Cognition in black-handed spider monkeys (*Ateles geoffroyi*): A battery of behavioral tests

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Titel
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Författare
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Sammanfattning
Abstract
Cognition allows animals to acquire, process, and store sensory information from the environment and use it to adapt to their surroundings. A battery of behavioral tests was used to assess the cognitive abilities of black-handed spider monkeys (*Ateles geoffroyi*). Black and white cups were used to assess (1) object permanence by showing the animals under which cup the reward was placed, (2) associative learning by concealing where the reward was placed, and (3) long-term memory by repeating the second task after a 4-month break; petri dishes with varying amounts of food were used to assess (4) relative quantity discrimination; and boxes fitted with dotted cards were used to assess discrete number discrimination with (5) equally-sized dots and (6) various-sized dots. For each task, one session comprised 10 trials (i.e. responses). All nine animals succeeded in all tests and, as a group, reached the learning criterion of 70% correct responses on session two in the object permanence and associative learning tasks; on session eleven in the quantity discrimination task; on session sixteen in the numerosity task with equally-sized dots; on session three in the numerosity task with various-sized dots; and averaged 84.4% correct responses in the long-term memory task. Their prompt high score in the numerosity task with various-sized dots suggests that the animals acknowledged the task for its numerical properties as opposed to the size or pattern of the dots. These cognitive abilities are thought to shape the necessary behaviors for the ecological and social needs of the species.

Nyckelord
Keyword
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Contents

1. Abstract

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2. Introduction

Animal cognition refers to the mechanisms involved in the acquisition, perception and storage of sensory information as well as the use of that information to modify and adapt behavior in the environment (Shettleworth, 2010). This processing of information allows animals to be flexible in their behavior which may change according to the situation, motivational level and environmental pressures (Parrish and Brosnan, 2012). As animal cognition encompasses a wide array of cognitive abilities, such as learning, memory, decision making and problem solving, it plays a key role in a broad spectrum of behaviors, from foraging to social interactions (Kamil, 1998; Shettleworth, 2001). The multifunctional basis of cognition, as well as its association

with the concept of intelligence (Roth and Dicke, 2005), make it a topic of interest both to gain a better understanding of the evolution of cognitive abilities and to further unfold the mechanisms underlying behavior.

Primates are particularly suitable for this purpose as they comprise a large variety of lifestyles and therefore a wide range of concurrent cognitive abilities (Lefebvre and Sol, 2008). Additionally, primates have a long-lasting reputation of being intelligent, which often makes them favored candidates in cognitive studies. Great apes in particular are usually prioritized due to the human interest in our phylogenetically closest relatives (Bekoff et al., 2002). Less is known, however, about the cognitive abilities of other taxa, such as New World primates. Black-handed spider monkeys (*Ateles geoffroyi*) are highly specialized frugivores and they display strong fission-fusion dynamics, i.e. dividing and reassembling subgroups according to the availability and distribution of resources (Campbell, 2008). Both, the specialization in diet and the distinct social organization are thought to positively affect the evolution of cognitive abilities. Indeed, the complex spatiotemporal distribution of fruit has been suggested to require considerable processing capacity in order to remember the location of patchy food sources and to better predict times and places to forage (Milton, 1981). On the other hand, high levels of fission-fusion dynamics may require enhanced cognitive skills to enable individuals to better track changes in social relationships both within and between group members (Barrett et al., 2003; Aureli et al., 2008). The ecology and sociality of an animal are strongly believed to shape – to some degree at least – the cognitive abilities of the species (Lefebvre et al., 2004; Dunbar and Schultz, 2007). Furthermore, the information processing which cognition supports is particularly important when environments tend to vary within the lifetime of an individual, as it allows the animal to navigate through unpredictable conditions (Snell-Rood, 2013). Thus, the changing ecological and social environment of spider monkeys, along with their behavioral strategies and potential underlying cognitive processes, make this species an interesting subject in which to further explore cognition.

One way to assess cognition is via a battery of behavioral tests, i.e. a set of tests designed to evaluate an array of cognitive abilities through an animal's performance across various tasks (Burkart et al., 2017). The cognitive domains that have been selected for the battery of the present study include object permanence, associative learning, numerical cognition (quantity discrimination and numerosity), and long-term memory.

Object permanence is the ability to understand that an object continues to exist even after it has disappeared from view, i.e. to maintain a mental representation of the object when out of sight

(Piaget, 1954). For animals moving through structured environments, such as arboreal primates like spider monkeys brachiating through dense vegetation, the ecological relevance of object permanence is apparent. Keeping track of a kin, a mate, or a predator that appears, disappears, and reappears can be essential for the success and survival of an animal. Similarly, in a foraging context, such a cognitive ability may aid in locating and identifying food sources that are not directly perceptible. Indeed, if an object disappears without leaving a trace or perceptual cue to rely on, the search problem will require a solution of an abstract nature such as a cognitive ability for a mental representation of the absent object (Dumas and Wilkie, 1995).

Associative learning, i.e. the formation of positive and negative associations with various stimuli (Siwicki and Ladewski, 2003) is another cognitive ability that may be of interest to further investigate in spider monkeys. A learning mechanism such as learning by association seems to be particularly favorable in tracking continuous seasonal change and variations in the composition and availability of food sources that highly frugivorous species depend on (Milton, 1981). This is a highly valuable ability that allows animals to gain and maintain information on the edibility and nutrition value of certain food items, while learning to avoid unpalatable and/or toxic ones (Laska and Metzker, 1998).

Numerical cognition refers to the ability to perceive and represent the numerical properties of stimuli (Beran et al., 2015). The judgement of relative quantities, at least, is thought to be important for a wide variety of species (insects, Pahl et al., 2013; birds, Emmerton, 1998; fish, Piffer et al., 2012; terrestrial mammals, Ferkin et al., 2009, Perdue et al., 2012; marine mammals, Jaakola et al., 2005) depending on survival and reproduction needs. Indeed, the quantification mechanism which is utilized by animals is thought to reflect the type of numerical information that is most relevant in a given environment as well as the degree to which this ability to discriminate impacts fitness (Beran et al., 2015). For instance, in a foraging context, it is evident that being able to choose the larger of two quantities maximizes food intake and thus provides a subsequent survival advantage (Stephens and Krebs, 1986). In a social context as well may numerical cognition serve a valuable function such as during social decision making, where animals determine the movements of the group depending on the relative quantity of individuals heading in certain directions (Strandburg-Peshkin et al., 2015). During inter-group conflicts, being able to assess the relative size of a rival group allows for animals to decide whether to respond aggressively or retreat from a potentially harmful encounter (Kitchen, 2006). In this sense, spider monkeys are an interesting species in which to test this

aspect of cognition, being strongly dependent both on patchily distributed food sources as well as cohesive and cooperative social groups.

Long-term memory can encompass information retained over hours, days, weeks, months or even years (McGaugh, 2000). The concept of long-term memory refers to the ability to reliably integrate and memorize experiences, and to use this knowledge in future challenges or potentially changing environments (Stephens and Dunlap, 2017). Such a cognitive ability may for instance allow an animal to remember feeding routes and the location of a food patch where it had a successful feeding experience in the past and return to that area instead of a patch in which it was less successful (Janmaat et al., 2006; Di Fiore and Suarez, 2007). Indeed, memories can be used in daily foraging decisions but also in social contexts such as recognizing kin after a prolonged period of separation (Rendall et al., 1996). From this perspective, long-term memory may be an essential ability for highly social and fruit-foraging primates like spider monkeys.

In order to gain more insight into primate cognition, the present study aims at assessing the cognitive abilities of spider monkeys in object permanence, associative learning, quantity discrimination and numerosity, and long-term memory.

More specifically, I addressed the following questions:

1. Do spider monkeys possess the ability of object permanence?
2. Do spider monkeys possess the ability to learn by association?
3. Do spider monkeys possess the ability to discriminate relative quantities?
4. Do spider monkeys possess the ability to discriminate discrete numbers?
5. Do spider monkeys possess the ability to memorize visual information on a long term?

3. Material and methods

3.1. Animals

The study was carried out with nine adult black-handed spider monkeys (*Ateles geoffroyi*) (Figure 1). The group consisted of six males (Neto, Gruñon, Lucas, Neri, Cejitas and Soruyo) and three females (Margarita, Mari and Frida), aged between eight and twelve years. The animals were housed at the field station UMA Doña Hilda Ávila de O'Farrill of the Universidad Veracruzana, located in a nature reserve near Catemaco, in the state of Veracruz, Mexico. They were provided with fresh fruits and vegetables once per day and given seeds and edible foliage

interdum to supplement their diet. The enclosures were equipped with branches, ropes, tires and further fixtures designed for climbing and swinging. The experiments were carried out in the morning before feeding and no food deprivation scheme was adopted for this study. The animals had participated in previous studies on their cognitive abilities, namely in various memory tasks, as well as in sensory discrimination tasks and were thus accustomed to participating in behavioral tests. All monkeys were tested individually in order to prevent interference from, and distraction by, the other monkeys. Data collection took place between May and October of 2019.
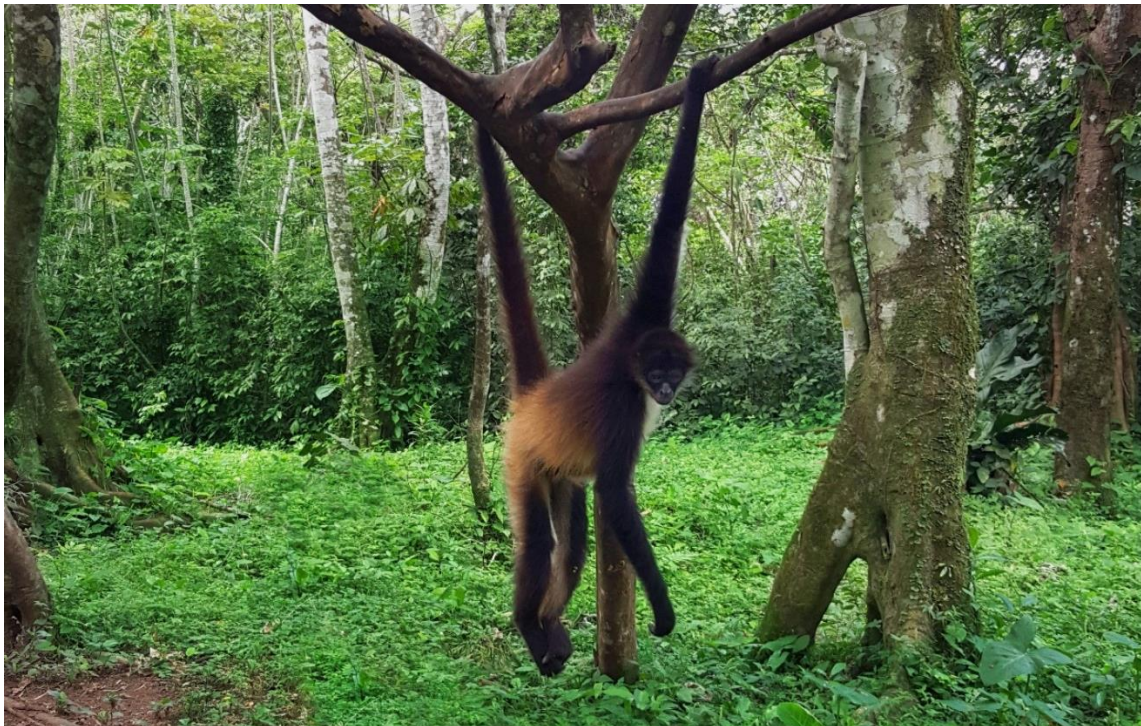
Figure 1. Black-handed spider monkey *Ateles geoffroyi*.

3.2. Experiment 1 – Object permanence

3.2.1. Test apparatus

The test apparatus consisted of an opaque white plexiglass board of 14 cm by 44 cm with two cylindrical plastic cups, one black and one white (height and diameter both of 5 cm) (Figure 2). The cups were attached to the board by a thin cotton twine, the purpose of which was to facilitate the handling of the cups during the experiment, i.e. to prevent the cups from falling as well as to prevent the monkeys from taking hold of the cups. The two cups were placed face down on the board at a distance of about 15 cm from one another in order to hide – under one or the other

cup – a food reward. The food rewards used in this test were raisins, dried cranberries or small pieces of cookie, depending on each individual's favored food item. Food preferences were assessed during the familiarization phase between experimenter and spider monkeys.

Figure 2. Test apparatus for the object permanence, associative learning, and long-term memory tests.

3.2.2. Behavioral test

The test apparatus represented a two-choice paradigm in which the spider monkeys were allowed to choose between one of the two colored cups that were presented to them, under one of which a food item was hidden (Figure 3). The other cup held nothing and thus did not present any reward if selected. The animals were allowed to observe under which of the two colored cups the food item was placed before the apparatus was presented to them. Once the cups were placed on the board, the apparatus was immediately presented to the animals. Therefore, the time interval between hiding the food item under the cup and presenting the apparatus to the animals was of a couple of seconds only. This short time interval was kept constant across trials and sessions. The monkeys' response in determining where the food reward was after it was covered by the cup assessed their object permanence abilities.

Figure 3. Spider monkey Mari selecting one of the two presented colored cups.

3.2.3. Experimental design

For this experiment, the experimenter stepped in front of the enclosure and called the monkey assigned to participate in the task. Once the animal was at the mesh, the experimenter – standing at about one meter distance – put a food item on the plexiglass board and placed both cups face down on the board, with one of them covering the reward. In order to avoid possible color biases, half of the animals were assigned one color (black), and the other half the other color (white), resulting in two possible combinations; 1) black cup with food item, and white cup without food, and 2) white cup with food item, and black cup without food. Neto, Neri, Soruyo, Mari and Frida were assigned black as the color that they were supposed to associate with a food reward, and Gruñon, Cejitas, Margarita and Lucas were assigned white as the color that they were supposed to associate with a food reward. The placement of the food item and cups was always done whilst ensuring the animal was paying attention to the process. The experimenter then approached the mesh, presenting the apparatus to the monkey and allowing the latter to select one of the two colored cups. The animals chose a certain cup by either simply touching one of the two cups – in which case the experimenter lifted the selected cup and allowed the monkey to grab the food reward – or by lifting the cup themselves and then retrieving the food reward. In the case that the animal decided for the empty cup, the experimenter lifted it, to show the monkey that no reward was underneath. Control trials were

performed prior to the experiment, and an independent observer repeatedly assessed the experimenter's behavior during the trials and found no indication of the latter giving unintended cues to the animal. The experimenter consistently looked at the animal's face during the trials – as opposed to any part of the apparatus – to avoid giving any cues by gaze, which also allowed the experimenter to ensure that the animal was focused on the task and not on her. N.B.: The same procedure was carried out for all further experiments as well. For each animal, the number of correct and incorrect responses were recorded, which corresponded to selecting the cup with the food item or the empty cup, respectively. The position of the cups (e.g. white cup on the left and black cup on the right) was pseudorandomized in order to minimize possible position preferences, and both color stimuli were presented equally often to the left and the right. The same color was presented a maximum of three times in a row on one or the other side. Ten trials formed one session, and one session was performed per animal, per day. At the end of each session, the experimenter gave a piece of cookie to the monkey, as to mark the end of the session. A total of 60 trials, i.e. six sessions were performed with each individual.

3.3. Experiment 2 – Associative learning

3.3.1. Test apparatus

The test apparatus used for this experiment was the same one that was used for Experiment 1 (see above), (Figure 2).

3.3.2. Behavioral test

As in Experiment 1, the animals were presented with the two-choice apparatus from which they were allowed to choose between one of the two colored cups, under one of which a food item was hidden. In this experiment, however, the animals were prevented from observing under which of the two colored cups the food item was placed, and which cup was left empty. As each individual was previously assigned either black or white as the color that was associated with a food reward (see Experiment 1), the animals' ability to associate a color with the presence or absence of a food item could be used to assess their associative learning capacities.

3.3.3. Experimental design

Similar to the previous task, the experimenter called the animal assigned to participate in the task and stood at a one meter distance while the latter came to the mesh. In this experiment, it was imperative that the monkey was not allowed to see under which cup the food item was

placed and the experimenter thus prepared the two-choice apparatus with her back turned to the animal. The experimenter manipulated the food items with her hands prior to the first trial to avoid potential olfactory biases. The cups also completely concealed the food items, leaving no openings that may have allowed for any olfactory cues to be picked up by the monkeys, and there was no indication from the animals' behavior suggesting that they might be able to use olfactory cues. The experimenter then turned around, approached the mesh and presented the apparatus to the monkey to decide for one of the two options either by touching or grabbing, one of the two colored cups. This process was repeated for each trial. In the case that the animal picked the empty cup, the experimenter lifted it, to show the monkey that no reward was underneath. For each animal, the number of correct and incorrect responses were recorded. The position of the cups was pseudorandomized, and both color stimuli were presented equally often to the left and the right. The same color was presented a maximum of three times in a row on one or the other side. Ten trials formed one session, and one to two sessions were performed per animal, per day. At the end of each session, the experimenter gave a piece of cookie to the monkey, as to mark the end of the session. A total of 200 trials, i.e. 20 sessions were performed with each individual.

3.4. Experiment 3 – Quantity discrimination

3.4.1. Test apparatus

The test apparatus consisted of an opaque white plexiglass board of 14 cm by 44 cm with attachable petri dishes (diameter of 9 cm) containing equally sized, but different quantities of, food items (Figure 4). A piece of magnetic band was taped under each petri dish, which allowed the experimenter to attach them to, and detach them from, the board which was fitted with two pieces of thin metal foil, taped at a 15 cm distance. The food items used in this experiment were pieces of raisins, pieces of cranberries, quarters of Cheerios, and unshelled sunflower seeds. Depending on their color, the food items were placed in petri dishes that were fitted with either a white background (Figure 4.A) or a black background (Figure 4.B), as to ensure a clear color contrast.

A.

B.

Figure 4. Test apparatus for the quantity discrimination test with A. dark food items (pieces of raisins) on a white background, and B. light food items (unshelled sunflower seeds) on a black background.

3.4.2. Behavioral test

The test apparatus represented a two-choice paradigm in which the animals were allowed to choose between one of the two petri dishes, which always contained varying quantities of food units. The spider monkeys' performance in recognizing two different quantities by selecting the petri dish with the higher number of food units allowed for the assessment of their discrimination abilities towards relative quantities.

3.4.3. Experimental design

The monkey assigned to participate in the task was called by the experimenter who stood at a one meter distance from the mesh and started the set up of the trial once the monkey was at the

mesh. The experimenter placed different food quantities in both petri dishes and covered them with their transparent lids before stepping forward and presenting them to the animal. The petri dish lids prevented the monkeys from grabbing the food items and required them to select one of the two dishes before getting access to the contents. Once the monkey made a choice by touching or placing its hand on one of the two petri dishes, the experimenter removed the lid of the chosen dish and handed its content to the monkey. A correct response was recorded if the monkey chose the larger quantity, and an incorrect response was recorded if the smaller quantity was chosen. Although it was assumed that the animals would select the higher quantity if they were able to discriminate it, it was uncertain whether they would. Therefore, even when the incorrect, i.e. smaller quantity was selected, the experimenter handed the contents of the petri dish to the monkey because – as the contents of both dishes were visible – this was considered an "informed choice". However, some individuals developed a side bias due to this, as they received a food reward by selecting either dish, and the experimenter ceased to hand the food items to an animal if the smaller quantity was selected, as to encourage the animals to pay further attention to both dishes and discourage any side biases. This change in tactics was implemented after about eight sessions, at which point the side biases had become evident. Each monkey was presented with the following ratios of food items: 1:2, 1:3, 1:4, 1:5, 2:3, 2:4, 2:5, 3:4, 3:5, 4:5. These ratios represent the number of food pieces. The position of the petri dishes (e.g. higher quantity on the left and lower quantity on the right) was pseudorandomized in order to minimize position preferences, and both – large and small quantities – were presented equally often to the left and the right. The larger quantity was presented a maximum of three times in a row on one or the other side. Each of the ten ratios mentioned above represented one trial, the ten trials represented one session, and one to two sessions were performed per animal, per day. At the end of each session, the experimenter gave a piece of cookie to the monkey, as to mark the end of the session. A total of 300 trials, i.e. 30 sessions were performed with each individual.

3.5. Experiment 4 – Numerosity with equally-sized dots

3.5.1. Test apparatus

The test apparatus consisted of a metal bar that was 50 cm long and 6 cm wide, with two PVC boxes (5 x 5 x 5 cm) that were attached to the bar at a 22 cm distance (Figure 5). Laminated white cards (5 x 5 cm) containing different numbers of black filled circles were fitted with a piece of magnetic tape, which allowed them to be attached to the boxes' slightly larger metal

lids (6 cm x 6.8 cm). The sizes of the circles were adjusted as to have the same amount of black and white surface on each card in order to ensure that the choice of the animals was made according to the absolute number of circles and not according to the amount of surface covered by the black circles. The boxes had a shallow opening which allowed the spider monkeys to retrieve a food reward in case of a correct response. The food rewards used in this test were raisins, dried cranberries or half Cheerios.
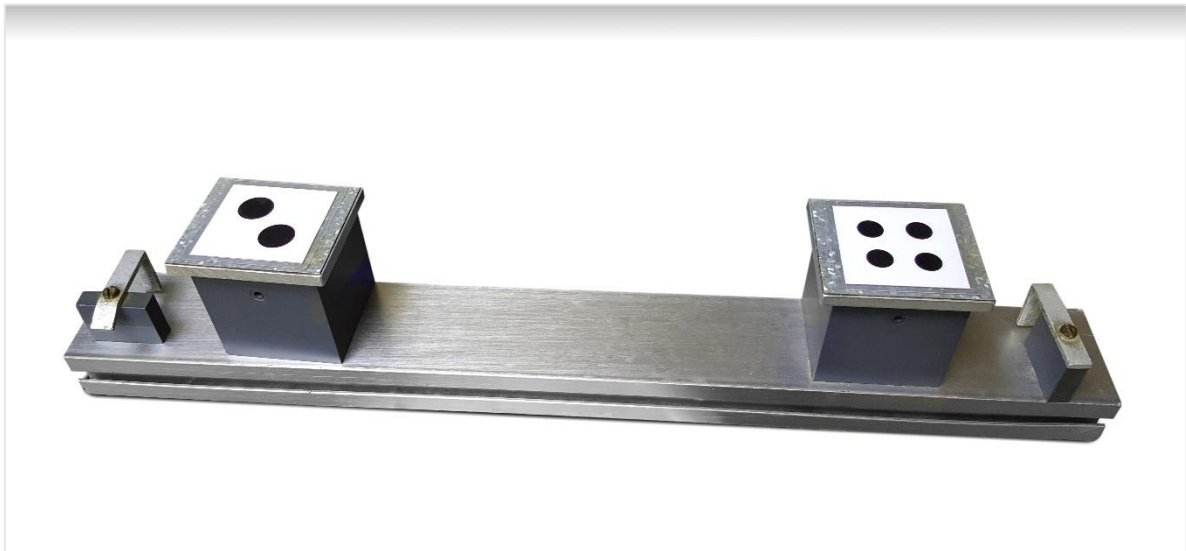

Figure 5. Test apparatus for the numerosity test with two number cards attached to the metal lids via magnetic band.

3.5.2. Behavioral test

The test apparatus represented a two-choice paradigm in which the animals were allowed to choose between one of the two numbered boxes, where the box fitted with the card with the higher number of filled circles contained a food item. The other box held nothing and thus did not present any reward if selected. The spider monkeys' performance in recognizing two different numerical properties by selecting the box with the higher numbered card allowed for the assessment of their numerical discrimination abilities towards discrete numbers.

3.5.3. Experimental design

As in the previous tasks, the experimenter called the monkey assigned to participate in the task and the session started with the animal at the mesh. A food item was placed in the box fitted with the higher numbered card and the other box fitted with the lower numbered card was left empty. This process was done with the experimenter's back to the animal being tested so that the latter could not see where the food reward would be located. The experimenter manipulated

the food items with her hands prior to the first trial to avoid potential olfactory biases. The boxes also closed tightly, leaving no openings that may have allowed for any olfactory cues to be picked up by the monkeys, and there was no indication from the animals' behavior suggesting that they might be able to use olfactory cues. The experimenter then turned around, approached the mesh and allowed the animal to select one of the two dotted boxes by either touching or lifting the lid of the desired box. If the animal only touched the box, the experimenter opened the lid, allowing the monkey to retrieve the reward in case of a correct response, or demonstrating the empty box in case of an incorrect response. A correct response was recorded if the animal chose the higher number, and an incorrect response was recorded if the lower number was selected. Each monkey was presented with the following combinations of dots: 1:2, 1:3, 1:4, 1:5, 2:3, 2:4, 2:5, 3:4, 3:5, 4:5. The position of the numbered cards (e.g. higher number on the left and lower number on the right) was pseudorandomized in order to minimize position preferences, and both – high and low numbers – were presented equally often to the left and the right. The card with the higher number of a given pair was presented a maximum of three times in a row on one or the other side. Each of the number combinations represented one trial, the ten trials represented one session, and one to two sessions were performed per animal, per day. At the end of each session, the experimenter gave a piece of cookie to the monkey, as to mark the end of the session. A total of 300 trials, i.e. 30 sessions were performed with each individual.

3.6. Experiment 5 – Numerosity with various-sized dots

3.6.1. Test apparatus

The test apparatus used for this experiment was the same one that was used for Experiment 4 (see above), (Figure 5). However, in this experiment, the sizes of the filled circles were modified so that various-sized dots were present on a given card in order to control for the possibility that the animals would base their decision for one of the two options on the size of the dots rather than on their numerical properties (Figure 6). The overall surface that the black circles and the white background covered were still equal to ensure that the animals' choice was made according to the absolute number of dots and not on amount of surface covered by the dots.

Figure 6. Test apparatus for the numerosity test with two number cards of various-sized dots.

3.6.2. Behavioral test

The procedure for this test was the same as for Experiment 4 (see above).

3.6.3. Experimental design

The experimental design for this test was the same as for Experiment 4 (see above).

3.7. Experiment 6 – Long-term memory

3.7.1. Test apparatus

The test apparatus used for this experiment was the same one that was used for Experiments 1 and 2 (see above), (Figure 2).

3.7.2. Behavioral test

With each spider monkey that had previously been assigned either black or white as the color to associate with a food reward (see Experiments 1 and 2), the animals were presented with the two-choice apparatus again at the end of all other experiments in order to test their long-term memory for a previously learned visual association. More specifically, the time between the end of the second experiment and the start of this experiment marked a four-month interval. Therefore, this last experiment allowed to assess the animals' long-term memory for the associative learning task that they had mastered previously.

3.7.3. Experimental design

The experimental design for this experiment was the same as for Experiment 2 (see above). In order to assess the animals' long-term memory, one single session of ten trials was performed with each individual. A single trial may have resulted in the monkeys' performance being at random, and more than one session may have allowed them to "relearn" the color combinations in the case that they did not remember them.

3.8. Data analysis

In each trial of each experiment, the animals had two possible responses; to select the correct side, i.e. the rewarded side of the test apparatus, or to select the incorrect side, i.e. the non-rewarded side of the test apparatus. In Experiments 1, 2 and 6 (object permanence, associative learning and long-term memory), a correct response corresponded to the animals selecting their assigned color of cups. In Experiment 3 (quantity discrimination), a correct response corresponded to the animals selecting the petri dish with the larger quantity of food items. In Experiments 4 and 5 (numerosity with equally-sized dots and numerosity with various-sized dots), a correct response corresponded to the animals selecting the box with the higher number of dots. The learning criterion was set at 70% correct responses over two consecutive sessions, i.e. at least 14 correct responses over 20 trials ($p<0.05$, two-tailed binomial). The mean performances of the group across tasks were calculated in order to assess the direction and intensity of the trendlines, that is, of the potential progress of the group across sessions in each task (Spearman's rho correlation test).

In the experiments involving test apparatuses with numerical properties (quantity discrimination, numerosity with equally-sized dots and numerosity with various-sized dots), the possible correlation between the animals' performance and the task difficulty – in terms of how similar or different the discriminanda were – was also assessed (Spearman's rho correlation test). The animals' performance was again assessed in terms of percentage of correct responses, while the task difficulty was assessed according to the number of food items, or number of dots, the various combinations differed by. These corresponded to quantity or number combinations differing by one food item or dot (1:2, 2:3, 3:4, 4:5), by two food items or dots (1:3, 2:4, 3:5), by three food items or dots (1:4, 2:5), and by four food items or dots (1:5).

Task difficulty was assessed by comparing the number of sessions each individual needed in each task in order to reach the learning criterion (Wilcoxon signed-rank test).

4. Results

4.1. Experiment 1 – Object permanence

In the object permanence task, all nine animals reached the learning criterion of scoring at least 70% correct responses in two consecutive sessions already at the end of the second session (Figure 7). After reaching the learning criterion, all animals also remained above the latter.
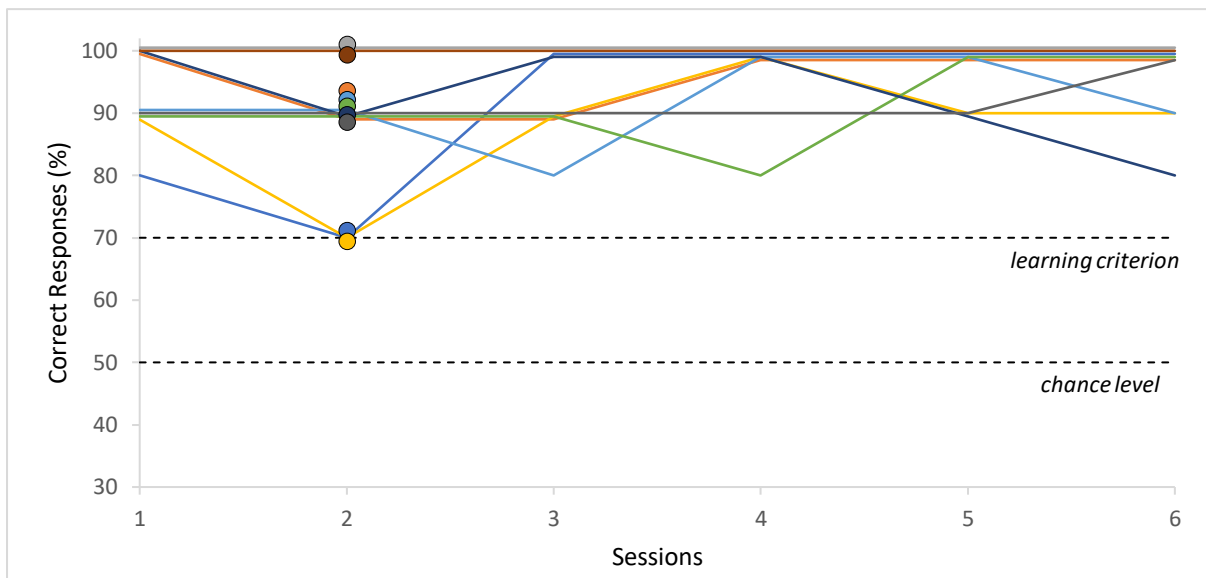

Figure 7. Performance of the nine spider monkeys during the object permanence task. Each data point represents the percentage of correct responses of a given animal in one session of ten trials. The colored dots represent the number of sessions needed for each individual to reach the learning criterion. –– Neto –– Gruñon –– Neri –– Cejitas –– Soruyo –– Margarita –– Mari –– Frida –– Lucas

Regarding the animals' performance as a group, the spider monkeys already performed above the learning criterion of 70% correct responses in the first two sessions and always remained there in all six sessions (Figure 8). Though the group's performance did not increase significantly across the sessions (p=0.117, r_s=0.706, two-tailed Spearman's rho), the animals' mean performance remained in the range of 90% to 100% correct responses.
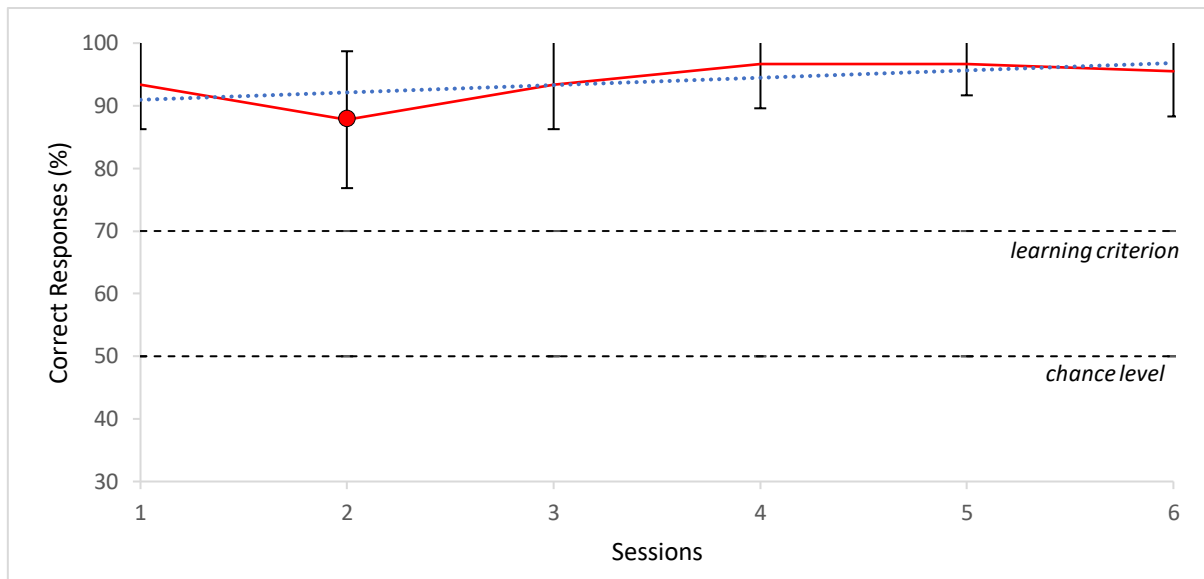
Figure 8. Mean performance of the nine spider monkeys during the object permanence task. Each data point represents the mean (±SD) percentage of correct responses in one session of ten trials. The red dot represents the number of sessions needed for the group to reach the learning criterion. The dotted blue line shows the trendline of the group's performance.

4.2. Experiment 2 – Associative learning

The number of sessions that the animals required to reach the learning criterion in the associative learning task ranged between two sessions for Neto, Gruñon, Neri, Cejitas, Mari and Lucas, and five sessions for Frida (Figure 9). Margarita required three sessions to reach the learning criterion, and Soruyo required four. After reaching the learning criterion, Neto, Gruñon, Margarita, Mari and Lucas remained above the latter, while Neri Cejitas, Soruyo and Frida displayed an occasional drop to between 50% to 60% correct responses, but generally stayed above the learning criterion of 70% correct responses.
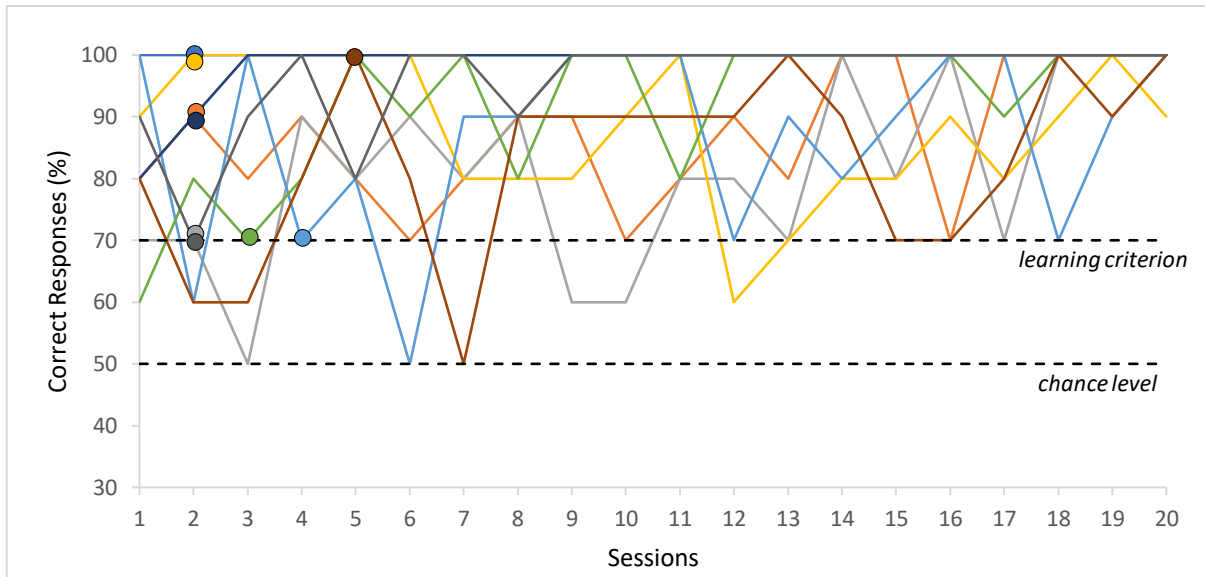
Figure 9. Performance of the nine spider monkeys during the associative learning task. Each data point represents the percentage of correct responses of a given animal in one session of ten trials. The colored dots represent the number of sessions needed for each individual to reach the learning criterion. –– Neto –– Gruñon –– Neri –– Cejitas –– Soruyo –– Margarita –– Mari –– Frida –– Lucas

Regarding the animals' performance as a group, their mean performance was already above the learning criterion of 70% correct responses in the first two sessions and always remained there in all 20 sessions (Figure 10). Nevertheless, the group's performance increased significantly across the sessions ($p<0.01$, $r_s=0.836$, two-tailed Spearman's rho) as illustrated by the trendline showing a positive slope.
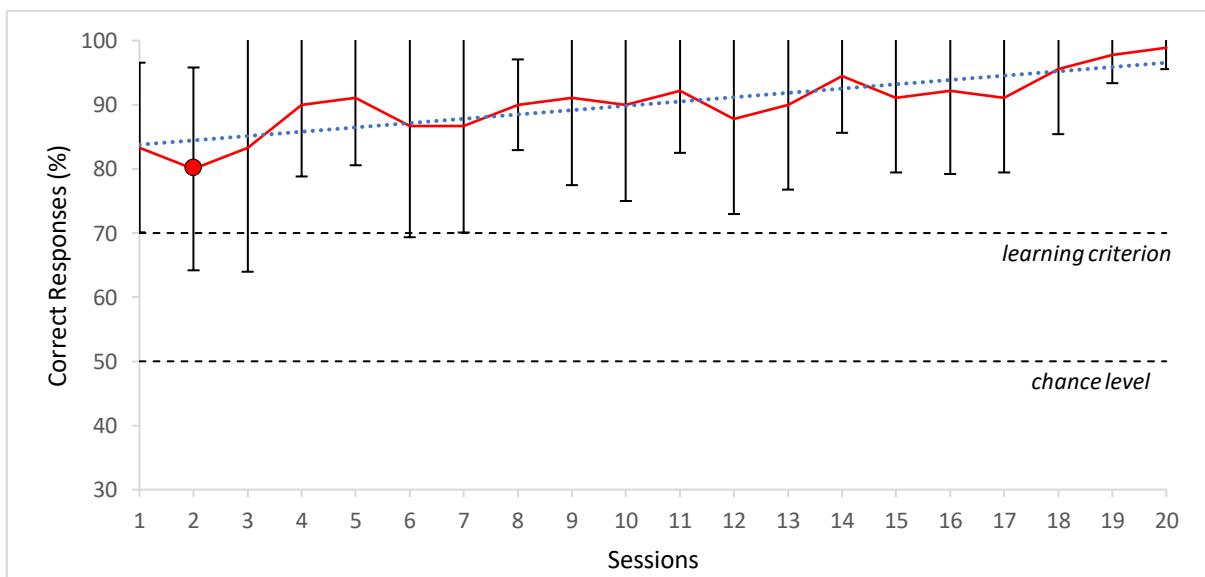
Figure 10. Mean performance of the nine spider monkeys during the associative learning task. Each data point represents the mean (±SD) percentage of correct responses in one session of ten trials. The red dot represents the number of sessions needed for the group to reach the learning criterion. The dotted blue line shows the trendline of the group's performance.

4.3. Experiment 3 – Quantity discrimination

The number of sessions that the animals required to reach the learning criterion in the quantity discrimination task ranged between two sessions for Neto, Cejitas and Soruyo, and twelve sessions for Lucas (Figure 11). Gruñon required six sessions to reach the learning criterion, Neri and Frida required three, and Margarita required seven. Due to Mari experiencing digestive upset during several days of the quantity discrimination experiment, she did not participate in this task. After reaching the learning criterion, Lucas remained above the latter, while the other individuals displayed occasional drops to between 30% to 60% correct responses, but generally stayed above the learning criterion of 70% correct responses.
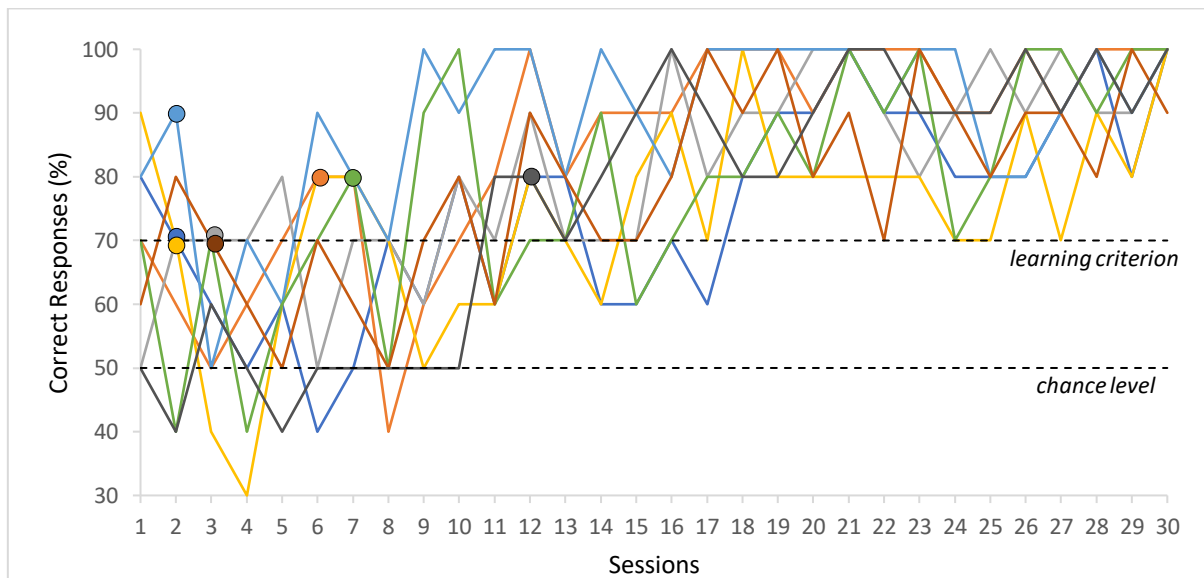

Figure 11. Performance of the eight spider monkeys during the quantity discrimination task. Each data point represents the percentage of correct responses of a given animal in one session of ten trials. The colored dots represent the number of sessions needed for each individual to reach the learning criterion. — Neto — Gruñon — Neri — Cejitas — Soruyo — Margarita — Frida — Lucas

Regarding the animals' performance as a group, the spider monkeys reached the learning criterion of 70% correct responses for the first time in session eleven and remained above the learning criterion in all following sessions (Figure 12). The group's performance increased significantly across the sessions ($p<0.01$, $r_s=0.887$, two-tailed Spearman's rho) as illustrated by the trendline showing a positive slope.
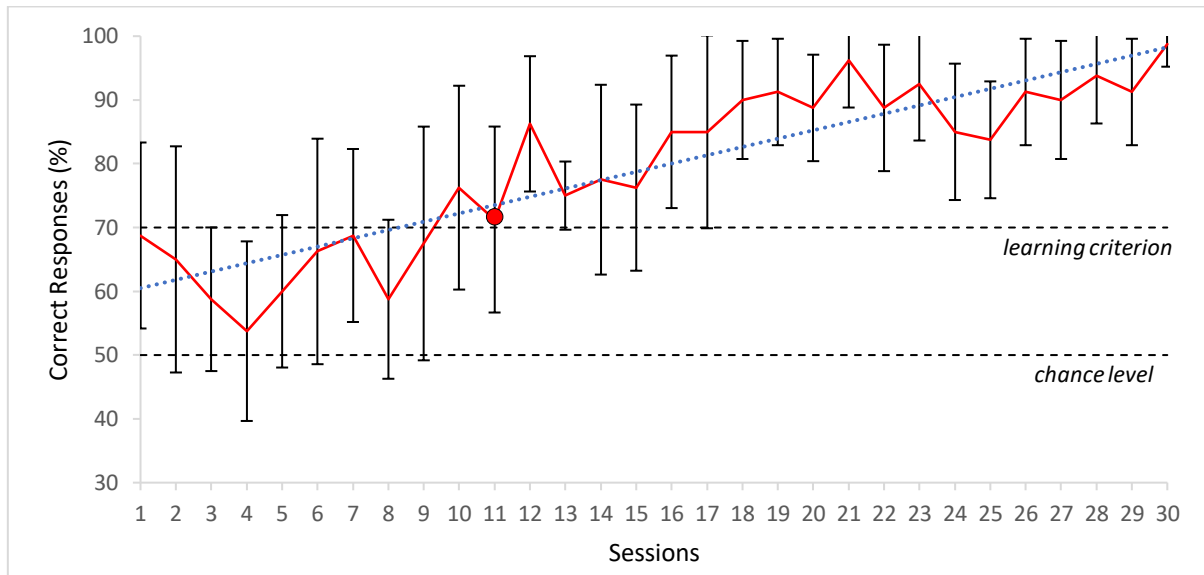
Figure 12. Mean performance of the eight spider monkeys during the quantity discrimination task. Each data point represents the mean (±SD) percentage of correct responses in one session of ten trials. The red dot represents the number of sessions needed for the group to reach the learning criterion. The dotted blue line shows the trendline of the group's performance.

The monkeys' performance as a group significantly correlated with task difficulty ($p<0.01$, $r_s=1$, two-tailed Spearman's rho) (Figure 13). Trials in which the number of food items differed only by one (Δ1) yielded the lowest mean scores of correct responses and trials in which the number of food items differed by four (Δ4) yielded the highest mean scores.
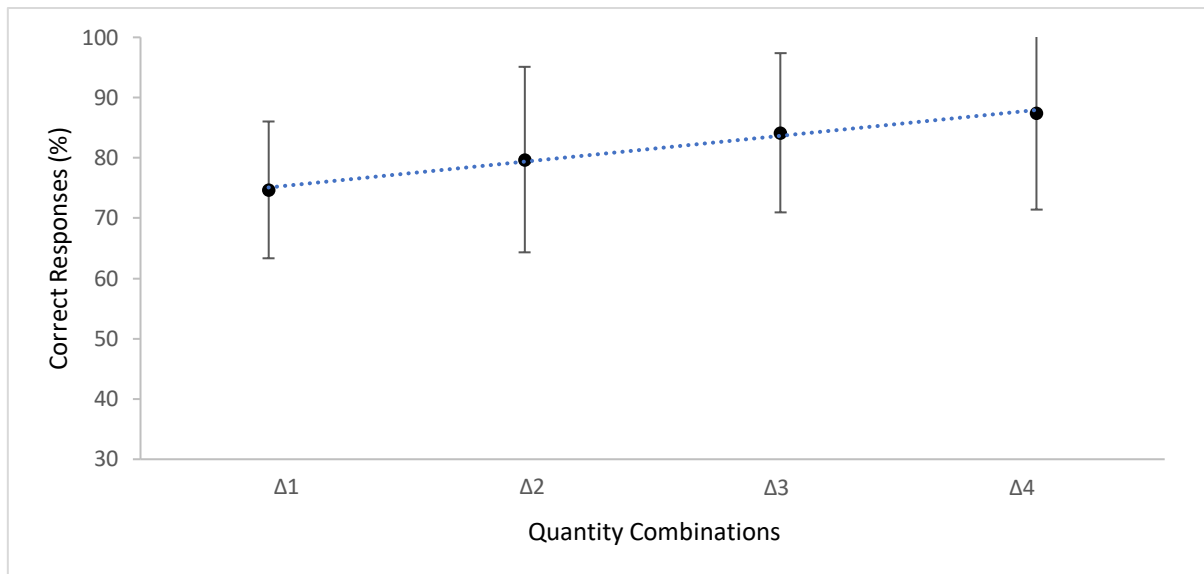
Figure 13. Mean performance of the eight spider monkeys in the quantity discrimination task according to the number of food items by which the various quantity combinations differed from each other. Each data point represents the mean (±SD) percentage of correct responses in one session of ten trials. Δ1 refers to the quantity combinations which differed by only one food item (1 vs 2, 2 vs 3, 3 vs 4, and 4 vs 5). Accordingly, Δ2, Δ3 and Δ4 refer to the quantity combinations which differed by two food items (1 vs 3, 2 vs 4, and 3 vs 5), three food items (1 vs 4 and 2 vs 5) and four food items (1 vs 5), respectively. The dotted blue line shows the trendline of the group's performance.

4.4. Experiment 4 – Numerosity with equally-sized dots

The number of sessions that the animals required to reach the learning criterion in the numerosity task with equally-sized dots ranged between two sessions for Neto, and twelve sessions for Gruñon (Figure 14). Neri required three sessions to reach the learning criterion, Margarita required four, Soruyo and Frida required five, Lucas required seven, Cejitas required eights, and Mari required nine sessions. After reaching the learning criterion, all individuals displayed intermittent drops to between 20% to 60% correct responses.

Figure 14. Performance of the nine spider monkeys during the numerosity task with equally-sized dots. Each data point represents the percentage of correct responses of a given animal in one session of ten trials. The colored dots represent the number of sessions needed for each individual to reach the learning criterion. — Neto — Gruñon — Neri — Cejitas — Soruyo — Margarita — Mari — Frida — Lucas

Regarding the animals' performance as a group, the spider monkeys reached the learning criterion of 70% correct responses for the first time in session sixteen and only dropped under the learning criterion once – to 64.44% – in the following sessions (Figure 15). The group's performance increased significantly across the sessions ($p<0.01$, $r_s=0.838$, two-tailed Spearman's rho) as illustrated by the trendline showing a positive slope.
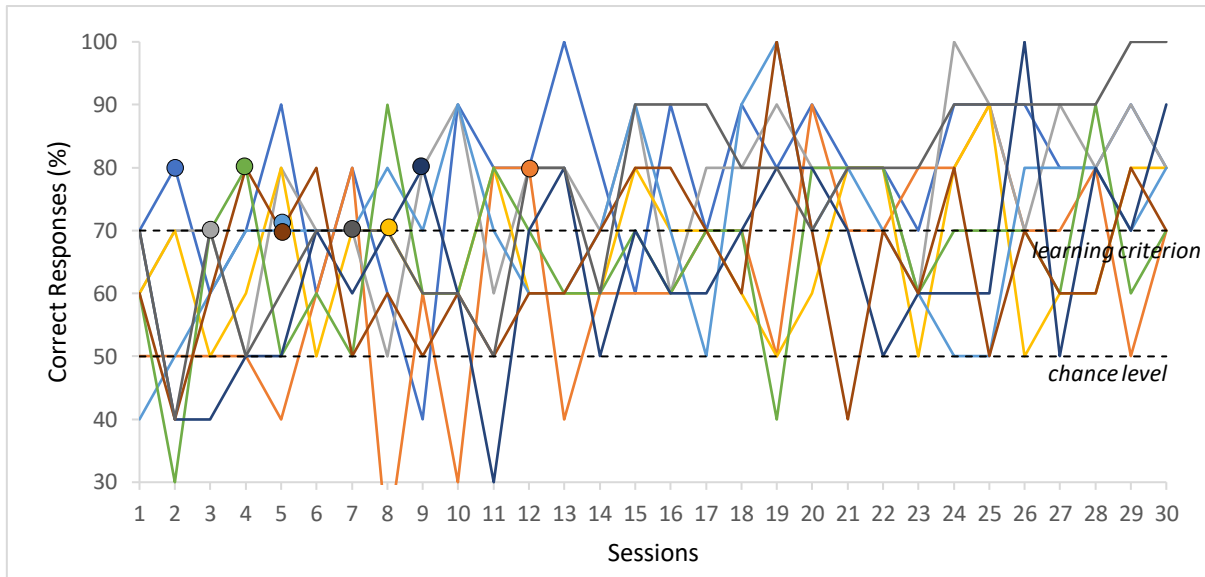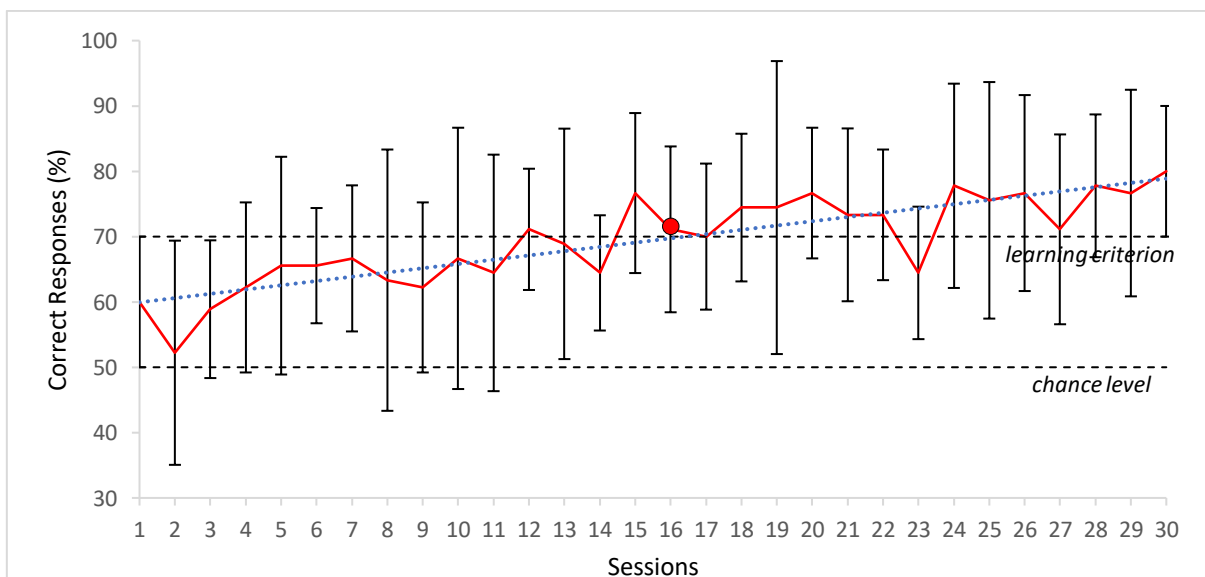
Figure 15. Mean performance of the nine spider monkeys during the numerosity task with equally-sized dots. Each data point represents the mean (±SD) percentage of correct responses in one session of ten trials. The red dot represents the number of sessions needed for the group to reach the learning criterion. The dotted blue line shows the trendline of the group's performance.

The monkeys' performance as a group significantly correlated with task difficulty ($p < 0.05$, $r_s = 1$, two-tailed Spearman's rho) (Figure 16). Trials in which the number of dots differed only by one (Δ1) yielded the lowest mean scores of correct responses and trials in which the number of dots differed by four (Δ4) yielded the highest mean scores.
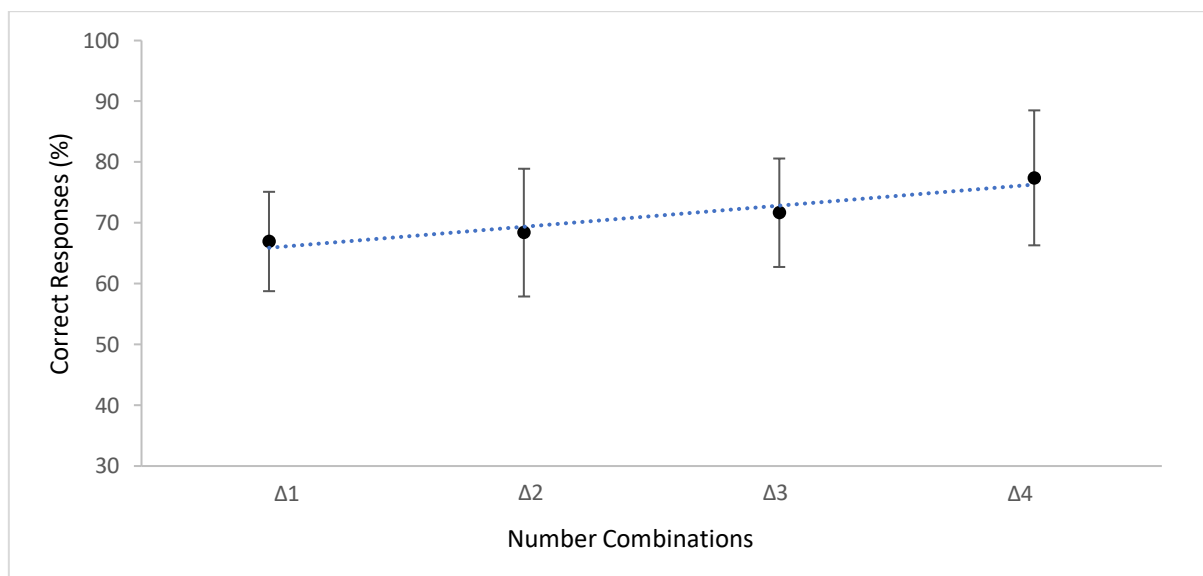
Figure 16. Mean performance of the nine spider monkeys in the numerosity task with equally-sized dots according to the number of dots by which the various number combinations differed from each other. Each data point represents the mean (±SD) percentage of correct responses in one session of ten trials. Δ1 refers to the number combinations which differed by only one dot (1 vs 2, 2 vs 3, 3 vs 4, and 4 vs 5). Accordingly, Δ2, Δ3 and Δ4 refer to the number combinations which differed by two dots (1 vs 3, 2 vs 4, and 3 vs 5), three dots (1 vs 4 and 2 vs 5) and four dots (1 vs 5), respectively. The dotted blue line shows the trendline of the group's performance.

4.5. Experiment 5 – Numerosity with various-sized dots

The number of sessions that the animals required to reach the learning criterion in the numerosity task with various-sized dots ranged between two sessions for Gruñon, Neri, Mari and Lucas, and thirteen sessions for Soruyo (Figure 17). Neto, Cejitas and Margarita required three sessions to reach the learning criterion, and Frida required seven. After reaching the learning criterion, Neto and Lucas remained above the latter, while the other individuals displayed intermittent drops to between 30% to 60% correct responses.

Figure 17. Performance of the nine spider monkeys during the numerosity task with various-sized dots. Each data point represents the percentage of correct responses of a given animal in one session of ten trials. The colored dots represent the number of sessions needed for each individual to reach the learning criterion. –– Neto –– Gruñon –– Neri –– Cejitas –– Soruyo –– Margarita –– Mari –– Frida –– Lucas

Regarding the animals' performance as a group, the spider monkeys already reached the learning criterion in session three and displayed only occasional drops under the learning criterion – to 65.55% and to 67.77% – in the following sessions (Figure 18). It is interesting to note that while the group's performance in the numerosity task with equally-sized dots gradually and significantly increased from around 60% to 80% across the sessions (Figure 15), the group's performance in the numerosity task with various-sized dots already starts between 70% and 80%, and mostly remains in that range throughout the sessions ($p=0.580$, $r_s=-0.105$, two-tailed Spearman's rho) as illustrated by the trendline showing a relatively straight slope.
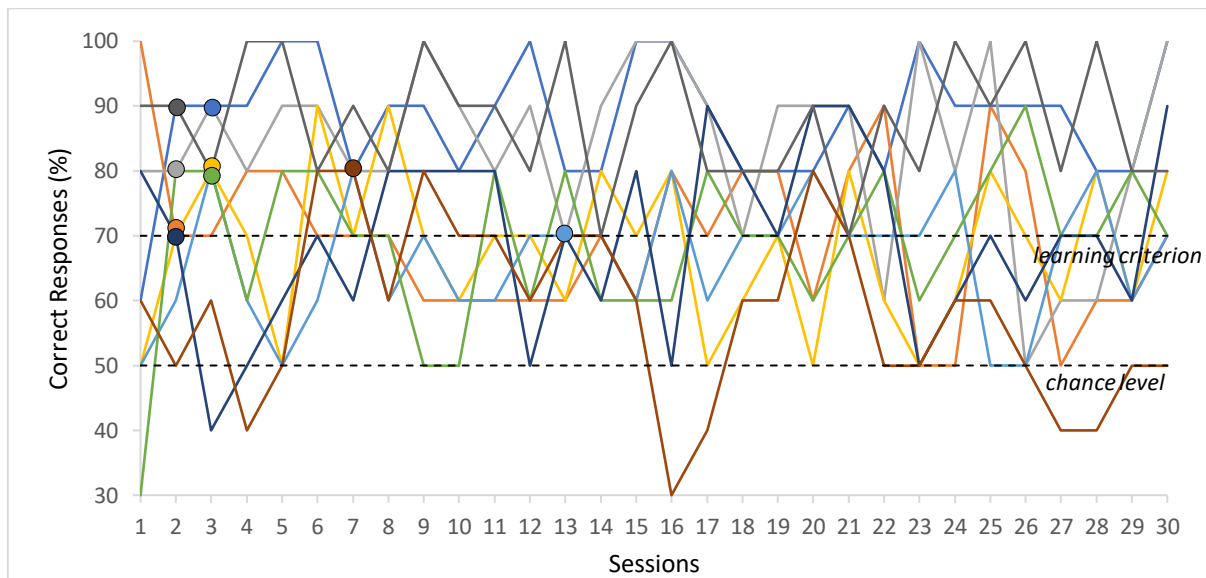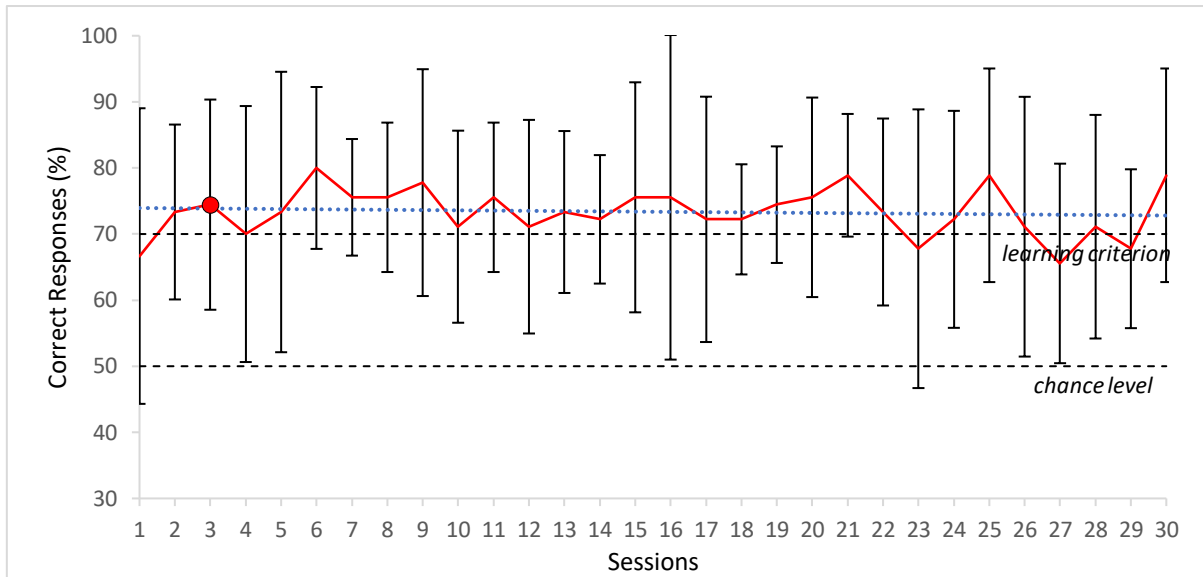
Figure 18. Mean performance of the nine spider monkeys during the numerosity task with various-sized dots. Each data point represents the mean (±SD) percentage of correct responses in one session of ten trials. The red dot represents the number of sessions needed for the group to reach the learning criterion. The dotted blue line shows the trendline of the group's performance.

The monkeys' performance as a group significantly correlated with task difficulty ($p<0.05$, $r_s=1$, two-tailed Spearman's rho) (Figure 19). Trials in which the number of dots differed only by one (Δ1) yielded the lowest mean scores of correct responses and trials in which the number of dots differed by four (Δ4) yielded the highest mean scores.
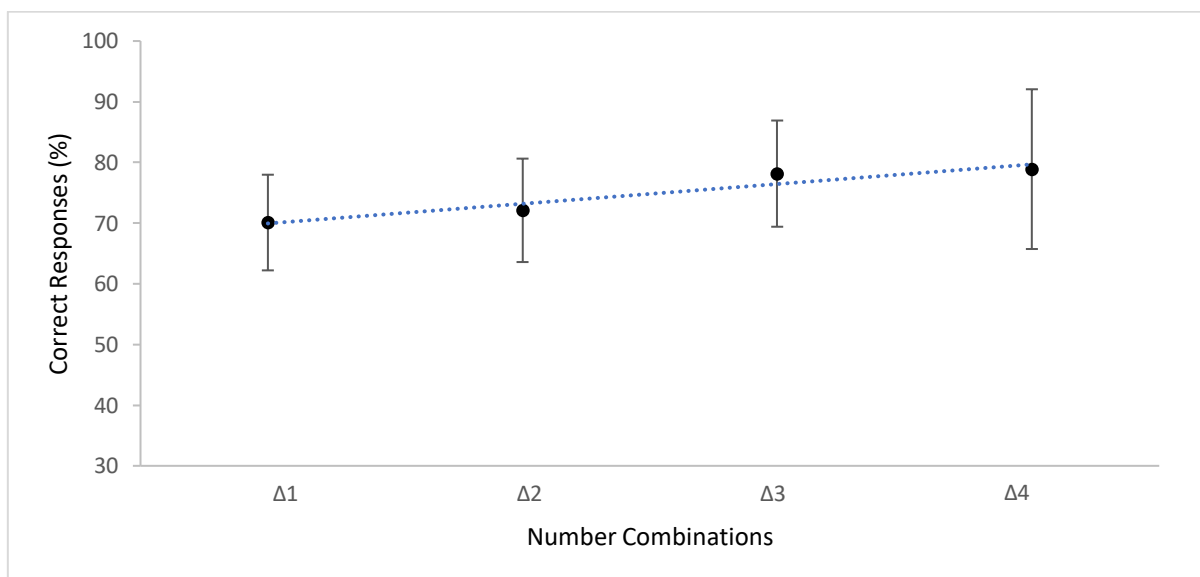
Figure 19. Mean performance of the nine spider monkeys in the numerosity task with various-sized dots according to the number of dots by which the various number combinations differed from each other. Each data point represents the mean (±SD) percentage of correct responses in one session of ten trials. Δ1 refers to the number combinations which differed by only one dot (1 vs 2, 2 vs 3, 3 vs 4, and 4 vs 5). Accordingly, Δ2, Δ3 and Δ4 refer to the number combinations which differed by two dots (1 vs 3, 2 vs 4, and 3 vs 5), three dots (1 vs 4 and 2 vs 5) and four dots (1 vs 5), respectively. The dotted blue line shows the trendline of the group's performance.

4.6. Experiment 6 – Long-term memory

The animals' performance in the long-term memory task – that is, their performance in the first associative learning session after a 4-month break – ranged between 60% for Gruñon and 100% for Mari and Lucas (Figure 20). Frida scored 70% correct responses, Neri and Cejitas scored 80% correct responses, and Soruyo and Margarita scored 90% correct responses. Accordingly, eight out of the nine animals scored at least 70% correct responses after the 4-month break and thus immediately reached the learning criterion. Regarding the animals' performance as a group, their mean performance was 84.44%.
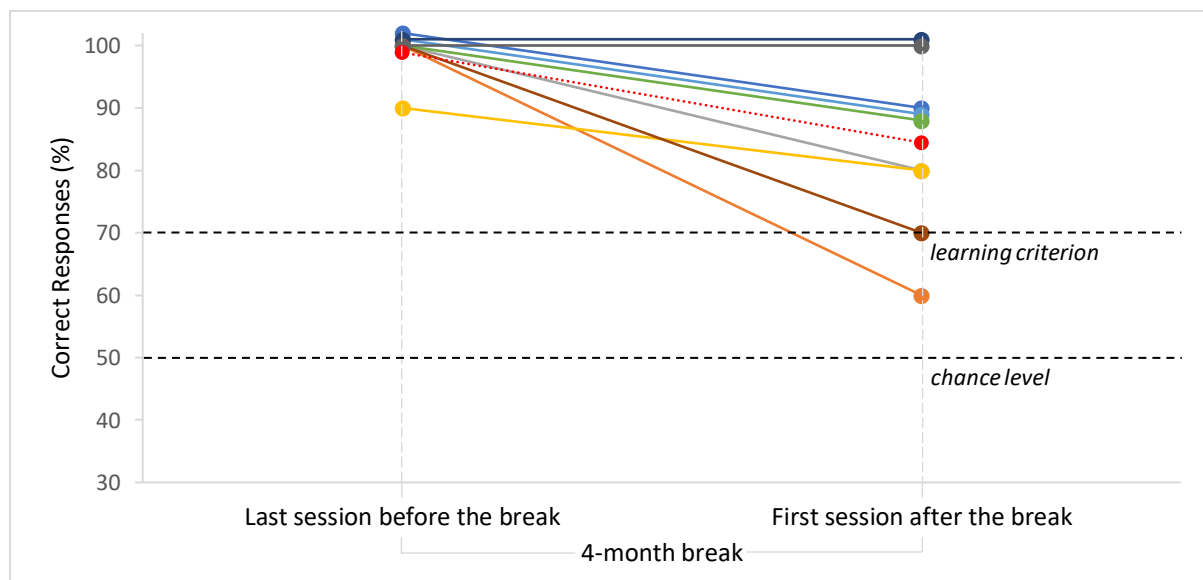
Figure 20. Performance of the nine spider monkeys in the long-term memory task. Each score represents the percentage of correct responses in one session of ten trials both, in the last associative learning session before the break and in the first session after the break. The dotted red line shows the mean performance of the group. — Neto — Gruñon — Neri — Cejitas — Soruyo — Margarita — Mari — Frida — Lucas

4.7. Task difficulty

According to the number of sessions that each individual required in each task to reach the learning criterion, the object permanence task and the associative learning task did not present a significant difference in difficulty ($p=0.109$, $Z=-1.604$, Wilcoxon signed-rank test), the quantity discrimination task and the numerosity task with equally-sized dots were more difficult than the associative learning task ($p<0.05$, $Z=-2.041$ and $p<0.01$, $Z=-2.536$ respectively, Wilcoxon signed-rank test), the quantity discrimination task and the numerosity task with equally-sized dots did not present a significant difference in difficulty ($p=0.306$, $Z=-1.023$, Wilcoxon signed-rank test), and the numerosity task with equally-sized dots was significantly more difficult than the numerosity task with various-sized dots ($p<0.05$, $Z=-2.325$, Wilcoxon signed-rank test).

5. Discussion

The results of the present study show that the spider monkeys mastered all cognitive tasks presented to them. Though there was variation both in individual performance and in group performance across tasks the animals succeeded in object permanence, associative learning, quantity discrimination, numerosity with equally-sized dots, numerosity with various-sized dots, and long-term memory.

5.1. Object permanence

The animals' performance in the object permanence task suggests that spider monkeys do indeed possess the cognitive abilities for object permanence. All nine individuals scored above the learning criterion from the beginning of the task and remained above the latter across the sessions. The slightly increasing yet statistically insignificant trendline of the group's performance indicates that the animals required only minimal – if any – learning in order to master the task. Object permanence is thought, however, to require some sort of visual representation of objects as well as a working memory, which can be described as the maintenance of information during short temporal intervals (Goldman-Rakic, 1987; Vallortigara, 2004).

According to Piaget (1953, 1954), object permanence in humans develops relative to progressive stages which manifest at different ages. In Stage 1 (birth to 1 month), children will

not search for an object which they see disappear and will track the movement of the object in Stage 2 (1 to 4.5 months). Children will be able to retrieve a partly occluded object in Stage 3 (4.5 to 7-8 months) and finally, a fully occluded object in Stage 4 (7-8 to 11-12 months). Later, children will be able to retrieve an object that is hidden successively in various locations, i.e. hidden, uncovered, and hidden again several times, this is Stage 5 (11-12 to 18 months). Lastly, in Stage 6 (18 to 24 months) children will be able to master the retrieval of an object, the location and movements of which they do not see, i.e. an object is hidden in a container, the latter is then moved behind another occluding apparatus, the object is relocated to the second apparatus, the first and empty container is shown to the children, who deduce the current location of the object. Stages 1 to 5 are referred to as visible displacements, whereas Stage 6 is referred to as an invisible displacement (Piaget, 1954).

Though there is some debate regarding Piaget's interpretation (discussed in Moore and Meltzoff, 1999), the six stages are often still used in the study of object permanence as a way to describe the level of object permanence that a certain species reaches, which is convenient for comparative studies. In the present study, the spider monkeys reach Piaget's Stage 4 of object permanence and thus succeeded in most stages involving visible displacements. As no further object permanence tasks were presented to the animals, no affirmation can be made with regard to whether spider monkeys would or would not succeed in the further stages of object permanence.

Much research on object permanence has been conducted on other nonhuman primates, namely on Old World primates. Species that have been demonstrated to succeed in visible displacement tasks as well as in invisible displacements tasks include chimpanzees (Mathieu et al., 1976; Call, 2001; Barth and Call, 2006), bonobos (Barth and Call, 2006), orangutans (De Blois, 1998; De Blois et al., 1998; Call, 2001; Barth and Call, 2006; Mallaravapu, 2009), gorillas (Barth and Call, 2006), and rhesus macaques (De Blois, 1998). Great individual variation was observed in gibbons where some individuals succeeded only in visible displacement tasks while others succeeded in invisible displacements tasks as well (Fedor et al., 2008).

As for other species of New World primates that have been tested, results vary depending on the taxon. Species that have been demonstrated to succeed in invisible displacement tasks include common marmosets (Mendes and Huber, 2004) and cotton-top tamarins (Neiworth et al., 2003). Results vary in capuchins with white-faced capuchins having solved invisible displacement tasks (Mathieu et al., 1976), while tufted capuchins failed in invisible displacement tasks (Dumas and Brunet, 1994). Squirrel monkeys and woolly monkeys

succeeded in visible displacements tasks, but not in invisible displacement tasks (De Blois et al., 1998; Mathieu et al., 1976). While prosimians are relatively understudied with regard to object permanence, the lemurs that have been tested failed most visible and invisible displacement tasks (Mallavarapu, 2009).

Various species of birds have been studied in object permanence as well. Ring doves (Dumas and Wilkie, 1995), kakarikis (Funk, 1996), mynahs (Plowright et al., 1998), and magpies (Pollock et al., 2000) have been demonstrated to succeed in visible displacement tasks while Eurasian jays (Zucca et al., 2007), Goffin cockatoos (Auersperg et al., 2013), as well as an African grey parrot, an Illiger mini macaw, a parakeet and a cockatiel have also succeeded in invisible displacement tasks (Pepperberg and Funk, 1990).

Domestic cats have been demonstrated to succeed in visible displacement tasks (Dumas and Doré, 1989; Goulet et al., 1994) and contradicting results were found as to whether dogs are able or not to succeed in invisible displacement tasks (Gagnon and Doré, 1992, 1993, 1994; Collier-Baker et al., 2004; Fiset and LeBlanc, 2007). More species have been tested in the last decade, such as dwarf goats (Nawroth et al., 2015), Atlantic bottlenose dolphins and California sea lions (Singer and Henderson, 2015), and giraffes (Caicoya et al., 2018), all of which have been demonstrated to succeed in visible displacement tasks. Asian elephants have been tested as well and were shown to succeed in visible as well as invisible displacement tasks (Miller, 2019).

Caution is necessary, however, in interpreting these data as some issues are not unlikely to present themselves in comparative analyses of object permanence tasks. For example, only small modifications in the behavioral tasks can result in drastic changes in the animals' performance (Regolin et al., 1995; Vallortigara, 2004; Nawroth et al., 2015). There have also been developments in the tasks used to assess object permanence, namely in the types of tasks, such as single, sequential, alternate, double, triple visible or invisible displacements, adjacent or non-adjacent displacements, and so forth (Call, 2001; Mallavarapu, 2009). It can also be difficult to make valid species comparisons because of the frequent lack of appropriate control trials across studies (Mallavarapu, 2009).

Tomasello and Call (1997) proposed a theory for the evolution of object permanence which suggests that basic object permanence skills, where an individual understands that an object continues to exist even when the latter is out of sight, may have evolved within the context of foraging. This supports Milton's (1981, 1988) theory which suggests that complex cognitive

skills evolved according to specific foraging demands, where animals, namely primates which forage on patchily distributed foods, for example, evolved cognitive skills like object permanence to locate and identify food sources. Parker and Gibson (1977, 1979) support a similar theory, though focused on extractive foraging, where extractive foragers must have evolved cognitive skills such as object permanence, thus a capacity for mental representation, due to the fact that the foods on which they feed are not directly perceptible. Tomasello and Call (1997), however, add that the ability to represent the unperceived movements of objects, thus referring to Piaget's Stage 6, i.e. invisible displacements, may have evolved in animals that are required to track moving prey, predators or conspecific group members. The authors therefore hypothesize that there are likely only few differences to be found in primate species with regard to object permanence as most primate species require this skill, whether it be for tracking food sources, predator avoidance, or maintenance of group cohesion (Call, 2000a).

In this sense, object permanence would be an essential skill for spider monkeys given their strong dependence on patchily distributed food sources and fission-fusion social dynamics (Campbell, 2008). Though the results of the present study demonstrate that spider monkeys do possess object permanence, further research is needed to determine the extent of the species' abilities in this cognitive domain.

5.2. Associative learning

The animals' performance in the associative learning task suggests that spider monkeys do indeed possess the cognitive abilities for learning by association. Six out of nine individuals reached the learning criterion already in the first two sessions while the remaining individuals needed only one to three additional sessions to reach the learning criterion. The statistically significant increasing trendline of the group's performance indicates that the animals displayed an increase in performance across sessions and thus – as the term suggests – a learning process.

Learning by association is a cognitive skill that has long been studied, namely by Pavlov (1927) who observed that the dogs he was doing research with started to salivate simply at the sight of the person who fed them. This concept became known as classical conditioning, i.e. learning through association where two items become associated as a result of their contiguous occurrence (Gormezano and Moore, 1966; Rescorla and Holland, 1982). In the case of the present study, the spider monkeys learned to associate the color of their assigned cup (i.e. black or white) with the food reward hidden under it.

It has also been suggested, however, that associative learning might be mediated by other mental processes rather than a learning mechanism, such as memory (Shettleworth, 1993) or problem solving (DeHouwer et al., 2016). Presuming that the spider monkeys resolved to their memory skills to master the associative learning task may actually be a potential explanation for the fact that the animals performed so well from the start of the experiment. Indeed, most individuals reached the learning criterion right away, which could suggest that they remembered the color of their assigned cup from the object permanence task rather than learned to associate the color of the cup with the food reward. More so, these different processes might not necessarily be mutually exclusive but rather, associative learning may be mediated by a variety of cognitive processes (DeHouwer et al., 2016).

Associative learning is a skill that can play a fundamental role in animal behavior, namely due to the fact that it allows animals to adapt to biologically significant events (Hollis, 1997). In addition, it appears reasonable to assume that an animal's learning skills are dependent on the specific habitat and feeding demands of that animal (Nachmann et al., 1977). For instance, the frugivorous diet of spider monkeys seems particularly reliant on a learning mechanism such as associative learning, which may be favorable to track seasonal changes and variations in the composition and availability of their food sources (Milton, 1981).

5.3. Quantity discrimination

The animals' performance in the quantity discrimination task suggests that spider monkeys do indeed possess the cognitive abilities to distinguish between two sets of quantities. Five out of eight individuals reached the learning criterion in the first two or three sessions, two individuals reached the learning criterion in the sixth and seventh sessions and only one individual reached the learning criterion somewhat later, in the twelfth session. The statistically significant increasing trendline of the group's performance indicates that the animals displayed an increase in performance across sessions, and the animals' performance in terms of percent of correct responses was higher as the ratio between the various quantity combinations of food items increased, and was lower with smaller ratios.

The animals were initially given the contents of the petri dishes regardless of whether they selected the larger or smaller quantity of items, since – as the contents of both dishes were visible – this was considered an "informed choice". However, due to this, some individuals developed a side bias, which hindered the efficiency in assessing their quantity discrimination

abilities. Therefore, a change of tactics was implemented, rewarding the animals only when they selected the larger quantity of items. This phenomenon, i.e. animals developing a side bias as a result of being rewarded for either response, is not uncommon in quantity discrimination tasks. Indeed, a similar behavior was observed in studies involving cotton-top tamarins and tufted capuchins for instance (vanMarle et al., 2006; Stevens et al., 2007). From a game-theoretical point of view, a side bias may be a "cheap" and easy way to increase speed and efficiency in feeding (McGrew and Marchant, 1999), as demonstrated in this context by the spider monkeys initially retrieving a food reward in every trial.

Distinguishing between two quantitatively different sets of items is referred to as relative quantity discrimination, i.e. choosing one or the other set of items based on a "more-than" or "less-than" rule (Beran et al., 2015). This ability to correctly evaluate quantities allows for numerical judgements not by counting, but rather by mentally representing the approximate number of items in a set, in an analog format (Cantlon, 2012). The common methodological approach to test relative quantity discrimination – which was used for the present study as well – consists of presenting the animals with two sets of biologically relevant stimuli (e.g. food items or conspecifics) differing in number. With the assumption that if the animals are indeed able to discriminate between the two given quantities, they will spontaneously select the larger, or smaller, quantity, depending on the nature of the stimulus (Agrillo and Bisazza, 2014).

Indeed, from an evolutionary point of view, being able to evaluate quantities of food, mates, competitors or predators would serve a critical survival function. Such a quantificational system allows to recognize and make appropriate decisions regarding relevant numerical information, such as, for example, $\times\times\times$ is better than $\times$ when it comes to food items, but worse when it comes to predators (Ansari, 2008). Given its comprehensive relevance, this ability is shared across taxa, and primates are no exception (chimpanzees, Rumbaugh et al., 1987, Beran, 2001; orangutans, Call, 2000b; olive baboons, Barnard et al., 2013; rhesus macaques, Wood et al., 2008; capuchins, vanMarle et al., 2006, Addessi et al., 2008; Beran et al., 2008; squirrel monkeys, Terrell and Thomas, 1990, Olthof et al., 1997; cotton-top tamarins, Stevens et al., 2007; common marmosets, Stevens et al., 2007; mongoose lemurs, Lewis et al., 2005). It has even been reported that 1-year-old, experiment-naïve, olive baboon infants are able to make spontaneous quantitative judgements between sets of objects, which suggests that quantitative reasoning emerges early in the development of primates, within this species at least, as it also does in human infants (Brannon and Van de Walle, 2001; Ferrigno et al., 2016).

Perhaps unsurprisingly, not only do the spider monkeys in the present study share this quantitative ability with other previously tested primates, but their performance with regard to discriminating quantities according to various quantity combinations is similar as well. Indeed, other studies have also found that the accuracy in the performance of the animals decreases as the ratio between the numerical values in the two sets of stimuli approaches 1 (e.g. Beran, 2001; vanMarle et al., 2006; Barnard et al., 2013). These results are consistent with Weber's law, which states that the successful discrimination of two stimuli along a certain continuum will depend on their ratio rather than their absolute values (Bonn and Cantlon, 2012). In other words, the closer in amount the quantities will be, the harder they will be to compare. From a foraging perspective, for instance, this concept is sensical as choosing a food patch with ten fruits instead of a food patch with two fruits will lead to a definite nutritional benefit, whereas being able to tell apart ten fruits from nine fruits will not result in a similar benefit since there will be less of a relative difference between the two options (Beran et al., 2015). This particular example is a good illustration of the relevance of quantity discrimination for the highly frugivorous spider monkeys and a legitimate interpretation for the performance of the animals in the present study.

5.4. Numerosity with equally-sized dots

The animals' performance in the numerosity task with equally-sized dots suggests that spider monkeys do indeed possess the cognitive abilities to distinguish between two sets of discrete numerical stimuli. While there was variation in individual performance, all individuals reached the learning criterion within two to twelve sessions. The statistically significant increasing trendline of the group's performance indicates that the animals displayed an increase in performance across sessions, and the animals' performance in terms of percent of correct responses was higher as the ratio between the various number combinations of dots increased, and was lower with smaller ratios.

Distinguishing between two sets of discrete stimuli means being able to evaluate the number of given elements, independent of the amount, i.e. choosing one or the other set based on a "how many?" basis rather than a "how much?" basis (Wiese, 2003). The common methodological approach to test discrete number discrimination – which was used for the present study as well – consists of presenting the animals with two sets of neutral stimuli (e.g. dotted cards) which they will then be trained to associate with a reward. The animals' capacity to learn a numerical rule is thus interpreted as evidence of their numerical abilities (Agrillo and Bisazza, 2014). As

opposed to the spontaneous numerical abilities involved in quantity discrimination (see 5.3. Quantity discrimination) – and due to the shaping procedure an animal undergoes in this methodology – discrete number discrimination is said to be assessed through trained numerical abilities (Agrillo and Bisazza, 2014). In the case of the present study, the spider monkeys were trained to learn that the box fitted with the card bearing the higher number of dots would result in a food reward.

The two approaches differ not only in procedure but may also demonstrate different numerical abilities. Indeed, from an ecological perspective, in spontaneous choice tests the animals are thought to display natural behavioral responses due to the biologically relevant nature of the presented stimuli. In this sense, the animals' performance in such tasks likely reflects the cognitive functions that should be stimulated in a similar challenge encountered in the wild. On the other hand, training procedures involving so-called neutral stimuli will presumably give no insight into the practical application of numerical abilities in a natural setting (Agrillo and Bisazza, 2014). In addition, it is possible that the training process itself may lead to the recruitment of other neural systems in order to adapt to the extensive demand of the cognitive task, systems which may not usually be involved in number processing (Hauser and Spelke, 2004).

The use of training procedures, however, presents the advantage of preventing the animals' performance to be affected by individual motivation and personal preference for the presented stimuli. In the present study, for instance, different food items were used in the quantity discrimination task (raisins, dried cranberries or Cheerios) in order to cater for the monkeys' food preferences, which is surely a factor to be considered in the methods. Furthermore, the use of abstract stimuli such as dots allows for a meticulous manipulation of the latter such that a wide variety of stimuli can be presented within the same numerical contrast and prevent the animals to base their responses upon patterns instead of numerical properties (Ashkenazi et al., 2013). Abstract stimuli also allow researchers to use the same stimuli across species and thus permit precise intra- and inter-specific comparative studies (Scarf et al., 2011).

Success in discrete number discrimination has been reported in chimpanzees (Tomonaga and Matsuzawa, 2002), an orangutan (Vonk, 2014), a hamadryas baboon (Smith et al., 2003), rhesus macaques (Jordan and Brannon, 2006; Beran, 2008), capuchins (Judge et al., 2005; Beran, 2008), squirrel monkeys (Thomas et al., 1980; Smith et al., 2003), and ring-tailed lemurs (Merritt et al., 2011). Non-primate species have also shown proficiency in learning numerical rules; a raccoon (Davis, 1984), black bears (Vonk and Beran, 2012), bottlenose dolphins

(Jaakkola et al., 2005, Yaman et al., 2012), birds (pigeons, Brannon et al., 2001, Scarf et al., 2001; crows, Bogale et al., 2011), fish (guppies, Pfiffer et al., 2012, Agrillo et al., 2014) and honeybees (Giurfa, 2019).

Not unlike the phenomenon encountered in quantity discrimination tasks, Weber's law is often observed in discrete number discrimination tasks, with accuracy in performance decreasing when minimizing the numerical interval between the stimuli. The animals' performance in the present study is no exception to this rule. While caution is necessary regarding the use of different methodologies in quantity and numerosity tests with regard to comparative analyses, the present study supports previous findings in other species, as not only are spider monkeys able to discriminate on the basis on quantities, but they can also discriminate between abstract numerical stimuli.

5.5. Numerosity with various-sized dots

In this task, seven out of nine individuals reached the learning criterion in the first two or three sessions, one individual reached the learning criterion in the seventh session and one individual reached the learning criterion in the thirteenth session. Interestingly, while the average performance in the numerosity task with equally-sized dots increased from around 60% to 80% correct responses, the average performance in the numerosity task with various-sized dots already started between 70% and 80% and mostly remained in that range across the sessions, with only few occasional drops below the learning criterion. This may indicate that the numerosity task with various-sized dots was interpreted by the monkeys to be similar and/or continuous to the numerosity task with equally-sized dots. Therefore, this suggests that the animals did in fact base their decision for one of two number cards on their numerical properties rather than on the size of the dots. Additionally, what the results suggest with regard to the numerosity task with equally-sized dots being more difficult than the numerosity task with various-sized dots (see 4.7. Task difficulty) may in fact simply be attributed to an order effect. Hence, if the animals based their responses on dot size or pattern, their performance should have been similar in both tasks as their interpretation of the two tasks would have been that they are equally difficult.

Similar to the quantity discrimination task and the numerosity task with equally-sized dots, the animals' performance in terms of percent of correct responses was higher as the ratio between the various number combinations of dots increased, and was lower with smaller ratios. This

further refutes the possibility that the animals based their decision for one of the two options on the size of the dots or the patterns of the cards rather than on their numerical properties.

As discussed previously (see 5.4. Numerosity with equally-sized dots), the use of abstract, or neutral, stimuli allows for detailed control of aspects such size, shape, color, density (e.g. Brannon and Terrace, 1998) and ultimately permits to confidently dissociate between an animal's quantity discrimination abilities and its discrete number discrimination abilities.

5.6. Long-term memory

The animals' performance in the long-term memory task suggests that spider monkeys do indeed possess the cognitive abilities to memorize visual information on a long term. After a 4-month break since the last associative learning session, eight out of the nine individuals scored 70% or more correct responses when the task was presented to them again, thus unanimously reaching the learning criterion right away.

As opposed to short-term memory, which refers to the ability to memorize few items over a relatively short period of time, long-term memory can be defined as a broad store of knowledge and a record of past events, providing a lasting retention of information and skills (Cowan, 2008). Although there are varying opinions about what exactly defines a "short" or "long" period of time in this context, one accepted categorization is that a short-term memory ranges from seconds to hours, while a long-term memory ranges from hours to months or even years, in humans at least (Bahrick et al., 1975; McGaugh, 2000; Richardson, 2007). Indeed, any categorization will be relative when assessing long-term memory in animals namely due to the great variation in life history and lifespan of the different taxa. Spider monkeys have a relatively long lifespan and "slow" life history (Shimooka et al., 2008), and it is reasonable to assume that four months can be considered a long-term span. Hence, the results of the present study suggest that the spider monkeys remembered the associative learning task and were able to successfully replicate their past responses towards it.

When comparing the animals' performance in the long-term memory session and their performance in the first session of the associative learning task, their mean performance in terms of percent of correct responses was similar (84.4% and 83.3% correct responses, respectively). Thus, it would not be unreasonable to speculate that their immediate above-chance performance in the long-term memory task was due, not to their memory abilities, but

rather to their demonstrated skills in quickly learning by association. However, the long-term memory task, unlike the associative learning task, was not preceded by the object permanence task – or any other task operating the same apparatus – which served as a sort of training exercise for the associative learning task, and may have contributed to the animals' high scores from the first session on. In addition, the manner in which the animals approached the apparatus in the long-term memory task was considerably different from the way in which they approached it the first time they saw it, i.e. in the object permanence task. Indeed, when first being presented with the apparatus, the animals displayed more uncertainty with regard to how they should manipulate it, and several individuals pulled on the plexiglass board or the colored cups. In contrast, in the long-term memory task, none of the animals pulled on any parts of the apparatus and on the contrary, all individuals handled the apparatus with ease and apparent knowledge of its functionality – despite the fact that they had not seen the apparatus for a prolonged period of time. These details further support the notion that the spider monkeys did indeed remember the apparatus and the task to be performed.

The latter discussed point possibly refers to recognition memory, a component of long-term memory, which requires both the identification of a stimulus and the judgement concerning its prior occurrence (Fahy et al., 1993; Aggleton and Brown, 2006). An important function of recognition memory involves the ability to effortlessly identify known individuals, objects or sensory stimuli such as sounds or smells and to direct attention towards familiar elements that are of importance to the behavior of the moment (Murray, 2001; Moreno-Castilla et al., 2018). Naturally, recognition memory – and long-term memory in general – allows animals to store acquired information about the environment; sticklebacks memorize patches in which they have previously fed for at least eight days (Milinski, 1994), corvids remember the locations in which they have stored food up to six months prior (Brodin, 2005), elephants respond to contact calls from known conspecifics after years without contact (McComb et al., 2000).

For spider monkeys, long-term memory is likely to play a key role namely in foraging behaviors amidst seasonally changing environments (Stephens and Dunlap, 2017). The frugivorous spider monkeys may recognize the visual characteristics of nutritious fruits and locally abundant trees, as well as memorize the location of trees and tree patches that have previously yielded high-quality foods (Zuberbühler and Janmaat, 2010).

6. Conclusion

The spider monkeys were able to master all cognitive tasks that were presented to them: they successfully located the food items which they observed being hidden under one of two colored cups, thus demonstrating their ability of object permanence; they successfully located the food items hidden – out of their sight – under one of two colored cups, thus demonstrating their ability to learn by association via relating their assigned cup color to the food reward; they successfully selected the larger of two quantities of food, thus demonstrating their ability to discriminate relative quantities; they successfully selected the cards bearing the higher number of dots, both with equally- and various-sized dots, thus demonstrating their ability to discriminate discrete numbers, independent of dot size and pattern; and they successfully located the food items hidden under their assigned colored cup after a 4-month break, thus demonstrating their ability to memorize visual information on a long term.

The next possible steps in the assessment of primate cognition, namely in spider monkeys, may be to test further cognitive domains such as visual learning set formation and visual reversal learning. It is well established that primates possess highly developed visual systems on which they greatly depend for their survival (Fobes and King, 1982; Vallortigiara, 2004), and to further explore behavioral adaptations related to this sense may help to uncover more underlying cognitive processes in spider monkeys. The formation of a discrimination learning set studies the phenomenon of a suitable change in an animal's behavior based on previously learned experiences (Harlow, 1949). Reversal learning refers to a situation where an animal is trained to respond differentially to a set of stimuli and is then exposed to the same stimuli with their reward value reversed (Rumbaugh et al., 1996). In the wild, animals must constantly learn new discriminations and show remarkable behavioral plasticity according to their living circumstances (Ohta, 1983), and to delve deeper into the cognitive processes involved in how animals "learn to learn" would be utterly interesting.

7. Societal and ethical considerations

The experiments carried out in this study are in compliance with the *American Society of Primatologists' Principles for the Ethical Treatment of Primates*, as well as with current Swedish and Mexican laws.

The participation of the spider monkeys in the tasks was on a strictly voluntary basis. The animals were in no shape or form forced to take part in any of the tasks and on the contrary, the experiments relied on the animals' willingness and motivation to cooperate. If an animal was uninterested for any reason to participate in a session, the experimenter moved on to another individual and resumed the task at a later time or date. However, in the large majority of cases, the spider monkeys were willing, and often eager, to participate in the cognitive tasks. In fact, cognitive challenges are suggested to confer welfare benefits through the mental stimulation that they provide the animals with. The engagement in cognitive challenges is thought to be linked to positive emotional states in animals and has been demonstrated to reduce stereotypic behavior in captive populations. Hence, the cognitive tasks presented in this study may have positively contributed to the welfare of the spider monkeys by providing cognitive enrichment. Additionally, no food deprivation scheme was adopted, and the animals always had access to their regular diet, which further supports the notion that the spider monkeys freely, and perhaps enthusiastically, took part in the experiments.

The study of primate cognition is significant namely for comparative studies, to understand the evolution of cognitive abilities, as well as for the acquisition of deeper insights into the underlying mechanisms of primate behavior. On a broader scale, studies on the cognitive abilities and limitations of nonhuman primates, our closest relatives, may also contribute to a better understanding of human cognition and of age- or disease-related impairments of human cognition.

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9. References

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