. During the first session, we put avocado puree (approximately 2 g) partially covering the pictures to motivate the spider monkeys to consume the avocado and touch the pictures. After the individuals touched the pictures and removed the puree to eat it, we gave them vocal feedback ("Muy bien!") and rewarded the individuals with a piece of cereal before they consumed the avocado. In the second session, we did not put any avocado puree on the pictures; we gave them vocal feedback ("Muy bien!") and a piece of cereal as the reward. If the individuals refused to touch the pictures without the avocado, we gave them the avocado puree for 10 trials, but we reduced the amount of avocado each trial. For the rest of the training sessions, we gave the spider monkeys the vocal feedback ("Muy bien!") and one cereal piece after the monkeys touched the pictures.

The next step was to train the spider monkeys to touch a list of pictures for the sampling condition. For this, the individuals were trained to touch more than one picture to receive the vocal feedback and the reward, starting with two pictures. One card with a picture attached was presented; after the monkeys touched the picture, another card with a different picture was presented. After the monkeys touched the second picture, we gave them vocal feedback ("Muy bien!"), a piece of cereal was delivered as a reward, and the trial ended. We followed this procedure for two sessions of 30 trials each. After that, we increased the number of pictures to three, following the same procedure for three more sessions of 30 trials each. In this step of the training, we used three new pictures, different from step one, and these were assigned randomly to different positions in the list in each trial. Since some individuals were less motivated to work for one piece of cereal, we increased the reward to two pieces of cereal per trial for all the individuals. At the end of the training, the monkeys touched the pictures within an average of 2.56 s ( $SD = 0.22$  s), an amount of time similar to the experiment with chimpanzees (Beran, 2011).

After the training for the list of pictures, we trained the monkeys to do the matching. The first step in training the matching was to present one picture as the sampling condition, and, after the monkeys touched the picture, the matching condition started, and we presented that picture alongside a new picture. If the individuals touched the same picture they saw before, they received vocal feedback (“Muy bien!”) and a food reward (two pieces of cereal). If they touched the incorrect picture, they received different vocal feedback (“Mal!”), and they did not receive a reward, but we allowed the individuals to then touch the correct picture, after which they received the vocal reward (“Muy bien!”) and a smaller reward (a half piece of cereal). We repeated this procedure for one session, and, after that, the individuals received vocal feedback (“Mal!” or “Muy bien!”), but the reward was only delivered if the spider monkeys touched the correct picture. In each trial, the picture that was presented in the sampling condition was randomly selected from a bank of seven pictures, different from the pictures used before. Each session was 20 trials per subject per day, the same number of trials used previously with the chimpanzees (Beran, 2011), and we ran these sessions until their precision was equal to or higher than 80% for three consecutive sessions, a criterion used previously with macaques (Matzke & Castro, 1998).

For this training, the monkeys needed different numbers of sessions to reach the criterion and to continue to the next training step. Four monkeys (Lluvia, Camila, Paulina, and Brutus) reached the criterion in five sessions. The other three reached the criterion in different numbers of sessions: Nery in six, Neto in seven, and Mary in eight.

The last training step was the combination of the list of pictures and the matching. In this phase, we used all 12 pictures (all the pictures used during previous steps). For this training, we presented a list of pictures instead of one picture during the sampling condition, and then presented the matching condition using a picture from the sample list and another picture that was not part of the sample list. We started this training using a list of two pictures, and, after the individuals touched the pictures one after the other, we presented the matching condition. The picture used in the matching condition was counterbalanced between the first and second position in the list and counterbalanced between left and right. We ran this procedure until the individuals reached 80% accuracy for three consecutive sessions. In this step, the monkeys also needed different numbers of sessions to reach the criterion. Lluvia and Camila reached the criterion in 6 sessions, while Mary, Neto, and Brutus reached the criterion in 8 sessions; Nery and Paulina reached the criterion in 10 sessions.

After all the individuals reached the criterion for a list of two sample pictures, we increased the list length to three pictures, counterbalancing the pictures used in the matching condition between the three positions of the list and between left and right in the matching condition. We ran this condition for only three sessions of 10 trials each, to avoid a learning curve since the first condition of the experiment was a list of three pictures. During this training phase, we chose the pictures for the list of samples for each trial randomly. All the matching conditions started immediately after the last picture of the list was presented.

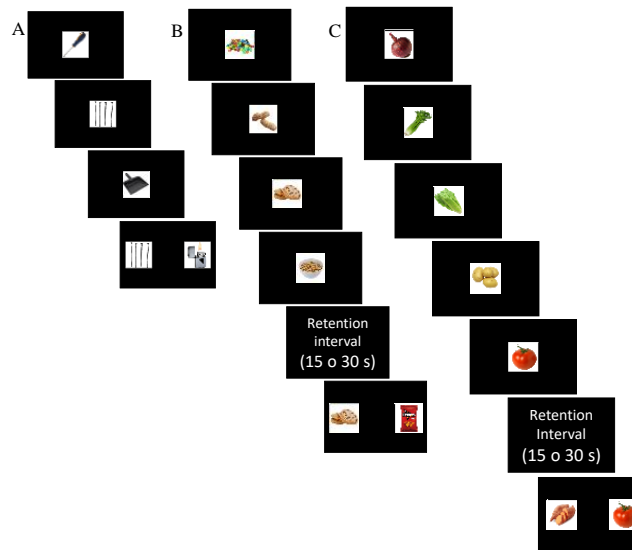
### ***Experimental Phase***

We ran daily sessions of 10 trials where the researcher was stationed outside the monkey’s enclosure presenting the plastic cards with the stimulus approximately 20 cm from the fence of the monkey’s enclosure. Once the monkey touched the picture, another one was presented, and so on until the sample list was completed. A black plastic card was presented during the retention intervals of 15 and 30 s but not for 0 s. In the 0-s retention interval, the matching condition was presented immediately after the last picture of the list. In the matching condition, as in the training, one of the pictures from the sample list was presented along with another picture that was not part of the list but belonged to the same category, one on the left and the other on the right. If the spider monkeys chose the correct picture during the matching condition, they received vocal feedback (“Muy bien!”) and two pieces of cereal as reward, but, if they chose the wrong picture, they received different vocal feedback (“Mal!”) but no reward. The correct picture was counterbalanced 50% to the left side and 50% to the right. Figure 1 shows the distribution of the cards and the pictures during the task.

The total number of trials per monkey was calculated by the list length and retention interval. Each position received 20 trials, and those were multiplied by the number of retention intervals (3). For the list of three pictures, we ran 180 trials per monkey: 60 trials per retention interval, divided into three positions in the list (20 trials per position) and two categories of pictures (10 trials per category). For the list size of four pictures, we ran 240 trials per monkey: 80 trials per retention interval, divided into four positions in the list (20 trials per position) and two categories (10 trials per category). Finally, for the list of five pictures, we ran 300 trials per monkey: 100 trials per retention interval, divided into five positions in the list (20 trials per position) and two categories (10 trials per category). The distribution of trials, the position of the correct response in the list, and the retention intervals are available at this link: <https://doi.org/10.6084/m9.figshare.13077962.v2>

**Figure 1**

*Arrangement of the Plastic Cards and the Pictures During DMS*



*Note.* All of the pictures presented during the sample condition were attached to the middle of the plastic cards and, during the matching condition, were presented on the left and the right. The distance between the cards during the matching condition was 6 cm. During the retention intervals of 15 and 30 s, a black plastic card was presented. (A) Distribution of cards in the condition with the list of three pictures. (B) Distribution of cards in the condition with the list of four pictures. (C) Distribution of cards in the condition with the list of five pictures.

***Experimental Controls***

We controlled that the pictures in each category were presented only two times per each retention interval as the correct stimulus in the matching condition, which means that every picture was used six times as the correct picture during the matching condition. We used this procedure and different categories of pictures to avoid familiarity with the pictures because this could increase recognition in primates (Basile & Hampton, 2010). To avoid the learning curve, we presented the retention interval randomly during the task as in a previous experiment (Basile, & Hampton, 2010), but list length increased arithmetically from three to five.

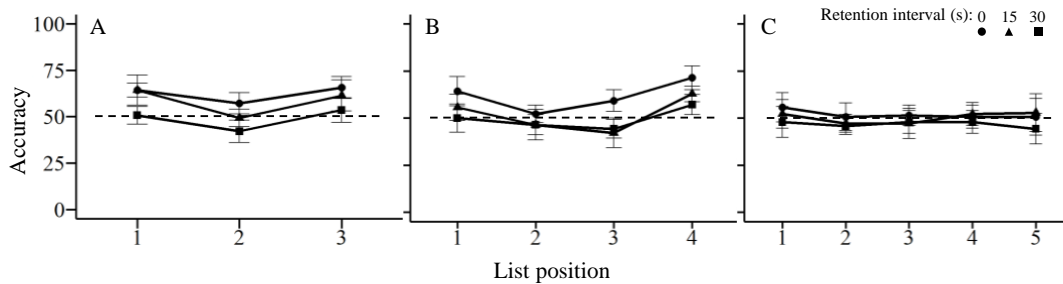
To avoid the “Clever Hans effect” or cueing the correct response to the spider monkeys via the researchers’ gaze, the researchers wore a cap and always looked down at the cards with the stimulus. The cap blocked the spider monkey’s view of the researchers’ faces and allowed the researchers to identify whether the selection of the monkeys was correct or not.

## Results

We calculated the percentage of correct responses (accuracy) of the monkeys based on sample list length, the position of the picture in the list, and the retention interval, and, then, we calculated the mean and 95% confidence interval (CI) for all monkeys, as Figure 2 shows. The data in Figure 2 show that the accuracy of the monkeys fell as the retention interval increased. The data also indicate that the accuracy decreased as list length increased and that the recognition of a picture was related with the position in which it was presented.

**Figure 2**

*Mean Accuracy of the Seven Monkeys*



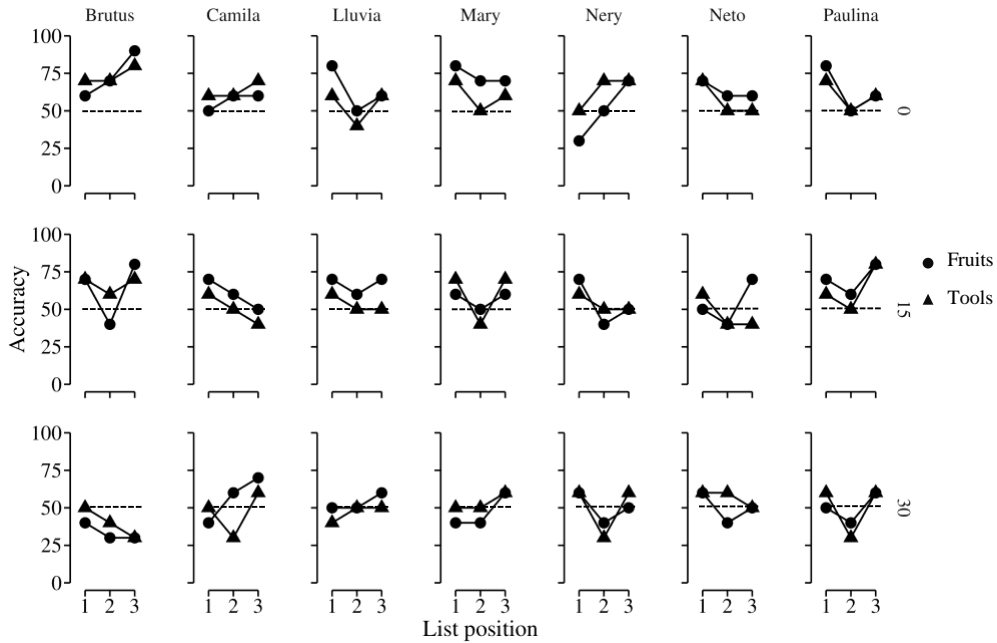
*Note.* The mean was calculated based on the position of the pictures in the list and the three retention intervals. The vertical bars in graphs A, B, and C show the 95% confidence interval. The dashed line in the three graphs shows the accuracy level by chance. (A) Accuracy for the list of three pictures. (B) Accuracy for the list of four pictures. (C) Accuracy for the list of five pictures.

The CI bars in Figure 2 show overlap between the retention interval and also across the positions in the list, which indicates variability within the monkeys. To analyze this variability, we plotted the accuracy of each monkey based on list length, the position in the list, the categories of the pictures used in the task, and the retention interval, as Figures 3-5 show.

For the sample list with three pictures (Figure 3), the data show, in almost all conditions, a similar percentage of accuracy between the categories of fruits and tools. However, Camila, Lluvia, and Neto showed differences in their recognition of tools and fruits for different retention intervals. The data show higher levels of accuracy with the 0-s retention interval, and the accuracy dropped as the retention interval increased, showing the lowest levels at the 30-s retention interval. In relation to the position of the picture in the list, the data show variability within the monkeys and across conditions. For example, Brutus showed higher accuracy for the last picture (recency) at the 0-s retention interval and higher accuracy for the first and last picture (primacy and recency) at the 15-s retention interval, but the accuracy levels at the 30-s retention interval were near the chance level. Other monkeys, like Mary, showed recency at the 0-s retention interval, primacy and recency at the 15-s retention interval, and recency at the 30-s retention interval, but, again, the levels of accuracy reached were at or near chance level. At the 30-s retention interval, the accuracy levels reached for the three positions in the list for almost all of the monkeys were at or near chance level.

**Figure 3**

*Accuracy Level Reached by Each Monkey for the List with Three Pictures*



*Note.* The number on the far right indicates the length of the retention interval. The dashed lines indicate the accuracy levels by chance.

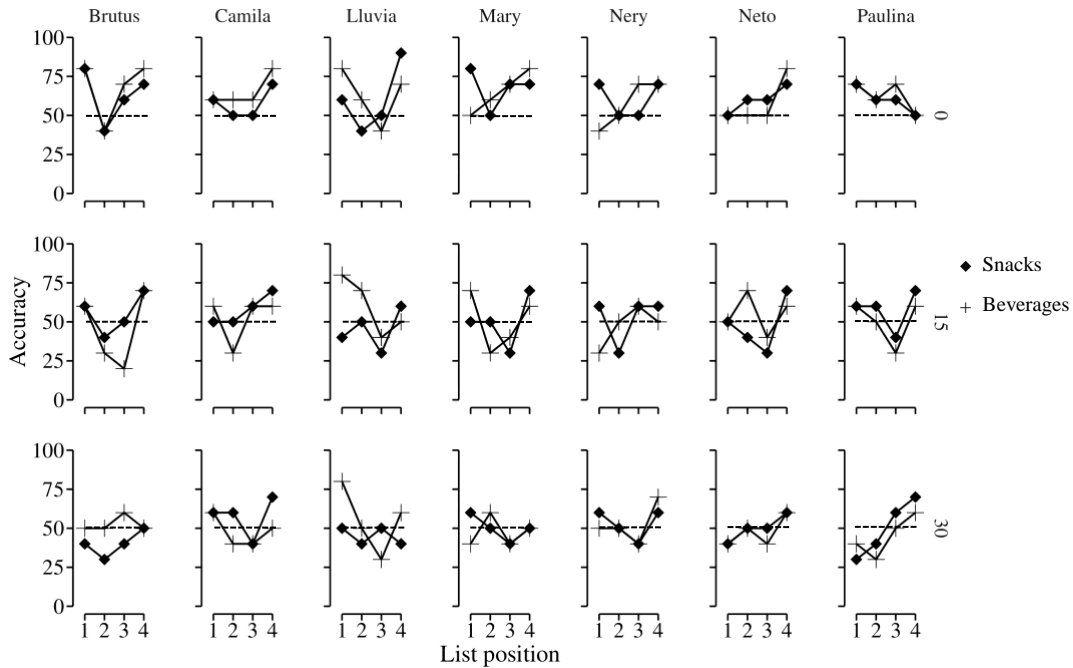
In the sample list with four pictures (Figure 4), the data show similar levels of accuracy between the pictures of snacks and beverages. However, some monkeys, like Camila and Lluvia, recognized one of the categories much better (higher accuracy). In Camila's case, she recognized the pictures of beverages better at the 0-s retention interval, but, at the 15- and 30-s retention intervals, she recognized the pictures of snacks better. In the condition with the 0-s retention interval, Lluvia recognized the pictures of beverages better in list positions one and two and the snacks better in list positions three and four. In the conditions with the 15- and 30-s retention intervals, Lluvia recognized the pictures of beverages better.

The data in Figure 4 show, as with the list size of three pictures, that accuracy fell as the retention interval increased. Also, we can see that each monkey followed different strategies to solve the task since the distribution of accuracy varied within the monkeys and within the retention intervals. For example, Brutus showed primacy and recency at the 0- and 15-s retention intervals and a flat distribution near the chance level at the 30-s retention interval, while Paulina showed a strategy that changed as the retention interval increased, with a tendency for primacy at the 0-s retention interval, primacy and recency at the 15-s retention interval, and recency at the 30-s retention interval. The accuracy levels at 30 s show that four out of seven monkeys reached accuracy levels above chance.

Finally, in the sample list with five pictures (Figure 5), the data show that the accuracy levels of the monkeys in the three retention intervals were near the level of chance or below; however, Brutus, Camila, Lluvia, Mary, Neto, and Paulina showed differences in their accuracy levels between the pictures of husbandry and vegetables. In Nery's case, his accuracy levels were near or below the level of chance and were similar in both categories. Only Brutus, in the condition with the 15-s retention interval, showed differences in the level of accuracy between categories.

**Figure 4**

*Accuracy Level Reached by Each Monkey for the List with Four Pictures*

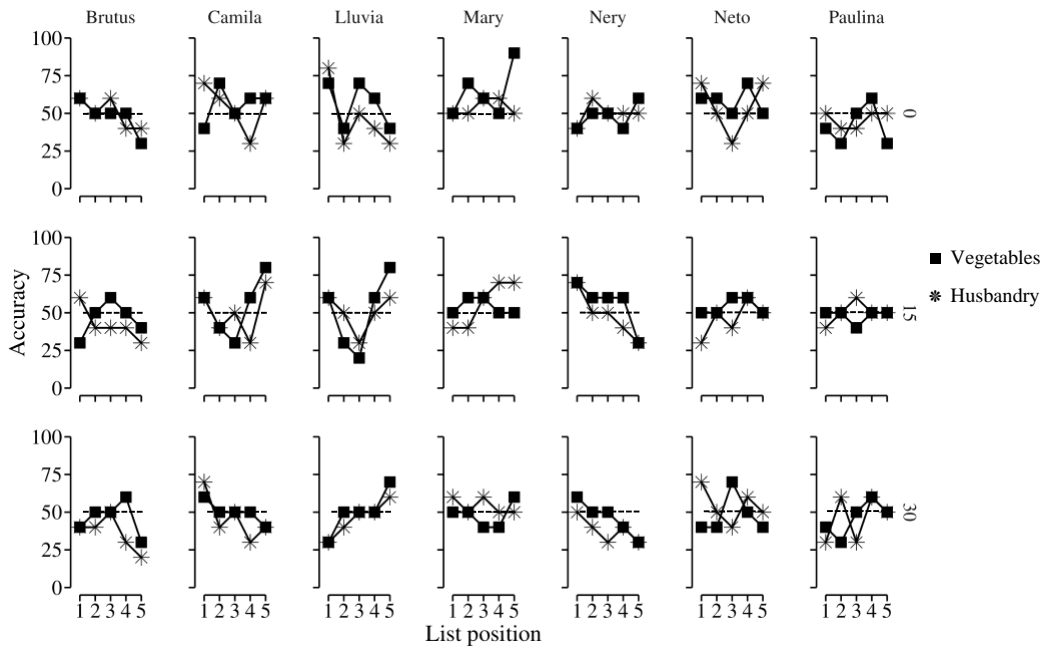


*Note.* The number on the far right indicates the length of the retention interval. The dashed lines indicate the accuracy levels by chance.

We analyzed the data using a nested ANOVA for repeated measures in the statistical software R (V. 4.0.2; R Core Team, 2020) using the function *aov* with the factors retention interval, list length, the interaction between retention interval and list length, the picture categories nested in the list length, and the position in the list nested in the list length because every list length used different categories of pictures, and the number of positions depended on the list length. The effect sizes with the 95% CI were calculated with omega squared ( $\omega^2$ ) using the function *omega\_squared* from the library *effectsize* (Ben-Shachar et al., 2020).

**Figure 5**

*Accuracy Level Reached by Each Monkey for the List with Five Pictures*



*Note.* The number on the far right indicates the length of the retention interval. The dashed lines indicate the accuracy levels by chance.

The results indicated a significant and medium-sized effect of the retention interval,  $F(2, 483) = 29.45$ ,  $p < .01$ ,  $\omega^2 = .10$ ,  $CI = [0.06, 0.16]$ , a significant but small effect of the sample list length,  $F(2, 483) = 16.02$ ,  $p < .01$ ,  $\omega^2 = .06$ ,  $CI = [0.02, 0.10]$ , a significant but small effect of the interaction between the retention interval and list length,  $F(4, 483) = 3.84$ ,  $p < .01$ ,  $\omega^2 = .02$ ,  $CI = [0.00, 0.05]$ , a nonsignificant effect of the categories nested in list length,  $F(3, 483) = 1.11$ ,  $p = .34$ ,  $\omega^2 < .001$ ,  $CI = [-0.01, 0.02]$ , and a significant and medium-sized effect of the position in the list nested in list length,  $F(9, 483) = 8.69$ ,  $p < .01$ ,  $\omega^2 = .12$ ,  $CI = [0.06, 0.17]$ .

We ran multiple comparisons using the Tukey Honestly Significant Differences function (*TukeyHSD*) in the statistical software R (V. 4.0.2; R Core Team, 2020) comparing the categories in each list length. The comparison for the list of three pictures showed a nonsignificant difference between tools and fruits,  $p = .99$ ,  $CI = [-0.09, 0.05]$ , for the list of four pictures the test showed a nonsignificant difference between snacks and beverages,  $p = 1.00$ ,  $CI = [-0.07, 0.06]$ , and, for the list of five pictures, the results also indicated a nonsignificant difference between the husbandry and vegetable categories,  $p = .98$ ,  $CI = [-0.03, 0.08]$ .

We wanted to know if the levels of accuracy were different from chance because the levels of accuracy reached by some monkeys appeared to be near the chance level. We compared the levels of accuracy reached by the monkeys for each list length and each retention interval with a hypothetical distribution of data at 50% that represented the accuracy by chance in each condition. For this comparison, we ran a Kruskal-Wallis test in the statistical software R (V. 4.0.2; R Core Team, 2020) using the function *kruskal.test*.

The results for the list of three pictures indicated that at the 0-s retention interval, the results were different from chance,  $X^2(1) = 38.61, p < .01$ . For the 15-s retention interval, the results also showed a significant difference from chance,  $X^2(1) = 15.09, p < .01$ , but were nonsignificant for the 30-s retention interval,  $X^2(1) = 0.00, p = 1.00$ . For the list of four pictures at the 0-s retention interval, the results indicated a significant difference from chance,  $X^2(1) = 33.17, p < .01$ , a nonsignificant difference for the 15-s retention interval,  $X^2(1) = 3.44, p = .06$ , and were also nonsignificant for the 30-s retention interval,  $X^2(1) = 0.60, p = .43$ . Finally, for the list of five pictures, the results indicated a nonsignificant difference for the 0-s retention interval,  $X^2(1) = 1.52, p = .21$ , and the 15-s retention interval,  $X^2(1) = 0.47, p = .48$ , but were significant for the 30-s retention interval,  $X^2(1) = 6.17, p = .01$ .

## Discussion

Our data show that the plots by group did not reflect the individual performances because the recognition memory of each monkey shows different serial-position effects (only primacy, only recency or primacy and recency), and the means in each condition did not reflect the variability of the individual performance. However, our nested ANOVA was able to capture some main effects that were also reflected in the individual plots of each spider monkey.

The ANOVA and the individual plots indicate that the performance fell as the retention interval increased; it was more difficult for the spider monkeys to recognize the pictures as the retention interval became greater. This result was different than that predicted by previous research with macaques and capuchin monkeys (Wright, 1999; Wright et al., 1985), in which the levels of accuracy reached at a greater retention interval were the same as a small retention interval. The difference of the spider monkeys' data from the prediction could be related to the amount of training the monkeys received. With the rhesus macaques and the capuchin monkeys, they were trained intensively until their precision was greater than 80% before they started the experiment, and, in the particular case of the capuchin monkeys, they were trained for 39,000 trials using a list of four pictures before the experiment started (Wright, 1999). The intensive training could prevent the fall in precision caused when the retention interval increases.

The reduction in accuracy as a function of the retention interval or delay has been reported previously in different primate species, including spider monkeys, in experiments of short-term memory (Altschul et al., 2019; Amici et al., 2010) and also in a review of the DMS task (Lind et al., 2015). The review also indicates that most animals performed at chance level when the delay was 27 s (Lind et al., 2015). The performance of the spider monkeys agrees with this observation because the spider monkeys reached the lowest precision at the 30-s retention interval.

The individual plots and the nested ANOVA detected a small effect of the list-length. This result was different than the one expected by the prediction since a previous experiment with squirrel monkeys showed similar levels of recognition when the list had three and six pictures (Roberts & Kraemer, 1981). Our spider monkeys showed lower accuracy levels as the number of pictures in the list increased. This difference could be related to the characteristics of the stimuli used with each species. In the experiment with the squirrel monkeys, the stimuli were geometrical designs (Roberts & Kraemer, 1981), while we used pictures with our spider monkeys. The number of stimuli was also different since the squirrel monkeys had only 10 geometrical stimuli (Roberts & Kraemer, 1981), while our spider monkeys had 120 pictures during the whole task, and we know from previous experiments that familiarity increases picture recognition (Basile & Hampton, 2010). These characteristics could explain why the list-length effect was found in the spider monkeys but not in the squirrel monkeys.

In the literature on humans, there has been discussion about the stimuli for which the list-length effect could be observed. A previous study on word recognition carried out with humans using a Bayesian analysis was not able to find the list-length effect (Dennis et al., 2008). However, two more recent studies were able to find the list-length effect using pictures instead of words (Brandt et al., 2019; Kinnell & Dennis, 2012). Although pictures are easier to recall than words (Defeyter et al., 2009; Paivio et al., 1968), the experiments of list-length effect on memory have proposed that the similarity between the stimuli is an important component for this effect, and, the more similar stimuli are, the more probable it is that the effect could be found (Brandt et al., 2019; Kinnell & Dennis, 2012). These results open the possibilities for future modifications to our task to test hypotheses related to the characteristics of the stimuli in other animal species, including nonhuman primates.

As for other aspects of the pictures used during the experiment, the results did not show higher recognition (greater accuracy) of pictures in the fruits and vegetables categories, categories with which the spider monkeys had previous experience since some pictures were items they consume regularly. This result indicates that previous experience with real and 3D stimuli did not increase recognition of 2D representations for the spider monkeys.

The ANOVA and the individual plots indicated differences in the level of accuracy reached for each position in the lists. The individual plots show that only primacy or only recency were more common to find in the 0-s retention interval; both primacy and recency effects were more common during the 15-s retention interval and happened for all three list lengths. At the 30-s retention interval, for all three list lengths, only primacy or only recency were more frequent again, but the precision reached by the spider monkeys was closer to chance levels. These results agree partially with our prediction that the retention interval would modulate the serial-position effect, and, as the length of the retention interval increased, the recency effect would dissipate and the primacy effect would increase, because the serial-position effects of the spider monkeys were modulated by the length of the retention interval; however, each spider monkey's serial-position effects were modulated individually. The prediction was based on previous tests with rhesus macaques and capuchin monkeys (Wright, 1999; Wright et al., 1985), and, as we mentioned, both species were trained extensively to solve the task. This could mean that the serial-position effects were also modulated by experience with the task, and, at higher levels of experience with the task, the serial-position effects changed tidily.

It is important to mention that the comparison of the performance of the monkeys against the hypothetical performance by chance indicated differences in the performance at the 0-s retention interval for the lists of three and four pictures but not for the list of five pictures. The data also indicated differences in the 15-s retention interval only for the list of three pictures, not for the lists of four or five pictures, and, for the 30-s retention interval, the analysis indicated differences only for the list of five pictures. However, the analysis by group did not reflect the performance of all individuals; five out of seven monkeys (Camila, Lluvia, Mary, Nery, and Neto) showed a level of accuracy higher than chance in at least one of the positions for the three list lengths and the three retention intervals.

Although previous research agreed with some results, there were also differences and disagreements between experiments. For example, the experiment with squirrel monkeys showed the effects of primacy and recency using retention intervals of .05 and 5 s (Roberts & Kraemer, 1981); one experiment with chimpanzees used a 1-s retention interval, and, when the list was homogeneous, they found only effects of recency, but, when the stimuli were heterogeneous, they found primacy and recency (Beran, 2011). With these retention interval lengths, the experiments with macaques and capuchin monkeys only found recency (Wright, 1999; Wright et al., 1985). The three experiments also used different tasks and experimental designs. The task with capuchin monkeys and macaques used a same-different task (Wright, 1999; Wright et al., 1985), while the task with the chimpanzees and the squirrel monkeys used a match-to-sample task (Beran, 2011; Roberts & Kraemer, 1981).

In the same experiments, the individual performance was reported only in the experiments with squirrel monkeys (Roberts & Kraemer, 1981), capuchin monkeys (Wright, 1999), and the two studies with chimpanzees (Kano et al., 2008; Beran, 2011). From these reports, the two studies with chimpanzees indicated variability within individuals. In Beran's (2011) experiment, the data indicated differences within individuals when the chimpanzees had to recognize a picture that belonged to a different category than the other stimuli in the list (isolation effect); half of the chimpanzees showed primacy and recency effects, while the other half showed only recency. In the study of Kano et al. (2008), the chimpanzees showed differences within individuals in the recognition of pictures with emotional value. However, this experiment involved two individuals and only one showed emotional enhancement, while the other one did not show this effect, and its performance was not different from pictures without emotional value (Kano et al., 2008). Based on this, it is not clear how large the variability within individuals could be in other species of primates in recognition memory experiments.

The variability within individuals has been shown in other experiments on memory with primates (Altschul et al., 2019; Egelkamp et al., 2019) and humans (Medrano et al., 2017). In the case of primates, an experiment carried out by the ManyPrimates Project to test short-term memory using the cups task showed a reduction in accuracy as the retention interval increased, but the data also indicated variability within individuals in 10 out of 11 species; only the orangutans showed very similar values of accuracy within individuals in the three retention intervals of the experiment (Altschul et al., 2019). Another study compared the capabilities of gorillas (*Gorilla gorilla*) and Japanese macaques (*Macaca fuscata*) to recall sequential information; the data indicated individual differences but no species differences in the acquisition of a three-component sequence (Egelkamp et al., 2019).

In the case of humans, previous research in neurobiology has identified individual differences in recognition memory associated with polymorphism in the production of transporters of dopamine; participants with a higher expression of genes that code for transporters of dopamine had a higher number of hits and slower reaction times compared with participants with a smaller number of dopamine transporters (Medrano et al., 2017). A similar effect could be happening in other primate species and could represent a possible explanation for the differences observed between individuals, but also a possible explanation for the differences observed between primate species in other memory experiments (e.g., Altschul et al., 2019). Polymorphism in the expression of genes that code for dopamine transporters has been reported previously in two species of macaques (*Macaca fascicularis* and *Macaca mulatta*) and has been linked to variations in social behavior (Miller-Butterworth et al., 2007). This evidence in primates opens possibilities for future projects testing the relationship between genes and recognition memory in other primates, like spider monkeys.

The heterogeneity in the results of previous studies reflects the importance of the experimental task and could also reflect that recognition memory is sensitive to different variables (e.g., type of stimulus, length of the list, retention interval length, etc.). In particular, the type of task used to test recognition memory could be an important characteristic to change. As we mentioned, the experiments carried out with humans to test the list-length effect were able to find the effect using pictures and a same-different task (Brandt et al., 2019; Kinnell & Dennis, 2012). The data from this kind of task allow the researcher to calculate rates of hits, false alarms, and correct rejections, calculate different psychophysical parameters, and apply Bayesian analysis (Brandt et al., 2019; Dennis et al., 2008; Kinnell & Dennis, 2012), which is a powerful data analysis tool that could be used to classify individual strategies, as researchers have done before with macaques and capuchin monkeys in an experiment on categorization (Whitham & Washburn, 2020). We encourage future research to take these characteristics into consideration in the development of behavioral tasks for testing recognition memory in primates.

In conclusion, our data indicate that the recognition memory of spider monkeys was modulated by the retention interval, the list-length effect, and the position on the list where the picture was presented, but every monkey has shown different serial-position effects. The change in the accuracy as the retention interval increased and the variability within individuals were not reported previously for recognition memory experiments and could represent a particular characteristic of spider monkeys that should be tested in the future.

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