Socijalno i nesocijalno učenje kod običnih marmozeta (Callithrix jacchus Linnaeus, 1758)

Vodjerek, Lea

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SOCIAL VERSUS NON-SOCIAL LEARNING IN COMMON MARMOSETS (*Callithrix jacchus* Linnaeus, 1758)

Master thesis

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Mnogo se godina socijalno učenje, zajedno s tradicijom i kulturom, vezalo isključivo uz čovjeka. S druge strane, u zadnjih nekoliko godina mnoga su istraživanja pokazala socijalno prenošenje informacija i zadržavanje istih tijekom vremena i/ili unutar generacija u mnogim životinjskim vrstama. Nedavna istraživanja na primatima pokazala su uspješnu upotrebu video prikaza prilikom istraživanja prenošenja tehnika rješavanja problemskih zadataka u laboratoriju i u prirodi. U ovom sam radu koristila video prikaze kako bih odredila da li obični marmozeti (*Callithrix jacchus*) preferiraju učenje od virtualnog ne-socijalnog prikaza ili virtualnog demonstratora iste vrste. Nadalje, zanimalo me da li će majmuni slijediti demonstratorov izbor, tj. otvarati kutijicu iste boje kao što je prikazano na videu. Rezultati su pokazali da nema preferencije ni za socijalnu niti ne-socijalnu inormaciju, te kako nema preferencije ni za demonstriranu niti ne-demonstriranu kutijicu. S druge strane, pozornost majmuna na video prikaze, te izbor demonstrirane ili ne-demonstrirane kutijice za manipulaciju, pod utjecajem je njihove obiteljske skupine. Također, pokazane su i individualne razlike u pozornosti na video prikaz unutar faze prikazivanja i faze testiranja.

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Master Thesis

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For many years, social learning as well as behavioral traditions and cultural phenomena, were thought to be distinctive to humans. In recent years, however, a lot of studies have shown evidence for the social transmission of information and its maintenance over time and/or generations in a variety of non-human animals. Recent studies on primates have shown successful use of video demonstration to investigate the transmission of techniques in problem-solving tasks in the laboratory and in the field. In this experiment, I used video demonstrations to determine if common marmosets (*Callithrix jacchus*) have a preference for learning from a virtual non-social demonstration or a virtual conspecific demonstrator. Further, I was interested to see whether the subjects follow a demonstrated choice i.e., opening of the same-colored container as shown in the videos. Results showed no preference for social or non-social demonstration, nor a preference for demonstrated or non-demonstrated box. However, both the monkeys' attention for a video demonstration and choice to manipulate demonstrated or non-demonstrated containers have been influenced by their group. Furthermore, I found large inter-individual differences in attention to video demonstrations in both the demonstration and test phases.

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Keywords: social learning, common marmoset, video demonstration, primates, social and non-social information use

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Ovaj rad, izrađen u Zavodu za kognitivnu biologiju i biologiju ponašanja Sveučilišta u Beču, pod voditeljstvom Prof.dr.sc. Thomasa Bugnyara i suvoditeljstvom Izv.prof. dr.sc Zorana Tadića, predan je na ocjenu Biološkom odsjeku Prirodoslovno-matematičkog fakulteta Sveučilišta u Zagrebu radi stjecanja zvanja **Magistar eksprimentalne biologije.**

This Thesis, completed at the Department of Behavioral and Cognitive Biology, University of Vienna, under the supervision of Prof. Dr. Thomas Bugnyar and co-supervision of Assoc. Prof. Dr. Zoran Tadić, was submitted for assessment to the Department of Biology, Faculty of Science at the University of Zagreb in order to acquire the **master's degree in experimental biology**.

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1 INTRODUCTION

1.1 BACKGROUND

Social learning, defined as learning that is influenced by observation of, or interaction with, another animal or its products (B. G. Galef, 1988) received a lot of attention in recent years. Most of the research focused on social learning resulting in matching behavior that can lead to the transmission of information and acquired patterns of behavior within a population and maintenance of these patterns over time (Galef, 1976). It is a relatively common and important form of adaptation, once thought to be characteristic for humans and great apes, but it was already shown in a variety of non-human animal species (Heyes et al., 1994; Zentall, 2004; Voelkl and Huber, 2007; Abramson et al., 2013; Van De Waal, Borgeaud and Whiten, 2013).

One of the key points that make social learning a topic of high interest is that it has been proposed to lead to tradition formation and the evolution of culture, as it entails a social component that is enhancing the process of information acquisition and transmission. Behavioral traditions are defined as a process of preservation of behavioral variants across generations through social learning. The criteria for behavioral traditions are that there needs to be a local behavioral variant, which is shown by some or most of the members of the group; it needs to be constant over generations and maintained through social learning (Fragaszy, 2003). Culture, on the other hand, has a different definition (largely depending on the academic discipline); in animal cognition, it is seen as either containing multiple traditions (Whiten et al., 1999) or as the accumulation of modification over time (Tomasello, 1999). In the last fifty years, the number of articles concerning the studies of culture and tradition in animals had an exponential growth rate, and this became a field of interest not only to biologists and psychologists but also to anthropologists and zoologists (Galef, 2004), as well as many applied animal sciences.

The earliest evidence of culture and behavioral traditions in animals were the studies of milk bottle openings by British tits (*Parus major*) (Fisher and Hinde, 1949) and sweet potato washing and wheat placer mining by Japanese macaques (*Macaca fuscata*) (Kawai, 1965). What Kawai and colleagues observed in Japanese macaques in 1953 was when one female named Imo started washing provided sweet potatoes. After

3 months, they observed this behavior in three other monkeys, her mother, and two playmates, and within 3 years, 40% of Imo's group started washing sweet potatoes. Now we can find similar studies throughout the animal kingdom conducted both on free-living and captive populations (Warner, 1990; Humle and Matsuzawa, 2002; Tebbich et al., 2002; Hunt and Gray, 2003; Gruber et al., 2009, 2019) mostly in apes, (chimpanzees and orangutans), rodents and cetaceans (B. G. Galef & Whiskin, 1997; Krützen, Willems, & Van Schaik, 2011; Whiten, Horner, & De Waal, 2005).

1.2 SOCIAL LEARNING MECHANISMS

We can also label social learning "observational learning" and define it as a change in behavior that follows the observation of another individual, mostly a conspecific, performing some behavior or the observation of the product of behavior (Zentall, 2012). Therefore, an animal can gain information about the environment, such as how to avoid predators or where to find food, by simply observing and copying another animal's behavior (C. Heyes, 2012). In theory, whether we call it "learning" depends on whether the performed behavior is new; if the behavior is already in the repertoire of the observer, we consider it a performance. In practice, sometimes it is hard to distinguish novel behavior because it is likely that some form of that behavior was already used by the observer prior to this observation. Thus, the term "observational learning" is used only when we consider that the observed behavior could not have occurred prior to the observation of a model (Zentall, 2012).

Since most types of social information can be gained by observing or interacting with a conspecific or heterospecific, there are many different types and categories of social learning (Byrne & Russon, 1998; C. M. Heyes, 1994; Kappeler, 2010). One way to classify social learning is to differentiate between processes that lead directly and indirectly to social learning. Processes that lead directly to social learning are observational conditioning, social enhancement of food preferences, production imitation, and emulation. Processes that lead indirectly to social learning are a local enhancement, response facilitation, and social facilitation. Stimulus enhancement is a process that can lead both directly and indirectly to social learning depending on the conditions (Hoppitt & Laland, 2008). All processes will be further defined below for better understanding.

Observational conditioning is a subset of stimulus-stimulus learning in which observation of a demonstrator exposes the observer to a relationship between stimuli at t_1. Exposure to this relationship results in a change of observer's behavior at t_2 (C. M. Heyes, 1994). Social enhancement of food preference in rats is perhaps the most studied social learning process of all (J. Galef et al., 1998). It is defined as a process that occurs when, after being exposed to a demonstrator carrying cues associated with a particular food diet, the observer is more likely to consume the same diet. The last process that leads directly to social learning is emulation. It occurs when after observing the demonstrator interacting with objects in its environment, there is a higher probability that the observer will perform any action that brings about a similar effect on those objects (Custance, Whiten, & Fredman, 1999).

Local enhancement is one of the processes that indirectly leads to social learning. It was first described by Thorpe (1963) as "apparent imitation resulting from directing the animal's attention to a particular object or particular part of the environment". The latter definition was broadened to entail that "local enhancement occurs when, after or during a demonstrator's presence, or interaction with objects, at a particular location, an observer is more likely to visit or interact with objects at that location" (Thorpe, 1963). The term "response facilitation" was first introduced by Byrne (1994) and it refers to instances when the presence of a demonstrator performing an act (i.e., in most cases resulting in reward) increases the probability of an observer animal to do the same (Byrne, 1994). The term social facilitation, on the other side, is used when the mere presence of a demonstrator results in behavior change in an observer (Zajonc, 1965). The last process, which can lead to direct and indirect social learning, is stimulus enhancement. It occurs when the observer is exposed to a single stimulus at time t_1 and it affects a change in its behavior at t_2 (Heyes, 1994).

1.3 COMMON MARMOSETS AS MODEL ORGANISM

Common marmosets (*Callithrix jacchus*, L.) (Figure 1) are small New World monkeys native to Brazil and the Atlantic coastal forests and semi-arid areas in South America (Clarke, 1994; Wahab, Drummer, & Behr, 2015). They belong to class Mammalia, order Primates, family Callitrichidae along with their close relative's tamarins (*Saguinus*, 15

species), lion tamarins (*Leontopithecus*, 4 species), Goeldi's monkeys (*Callimico*, 1 species), eastern Brazilian marmosets (Callithrix, 6 species), Amazonian marmosets (*Mico*, 14 species) and pygmy marmosets (*Cebuella*, 1 species) (Perelman et al., 2011; Rylands, Coimbra-filho, & Mittermeier, 2009).

Figure 1 Common marmoset (*Callithrix jacchus*). (Photo: https://www.pinterest.es/pin/294071050640754672/)

Members of the family Callitrichidae are one of the smallest primates and they represent the smallest true monkeys (simian primates) Adult body mass is on average 320 g – 360 g for wild common marmosets and 280 g – 530 g for the captive ones (Araújo et al., 2000). Distinguishing characteristics from other members of the Callitrichidae family are white ear tuffs (Figure 1). Claw-like nails grow on all fingers and toes except the big toe which has a flat nail. Also, the big toe is opposable to other fingers, as in all other primate species (Gale, 2003).

Common marmosets are endemic in Northeastern Brazil (Figure 2) but have also been introduced into areas outside their natural geographical range like East and Southeast Brazil

(Rylands et al., 1993). They live in different kinds of habitats: Atlantic coastal forests, gallery forests, and in forest patches within open habitats (De la Fuente et al., 2019; Digby & Baretto, 1996; Gale, 2003). According to The IUCN Red List of Threatened Species (2021), the common marmoset is considered to be at "Least Concern".

Figure 2 The distribution of common marmoset (*Callithrix jacchus,* L.) in Northeastern Brazil. (Photo: IUCN)

Marmosets are diurnal animals active for 11 – 12 hours a day, usually until sunset. During their activity period, they mostly socialize, forage, rest, and feed (Gale, 2003; Leonardo, Pinheiro, Rossano, & Pontes, 2015). Their diet can vary depending on the season and availability, but mostly it consists of fruit and insects along with seeds, flowers, small lizards, and plant exudates (primarily gums, with some sap) (Abbott, Barnett, Colman, Yamamoto, & Schultz-Darken, 2003; Clarke, 1994; Digby & Baretto, 1996; Digby, Ferrari, & Saltzman, 1999; Leonardo et al., 2015).

Common marmosets, as well as the other Callitrichidae, have a relatively complex social system, and accordingly a wide repertoire of vocalizations (Bezerra & Souto, 2008; Epple, 1968; Gale, 2003). Most of the calls are used as contact calls due to their arboreal habitat, but there is also a variety of mobbing, warning, submissive, aggressive, and social calls (Epple, 1968; Pistorio, Vintch, & Wang, 2006). Marmosets communicate also via olfactory and visual signals but mostly rely on auditory signals due to reduced visibility in their natural habitat. Their vocal repertoire consists of approximately 13 different calls that can be distinguished via both sonograms and human ears according to Bezerra and Souto (2008).

Common marmosets live in family groups ranging from 3 to 15 individuals (Gale, 2003). They are known for their cooperatively breeding social organization usually involving one breeding pair and "helpers" – adult relatives that contribute to raising infants (Caldwell & Whiten, 2004), that are usually twins (Wislocki, 1939) (Figure 3), but in captive colonies, triplets are the most frequent litter size (Tardif et al., 2003). The infants are carried on the back, and usually, all group members participate in infant carrying and food transfer to them. The care for infants is a very energy-consuming process for group members, but it decreases after 3 – 4 weeks after birth when young marmosets start to explore on their own (Gale, 2003). In captivity, marmosets are usually housed in groups that include an adult pair and their offspring.

Figure 3 Common marmoset taking care of the twins by carrying them on its back. (Photo: https://primatecarewelfare.wordpress.com/2018/03/30/helping-in-marmosets-new-study/)

Common marmosets are an ideal model species due to their small body size which facilitates the maintenance and handling, breading, and high reproductive efficiency in captivity (J. M. Burkart & Finkenwirth, 2015). Marmosets have been studied in the laboratory since 1960, and are widely used in social learning, imitation, foraging, vocalization research (Caldwell & Whiten, 2004; Gunhold, Massen, Schiel, Souto, & Bugnyar, 2014; Miller, Mandel, & Wang, 2010), but are also used as an alternative primate species in biomedical research (Yamazaki & Watanabe, 2009). They present a good model species for social learning research especially because of their cooperative breeding system and high sociability within the group, which was proven with a multitude of research papers (Bugnyar & Huber, 1997; Gunhold, Massen, et al., 2014; Gunhold, Whiten, & Bugnyar, 2014; Pesendorfer, Gunhold, Schiel, Souto, & Huber, 2009; Voelkl & Huber, 2000; Voelkl, Schrauf, & Huber, 2006).

1.4 SOCIAL LEARNING EXPERIMENTS IN COMMON MARMOSETS

There have been a few studies that show evidence for imitative social learning in common marmosets. In the study by Bugnyar and Huber (1997), inexperienced individuals observed an experienced individual demonstrate one of two techniques to earn food rewards from the apparatus. The demonstrator could either push or pull a pendulum door to reach a reward in the wooden box. The study found that individuals who watched the demonstrator showed a tendency to use demonstrators' technique, but later switched to a simpler technique – pushing. The results of the study indicated that marmosets are capable of learning simple motor skills through observing another conspecific (Bugnyar and Huber, 1997).

Furthermore, Voelkl and Huber (2000) proposed to have found clear evidence for imitative learning in marmosets. In their experiment, marmosets observed a demonstrator removing a lid from plastic canisters, using either their mouth or their hand, to obtain a reward. Marmosets that observed demonstrators using their hands or mouth also used the same opening technique. In a subsequent study in 2007, Voelkl and Huber showed that the subjects copied the response topography of a conspecific demonstrator in order to get a food reward (Voelkl and Huber, 2007). These findings are supporting the suggestion that learning through imitation is also possible in monkeys, and not just in great apes and humans. This study confirmed earlier findings (Bugnyar and Huber, 1997) and provided further evidence of marmoset's capability for imitation (Voelkl and Huber, 2000).

Caldwell and Whitten (2004) used an artificial fruit apparatus to test marmosets for social learning. Marmosets received full or partial demonstration for opening an artificial fruit, and the control group saw no opening demonstration before testing. None of the observers succeeded in solving the task during the test period, but they showed a demonstration-consistent effect, namely, the group that received a full demonstration showed more apparatus manipulation overall in contrast to the other groups. In their conclusion, the authors propose that a clear difference between the tested groups suggests that social learning mechanisms provide a real benefit for the animals in the matter of novel food-processing skills, such as the one presented in this experiment (Caldwell and Whiten, 2004).

Following up the experiment on imitative learning in marmosets (Voelkl and Huber, 2000), Range and Huber (2007) studied attention patterns, which differed both between species, but also between individuals. Thus, attention is likely to influence the amount and type of information that individuals will extract from given demonstration (Range and Huber, 2007). In this experiment, marmosets watched different conspecifics through two observational holes while the demonstrators were searching, manipulating an object, and feeding. Beside a huge individual variation in attention, they showed that marmosets were more attentive towards a problem-solving model than an exploratory one. Overall, attention in marmosets was short, and there was an increase in attention if the demonstrator was of the opposite sex.

In 2009, Pesendorfer and colleagues tested the maintenance of traditions in common marmosets in a field experiment. They used the two-action apparatus of Bugnyar & Huber (1997) to establish alternative behavioral patterns in six family groups (with a total of 36 individuals). These groups were exposed to only one technique during a training phase and were afterward tested with two techniques available. The monkeys used the first, trained, technique over a period of three weeks despite being provided with a choice between the two techniques. Three additional groups were used as a control group and were given the same number of sessions but could freely choose the method to obtain a reward. In the control groups, there has been an overall bias towards one of the two presented techniques, and those subjects that had a different preference did not adjust to the rest of the group. To conclude, it seems that the maintenance of the behavioral patterns within groups can be explained with habit formation when subjects receive a reward after the first successful manipulation. Even as it appeared there have been signs of social conformity because of overall bias towards one of the two presented techniques, this mechanism was not shown in this particular study (Pesendorfer et al., 2009).

The first study on common marmosets that used video demonstration in the wild was conducted by Gunhold, Whiten, and Bugnyar in 2014, who used an artificial visual stimulus to try to overcome socio-ecological factors that are thought to be responsible for the transmission patterns. In this field experiment, 6 groups of marmosets watched a video demonstration of conspecific opening an artificial fruit by either pulling the drawer or pushing the lid., and the other six groups watched a static image of a conspecific standing next to the artificial fruit. The subjects that were exposed to video demonstration were more manipulative and more successful at opening the artificial fruit in contrast to control

subjects, and had a higher probability of using the demonstrated technique and thus serve as models for their family members (Gunhold, Whiten and Bugnyar, 2014)

In 2014, Gunhold and colleagues have also published an experiment focusing on memory, transmission, and persistence of foraging techniques in common marmosets. They conducted a field experiment with 13 groups of wild common marmosets. In 7 groups were individuals that were already familiar with the task (from the previous study by Pesendorfer et al, 2009) and therefore could be used as potential models for naïve individuals. Furthermore, in four groups one individual was trained to use one of the two possible techniques and in the two control groups, there were no skilled individuals present. They investigated whether experienced individuals remembered how to solve a task, and if they would use their learned technique; whether the naïve individuals would learn socially from their family members, and if so, if they would they use the same technique as the demonstrator. Lastly, they explored if this behavior would persist over time in individuals and groups. The wild common marmosets were indeed able to memorize, learn socially and maintain their preference for a foraging technique (Gunhold et al., 2014).

Finally, Gunhold and colleagues (2015) tested marmosets for the long-term fidelity of foraging techniques in a captive setting. Three captive families were trained in a family group setting to open a wooden box with one of the two possible techniques (pushing or pulling a flap door) to reach a food reward. Most individuals used the technique that was learned in a group setting, in spite of that they could use the alternative technique during the test sessions, which was conducted individually. The subjects were re-tested six times over a period of more than four years to examine the fidelity of preferences for a foraging technique. In all tests, the marmosets shoved a similar preference as in the first test block. This study experimentally demonstrates the memory and fidelity of experimentally seeded information in a manipulation task over a time period of several years (Gunhold et al., 2015).

2 AIMS AND PREDICTIONS OF THE STUDY

This study aimed to examine whether common marmosets (*Callithrix jacchus*) prefer to use social or non-social information when provided with a choice.

Specifically, I asked the following questions: i) do the monkeys prefer social or non-social demonstration?, ii) do the monkeys subsequently have a preference for demonstrated or non-demonstrated containers?, iii) which factors (i.e. age, sex, group) do affect the monkeys' attention for a video demonstration?, iv) who is interested in a video demonstration (i.e., are there individual differences within the population)? and v) whether the monkeys' choice to manipulate demonstrated or non-demonstrated containers is influenced by sex, age, or group?

I expected that: i) monkeys will prefer social over the non-social demonstration, i.e. they will spend more time in front of the video with a conspecific, ii) there might be an initial preference for the demonstrated container, which could be lost after the initial trial (compare Bugnyar & Huber 1997), iii) monkeys' attention for video demonstrations will be affected by family group and age (compare Range & Huber 2007), but I do not expect that sexes will differ in this respect, iv) there will be individual differences within the population and within the family groups (compare Gunhold et al. video study 14), v) monkeys' choice to manipulate demonstrated or non-demonstrated container may be affected by family group and age (compare Gunhold et al. Anim Behav paper 14), but I do not expect a difference between sexes.

3 METHODS AND EXPERIMENTAL DESIGN

3.1 SUBJECTS

Twenty-six captive-born common marmosets, 17 males, and 9 females were used as experimental subjects in this study. The monkeys were housed in two separate rooms in five family groups (8 subgroups in total) and kept at the Animal Care Facility of the Department of Behavioral and Cognitive Biology, University of Vienna, Vienna, Austria. Each family group ranging from 2 to 8 individuals was housed without any visual contact between the neighboring family groups; however, they were kept in acoustic and olfactory contact. Visual contact between family groups was prevented by vertical blinds set between the cages, but if groups were temporarily separated into subgroups, the subgroup remains in visual contact. Detailed individual information, as well as that on the family group and subgroup, is shown in Table 1.

Table 1 Description of the test subjects: family group, subgroup, name, sex, and date of birth.

FAMILY GROUP	SUBGROUP	NAME	SEX	DATE OF BIRTHF
Pooh	Pooh	Fimo	♂	10.8.02.
		Locri	♂	13.8.03.
Sprichtel	Sprichtel	Sparrow	♀	23.3.06.
		Smart	♂	4.11.09.
		Simba	♂	28.1.16.
		Nala	♀	28.1.16.
		Herr Nilsson	♂	2.1.19.
V group	Double V's	Vento	♂	24.5.09.
		Valentino	♂	20.3.13.
	Romans	Ernesto	♂	20.7.04.
		Vincent	♂	29.8.12.
		Melvin	♂	19.7.14.
		Mathilda	♀	19.7.14.
Cleli	Cleli 1	Blinky Bill	♂	21.9.15.
		Wall-E	♂	21.9.15.
		Bambi	♂	7.6.16.
		Feline	♀	7.6.16.
	Cleli 2	Veli	♀	14.11.04.
		Clever	♂	4.11.09.
		Vaiana	♀	9.10.17.
		Maui	♂	9.10.17.
Kiri	Aurora	Jack	♂	23.3.06.
		Aurora	♀	15.10.12.
	Kobold	Kobold	♂	11.4.05.
		Oli	♀	15.10.05.
		Luna	♀	12.10.13.

The groups were kept in indoor-outdoor enclosures (each enclosure measuring approximately 250 x 250 x 250 cm) surrounded by wire mesh and equipped with wooden branches, hammocks, tunnels, resting places, and various other enrichment items (Figure 4).

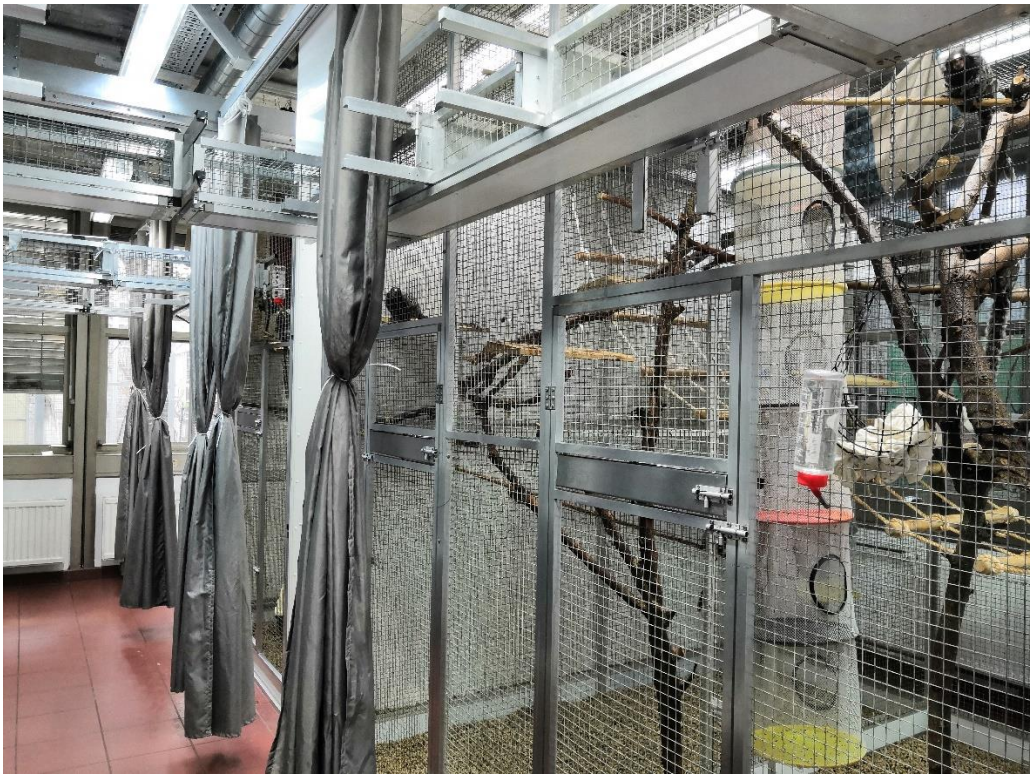

Figure 4 The indoor enclosures with a passage tunnel system. (Photo: Lea Vodjerek)

Monkeys were fed twice per day. The marmosets received a varied diet containing marmoset pellets, vegetables, fruits, dairy, grains, marmoset gum, marmoset jelly, insects, eggs, as well as protein and vitamin supplements twice a day at approximately 7:30 and 14:00. Access to water was provided *ad libitum* in all groups.

An automatic humidity system and indoor heating bodies ensured that temperature (21-26°C), humidity (30-60%), and dark/light cycle (12:12 hours) are held constant within the indoor facilities. Daylight was the main source of light, but additional solar lights, as well as the heating lamps, were available in both rooms.

3.2 EXPERIMENTAL SET-UP

All experiments were conducted in a separate experimental room every other day for 28 days. Each tested group was lured into an experimental room through a passageway system of tunnels. The group was waiting in a separate cage (Figure 5) in which they had access to water *ad libitum*. The cage was equipped with wooden branches, wood pallets, resting places, and tunnels.

Figure 5 Separate cage in which monkeys were waiting prior to the experiments and with a passageway system of tunnels that enabled separating the experimental subject from the group. (Photo: Lea Vodjerek)

Each marmoset was tested individually to eliminate any possible effects of the family group dynamics on the experiment. Every experimental subject was separated from the

family group and entered the experimental cage through a passageway of tunnels. The opaque guillotine door throughout the tunnels enabled luring a certain subject to enter the experimental cage, in a randomized sequence.

Figure 6 Experimental cage. (Photo: Lea Vodjerek)

Two wooden boxes were set in the back of the experimental cage (Figure 6). Each box contained a smaller wooden box (plexiglass was attached to the front, further referred to as “plexiglass box”) (Figure 7) in which tablets were placed. Marmosets had access to both boxes from three sides whereas the back was attached to the wall behind. In the test phase (see below, Chapter 3.4.3), I added two small plastic containers (blue and green) inside of the wooden box, half-closed with a plastic cover leaned on the container (Figure 8) which could be moved by monkeys when using mouth and/or hand (for clarification see text below).

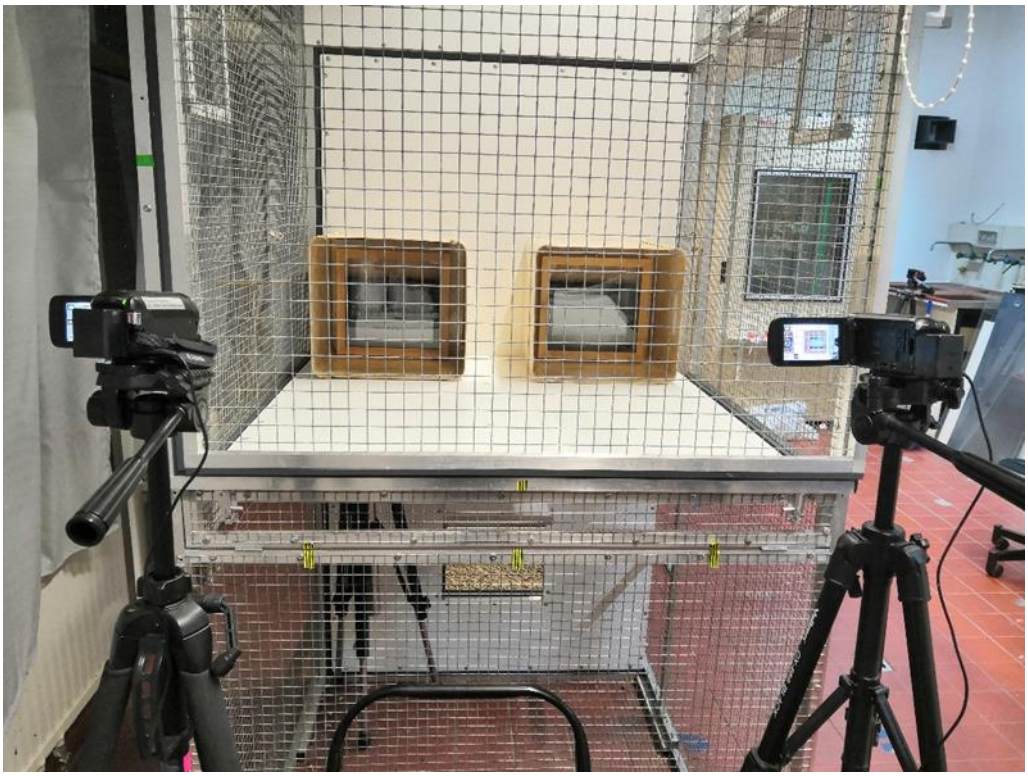

Figure 7 Experimental setup and position of the wooden boxes and the cameras. (Photo: Lea Vodjerek)

Both wooden boxes were covered in plastic wrapping so that marmosets could not damage them with teeth and/or by scent marking, and it also facilitated cleaning. Between the experimental subjects, the cage, boxes, and containers were cleaned with water-vinegar solution (ration 5:1) to prevent olfactory interference between different subjects and family groups.

3.3 EXPERIMENTAL CONDITIONS

For the video demonstration, one monkey (Sparrow) was trained to open the container and to take a piece of banana that was placed inside. In this video, the demonstrator opened one container by using its hand. In the other video only a solved problem was shown (i.e., the opened container and a half of banana inside it). In both videos, background noise was taken out and replaced with food calls emitted by an unfamiliar conspecific during each

video demonstration. The video consisted of several sequences that each lasted around 20 seconds, merged, and played for more than 5 minutes. The audio sequence was always the same (looped and matched in its occurrence on both social and non-social video).

Each video had two alternative containers presented: green and blue, but the demonstrated monkey was always opening and eating. All monkeys were randomly assigned to one alternative before the start of the experiment. Conditions were equally represented in both males and females and within family groups. The video was played within a PowerPoint presentation, and each PowerPoint presentation started with a slide showing a photo of a banana on a white background. Both presentations were played at the same time on a tablet placed in a plexiglass box and controlled via a Bluetooth controller. The position of the social demonstration and the solved problem (i.e., non-social side) was changed each day to avoid any side preference effect. Before the subject entered the cage, a first slide was shown (i.e., banana). Once the monkey was within the cage, I played the video (after approximately 3 seconds) (Figure 8).

3.4 TESTING PROCEDURE

Three cameras were used for filming the experiment. Two cameras were set on tripods and placed on the front side of the experimental cage and were used to focus on one of two wooden boxes (Figure 7). The third camera was handled by the second experimenter and was focused on the subject and its behavior.

Figure 8 Wooden box with plexiglass box that contains tablet and two containers with a cover. (Photo: Lea Vodjerek)

Marmosets were divided into two subgroups according to position in the keeping rooms (left and right groups from both rooms). In the first round of the experiment, I tested the "right groups": Kiri (Aurora), Kiri (Kobold), Double V's, and Romans, jointly 11 individuals. We excluded Nemo (family group Kobold) from the testing due to old age and incapability to perform the test. In the second round of the experiment, I tested the "left groups": Pooh, Sprichtel, Cleli 1, and Cleli 2, jointly 15 individuals.

Prior to the start of the experiments, all subjects were already familiar with the experimental cage and wooden boxes from the previous experiments. In this experiment, they were additionally habituated to the experimental cage and wooden boxes for two days during which they were rewarded with banana pieces ("habituation phase"). All monkeys were tested in three different phases of the experiment: demonstration phase (2 sessions), demonstration + test phase (5 sessions), and test phase (5 sessions). All the monkeys were

tested between 10h - 15h, every second day. Before the experiment monkeys were fed only with New World monkey pellets to increase their motivation and cooperation.

Before the start of the experiment wooden boxes and tablets were placed inside the experimental compartment. The tested subject was lured through the tunnel system to the "waiting hall" with a guillotine door that divided it from the experimental cage, just above the experimental cage. All three phases of the experiment, and the habituation phase, started after guillotine doors were opened and the monkey came into the cage with both hands and feet, but without a tail (Table 2).

Table 2 Experimental design showing sessions and experimental conditions.

The phase of the experiment	Day / session	Experimental condition
HABITUATION	Day 1 Day 2	Tablets turned off Black and white video playing on the tablet for 5 minutes
DEMONSTRATION	Session 1 and 2	Video demonstration played for 5 minutes
DEMONSTRATION + TEST	Sessions 3 - 8	Video demonstration played for 5 minutes Video demonstration played + containers added
TEST	Sessions 8 - 12	Video demonstration played + containers added

3.4.1 Habituation phase

The habituation phase was the first part of the experiment so that all subjects get used to the experimental cage and wooden boxes. On habituation day one, both wooden boxes were placed in an experimental compartment together with the plexiglass boxes. Inside the wooden boxes were placed four small banana pieces (2g) to encourage

monkeys to explore the inside of the box. Tablets were placed inside the plexiglass box but were turned off during this time. The test subject was then free to explore the experimental compartment and wooden boxes for 5 minutes. After five minutes subject came back to the waiting hall, and then through the tunnel system back to the separate cage where its family group was situated.

On the second habituation day, the set-up was the same with exception of the video demonstration on the tablet. On both tablets, the same pre-recorded black and white video showing natural landscape was played via Bluetooth controller. The purpose of this video was to habituate the monkeys to the screen that is turned on. The test subject was again free to explore the experimental compartment, wooden boxes, and Plexiglas boxes for 5 minutes. After five minutes a subject came back through the tunnel system to a waiting hall, and then back to the separate waiting cage, to its family group.

3.4.2 Demonstration phase

Session 1 and 2 were the start of the experimental phase when I play video demonstrations to all subjects. All test subjects were pre-assigned to one video demonstration alternative (i.e., green, or blue). Before the start of the experiment, all cameras were synchronized.

The start of the demonstration was when the monkey entered the experimental cage with both hands and feet (without tail), and at that moment guillotine doors were closed to prevent escape from the cage. First, a slide with bananas was shown, and then a video demonstration started approximately three seconds after closing the doors. The demonstration lasted for 5 minutes after which the subject was lured into the waiting hall and let back to a separate waiting cage with its family group.

3.4.3 Demonstration + test phase

This was a two-part phase in which the subjects had a demonstration part first for 5 minutes, and then a test part for another 5 minutes. The demonstration part was the same as mentioned in the previous section.

After the end of the demonstration part, the monkey was lured back into the waiting hall where it waited for the test part. In the meantime, I added containers (Figure 8) into a wooden box according to the position that was randomly added to every subject every day (Figure 9). Position of the boxes could be 1 or 2, with 1 being: blue on the right and green on the left, and 2: green on the right and blue on the left. Containers were added out of the sight for the waiting monkey. All boxes were filled with one banana piece (i.e., a half-moon of bananas; 6g). The cover of the container was leaned on the container, not fully closed, to facilitate an opening for the monkeys.

Figure 9 Test part of the experiment. (Photo: Lea Vodjerek)

The test part (Figure 9) began when the monkey entered the experimental compartment with both hands and feet, yet without the tail. The end of the test was either after 5 minutes or after the monkey opened one of the boxes and took a banana from it.

3.4.4 Test phase

The test phase was the final phase of the experiment. The procedure was the same as mentioned in the test part of the previous section (Figure 10). In sum, the monkeys had a chance to explore the containers. The test ended either after 5 minutes or after the monkey opened one of the boxes and took a banana from it.

Figure 10 Screenshot of Wall-E performing test and opening blue box on social demonstration side.

3.5 DATA CODING AND STATISTICAL ANALYSES

I merged all three videos (from three video cameras) into one video, using the video editing program *Shotcut.* After merging the videos, I analyzed the videos using *Solomon Coder beta* v. 17.03.22 (Péter, 2017), using an ethogram as shown in Table 3. All data were exported to Microsoft Excel 2016 and later evaluated statistically in *SPSS Statistics* v. 23 *(*IBM*).*

Table 3 Written description of all behaviors exhibited by the monkeys in the experimental cage. “Categories” represent a broader group of given behaviors, “Behavior” represents all actions that were coded in the experiment and that monkeys did in the experimental cage, and “Description” is a thorough explanation of each action that could be seen in the experiment.

CATEGORIES	BEHAVIOUR	DESCRIPTION
Markers	Open Demo/Test	The moment when the door was completely opened
	Start Demo/Test	The moment when the subject enters the experimental compartment with both his hand and legs.
	Stop Demo	300 seconds after start demo.
	End Test	300 seconds after start test or after the monkey opened one of the test boxes and took a banana.
Locomotion	Locomotion	The subject walks, runs, or jumps inside the experimental compartment
	Movement proxy	The number of locations subject has changed during the experiment
Latency (L)	Compartment	The time duration from opening the door until the subject enters the experimental cage with all four limbs.
	Slide change	The moment when the presentation slide changes to the video demonstration.
	Video starts	The moment when a video demonstration was played.
	Social/Nonsocial box	The time duration until the subject enters either of the wooden boxes (with at least one hand)
	Eat banana	The time duration until the subject takes a banana with his mouth.
	Touch Demo S/Nondemo S/Demo NS/Nondemo NS	The time duration until the subject touches either of the presented test boxes with his hands or head.
	Open Demo S/Nondemo S/ Demo NS/Nondemo NS	The time duration until the subject opens either of the presented test boxes with his hands or head.
	On the wire mesh	The subject is sitting, hanging, or moving on the wire mesh that surrounds the experimental cage.

Location	On the floor	The subject is sitting, standing, or moving on the floor of the experimental cage.
	On top of the S/NS box	The subject is sitting, standing, or moving on top of one of the wooden boxes
	In front of the S/NS box	The subject is sitting, standing, or moving at least 15 centimeters in front of one of the wooden boxes
	In the S/NS box	The subject is sitting, standing, or moving inside one of the wooden boxes. (Subject has to enter the wooden box with half of his body to be considered as in the box)
Vocalizations	Tsik	Mobbing call. Mostly used in the presence of a predator or when individuals are alarmed
	Tsik – Ek	Tsik and ek combined into one call. Made in situations of some alarm
	Ek	Mouth slightly open. Low pitched call; single or several in close succession.
	Phee	Sounds like a soft whistle. Constant in pitch over the whole call; made singly or several in close succession. Within-group contact call
	Chatter	Aggressive calls used in fights or during aggressive encounters. Companied by the vibration of the whole body
	Cough	Sounds like a soft whistle. Constant in pitch over the whole call. Mouth open or almost closed. Used as the contact call. .
	Twitter	Rapid series of elements regularly and closely spaced and each rising swiftly in frequency. Mouth opened.
	Chirp	Quiet, pleasant-sounding call, often emitted in the presence of preferred food
	See	Brief call rising slightly in frequency. Made in situations of some alarm
	Startle	The subject is suddenly scared away by some noise or other.

Stress-related behavior	Manipulating the cage	The subject is manipulating the wire mesh or any part of the cage with his mouth and/or hands.
	Manipulating the box	The subject is manipulating any surface of the wooden box with his mouth and/or hands.
	Defecate	The subject is defecating.
	Urinate	The subject is urinating.
	Scent mark	The subject is scent marking any surface in the experimental cage with his genitals/mouth/body.
	Piloerection	The subject's tail and/or body is piloerected.
Other behavior	Look to the side (S and NS)	The subject is looking at the side of either of the wooden boxes.
	Touch plexiglass	The subject is touching a smaller wooden box with plexiglass.
	Sniffing	The subject is sniffing any surface in the experimental cage.
Attention to videos	Attention social	The attention of the subject towards the social demonstration video.
	Attention non-social	The attention of the subject towards non-social demonstration video.
Manipulation	Manipulating demonstrated container S/non-demonstrated container S/demonstrated container NS/non-demonstrated container NS	The subject is manipulating either of the containers with his hands/legs/head.

4 RESULTS

To answer whether there was a difference in preference to the social and non-social demonstration, I compared the percentage of attention duration to the social and non-social demonstration using Wilcoxon Signed Rank Test. The percentage of attention for the demonstration phase, I got by dividing the duration of attention in one session with the full duration of video demonstration, which is 300 seconds, and I repeated that across all seven sessions. The numbers I got, I summarized and divided by the total number of sessions (i.e., 7 sessions). For the percentage of attention in the test phase, I used the duration of attention and divided it with the duration of the test (i.e., different for every individual) because the test phase could be finished after 300 seconds or after the container was opened. As I did for the percentage of attention in the demonstration phase, I summarized the values and divided the number with the total number of test sessions, which was 10.

There was no significant difference in the percentage of time spent observing social versus non-social in demonstration phase ($N_{subjects}$ = 26, Z = -1.029, p = 0.304, Figure 11) and in test phase ($N_{subjects}$ = 26, Z = -0.368, p = 0.713, Figure 12). Attention to a social demonstration was positively, but not significantly, correlated with the total number of openings of the demonstrated container on social side (rs= 0.339, p = 0.09), whereas the attention to the social demonstration was not correlated with opening of demonstrated container on the non-social side (rs= 0.181, p = 0.375). However, attention to non-social demonstration was significantly correlated with the number of openings of the demonstrated container on the social side (rs = 0.391, p = 0.048).

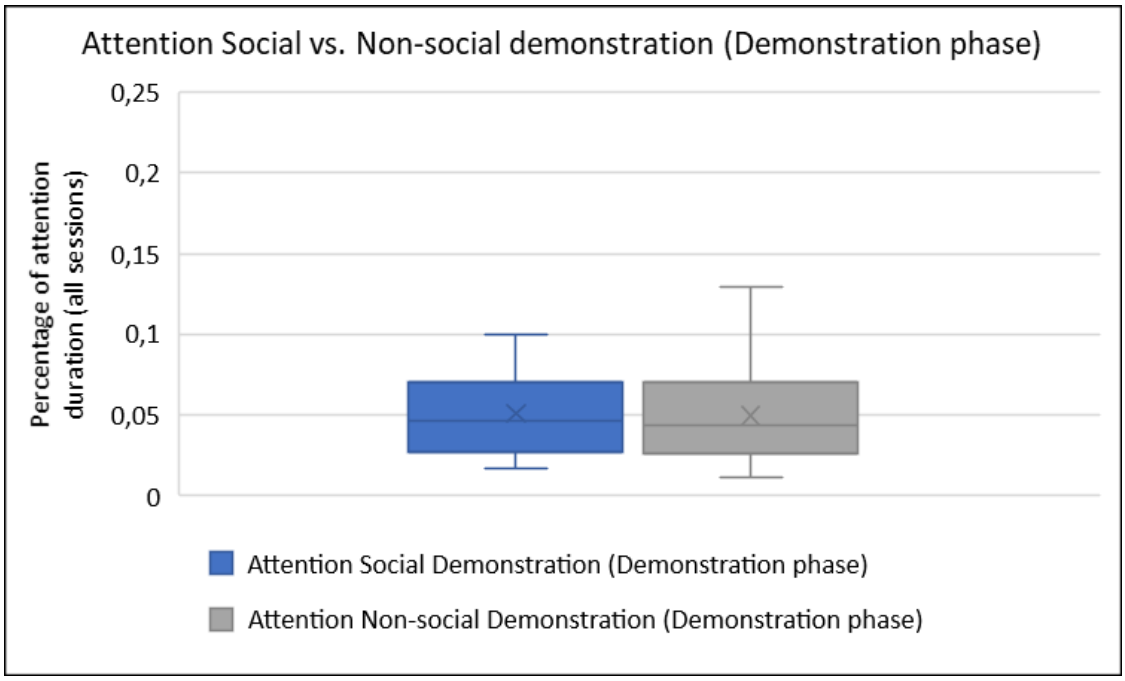

Figure 11 Boxplots showing the difference between the percentage of attention duration to the social and non-social demonstration in the Demonstration phase. The middle line of the box represents the median or middle number, the x in the box represents the mean and the whiskers (vertical lines) extend from the ends of the box to the minimum value and maximum value.

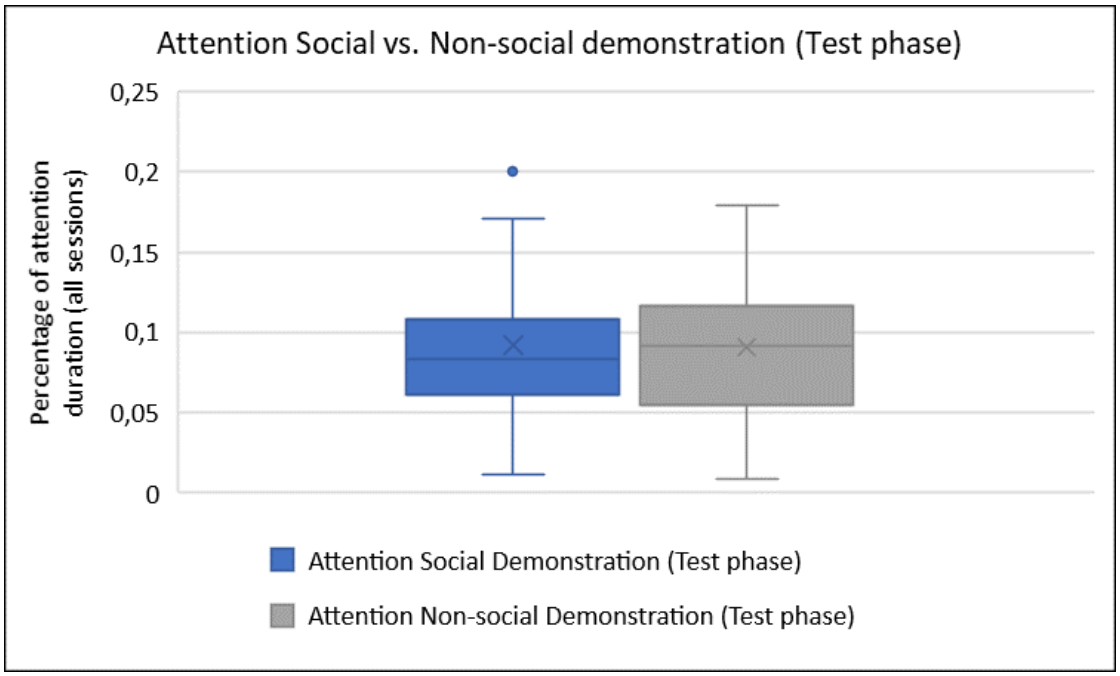

Figure 12 Boxplots showing the difference between the percentage of attention duration to the social and non-social demonstration in the Test phase.

To answer whether there was a difference between manipulation of demonstrated and non-demonstrated containers, I used Wilcoxon Signed-Rank test. I used the percentage of manipulation of demonstrated and non-demonstrated containers, on both social and non-social sides combined, in the test phase. The percentage of manipulation duration, I got by dividing the total duration of manipulation with the duration of the test (i.e., different for every individual) through all sessions for each individual separately. I summarized the values I got and divided them with the total number of test sessions (i.e., which was 10). I found that there was no significant difference between manipulation of demonstrated and non-demonstrated containers (Wilcoxon Signed Rank test, $N_{subjects}$ = 26, Z =-0.470, p = 0.638, Figure 13). Additionally, there is an individual difference in the choice for the first container monkeys touched in every test (i.e., demonstrated, or non-demonstrated container), but on the population level, there is no significant difference (Figure 14).

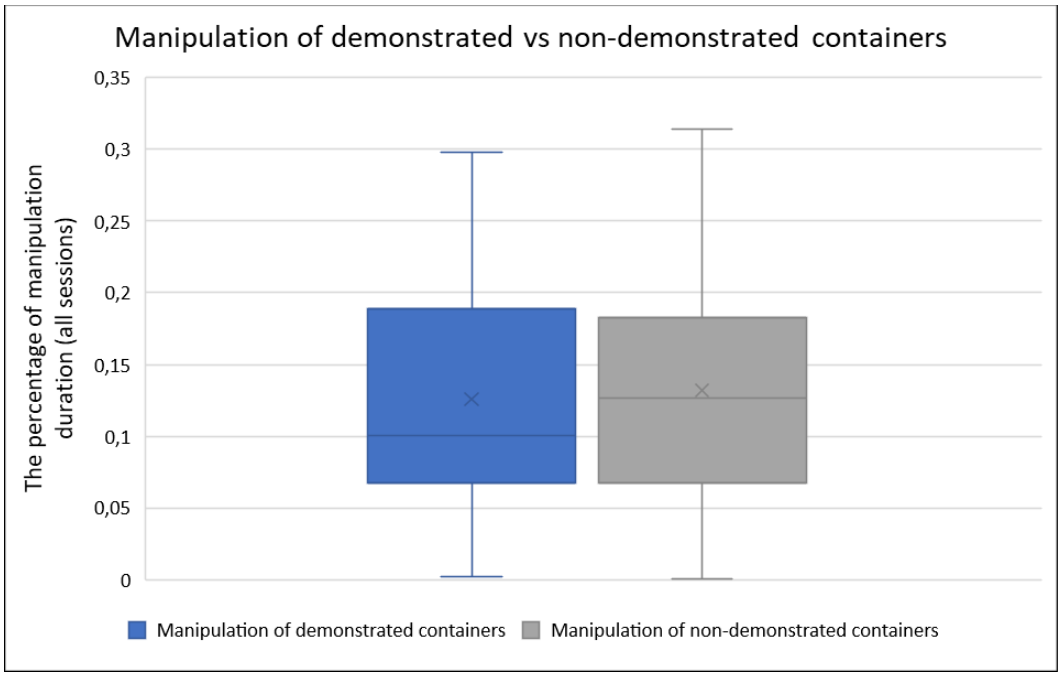

Figure 13 Boxplots showing the difference between manipulation of demonstrated and non-demonstrated containers in all sessions of the Test phase combined.

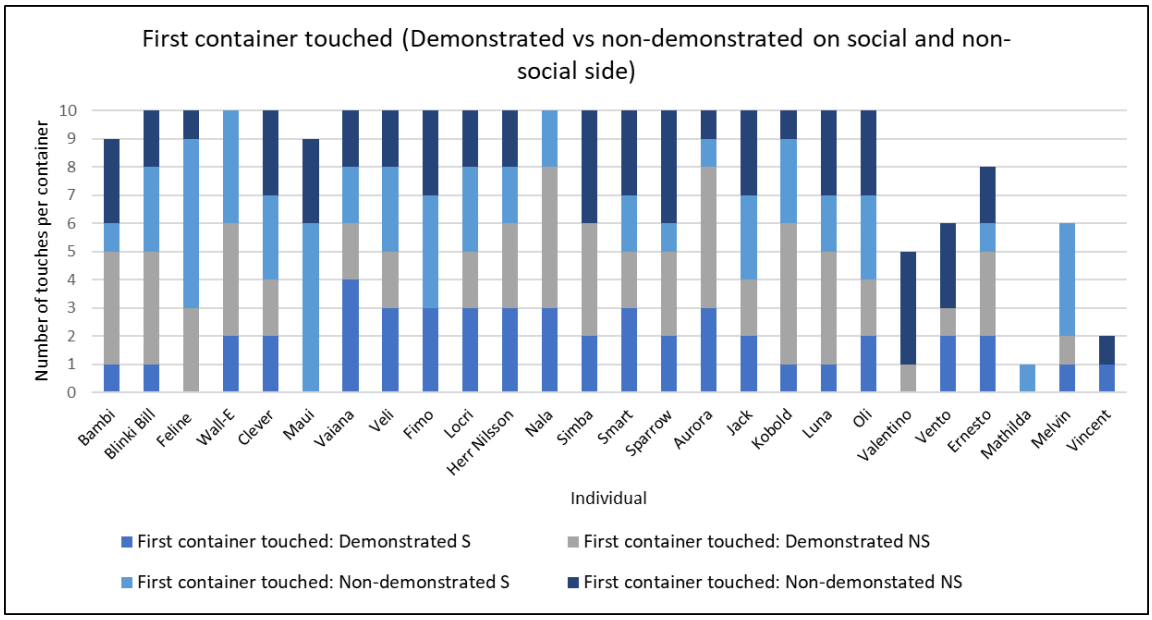

Figure 14 Graph showing the first touched container across all sessions for all individuals.

To assess whether there was the effect of age, sex, and group on monkeys' attention for a video demonstration, I used Generalized Linear Models (GLM). I compared the full to the null model, and if the full model was better than the null model, I continued performing a stepwise model selection (reducing factors from a full model) using Akaike's Information Criterion (AIC) to select the best model. The best model predicting attention to the social video demonstration was the one with a group as a predictor ($B = 0.045$, $p = 0.001$), in the Demonstration phase (Figure 15). For the Test phase, the best model predicting attention to the social demonstration was also the one with a group as a predictor ($B = 0.038$, $p < 0.001$, Figure 16).

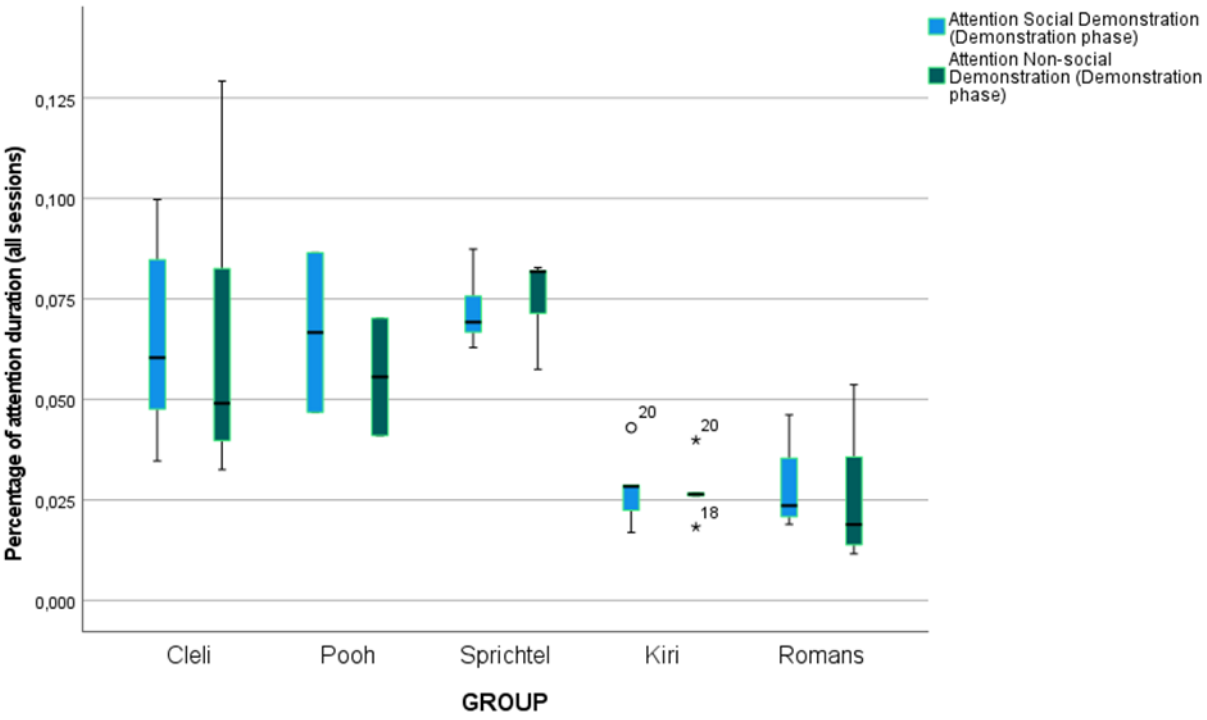

Figure 15 Boxplots showing group differences in attention to the social and non-social demonstration during the Demonstration phase.

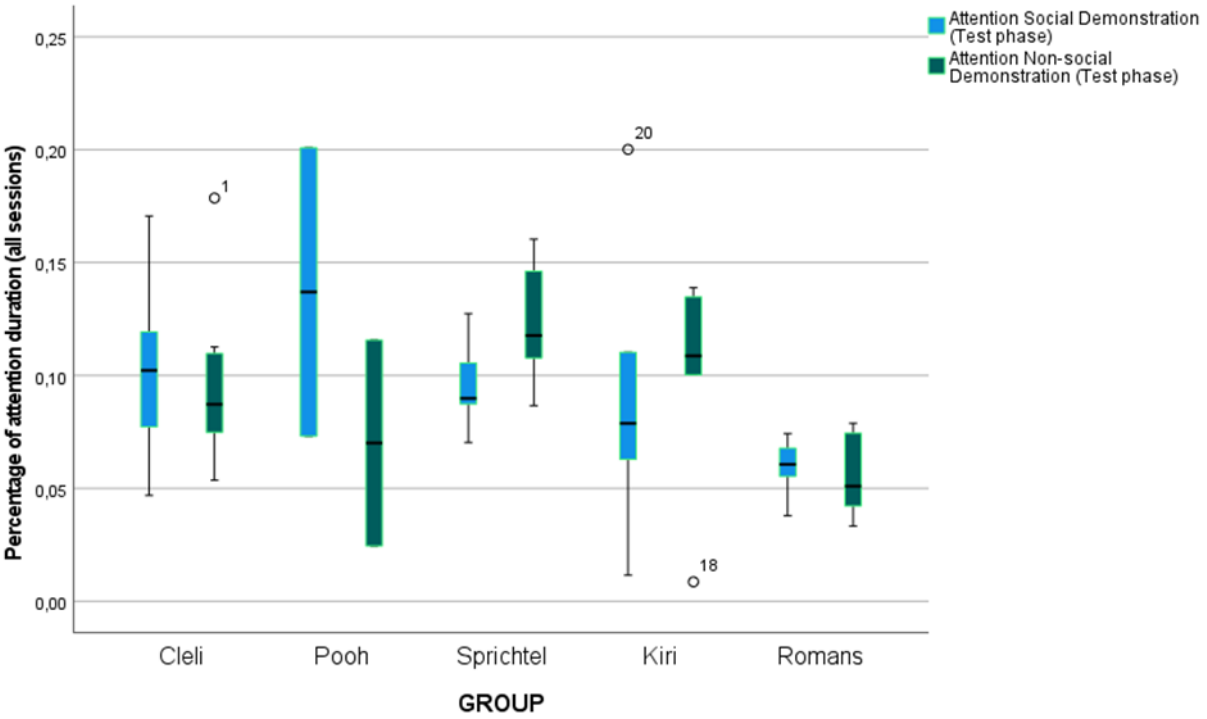

Figure 16 Boxplots showing group differences in attention to the social and non-social demonstration during the Test phase.

As I wanted to know if there were individual differences within the population regarding attention to video demonstration (i.e., social, and non-social), I plotted the percentage of attention across all sessions in the Demonstration and Test phase. Visual inspection of the graphs allowed me to see if there were differences in attention to social and non-social demonstration between individuals and if some individuals were more interested in video demonstrations than others (Demonstration phase: Figure 17 and test phase: Figure 18)

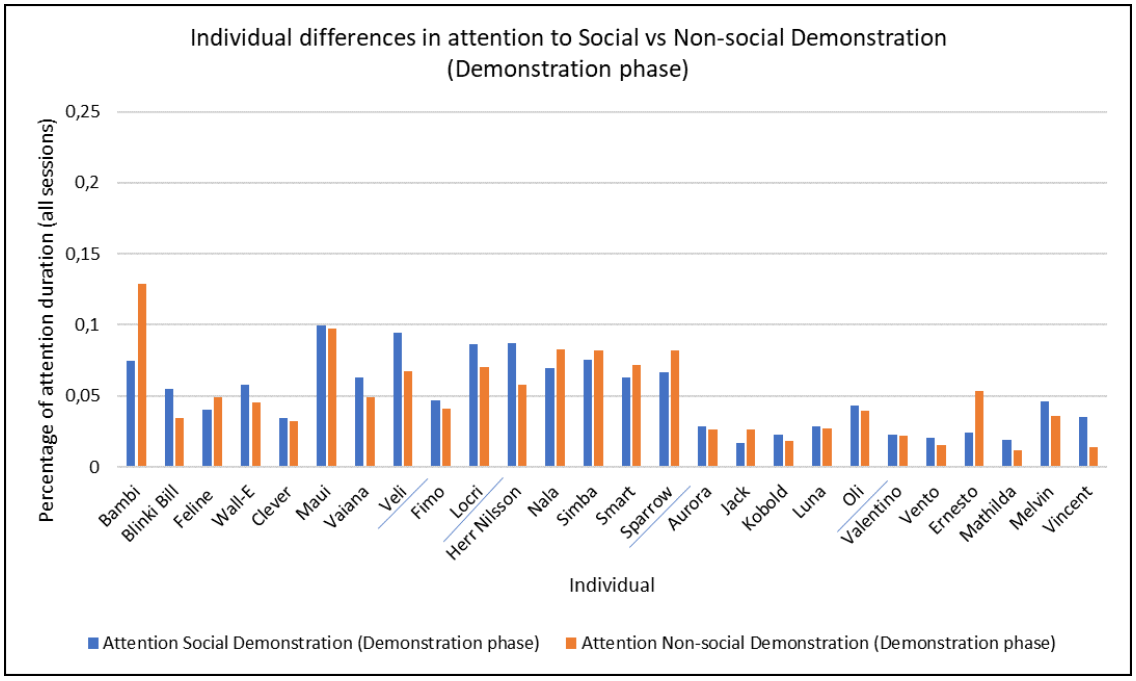

Figure 17 Graph showing the individual differences in the percentage of attention to the social and non-social demonstration during the Demonstration phase.

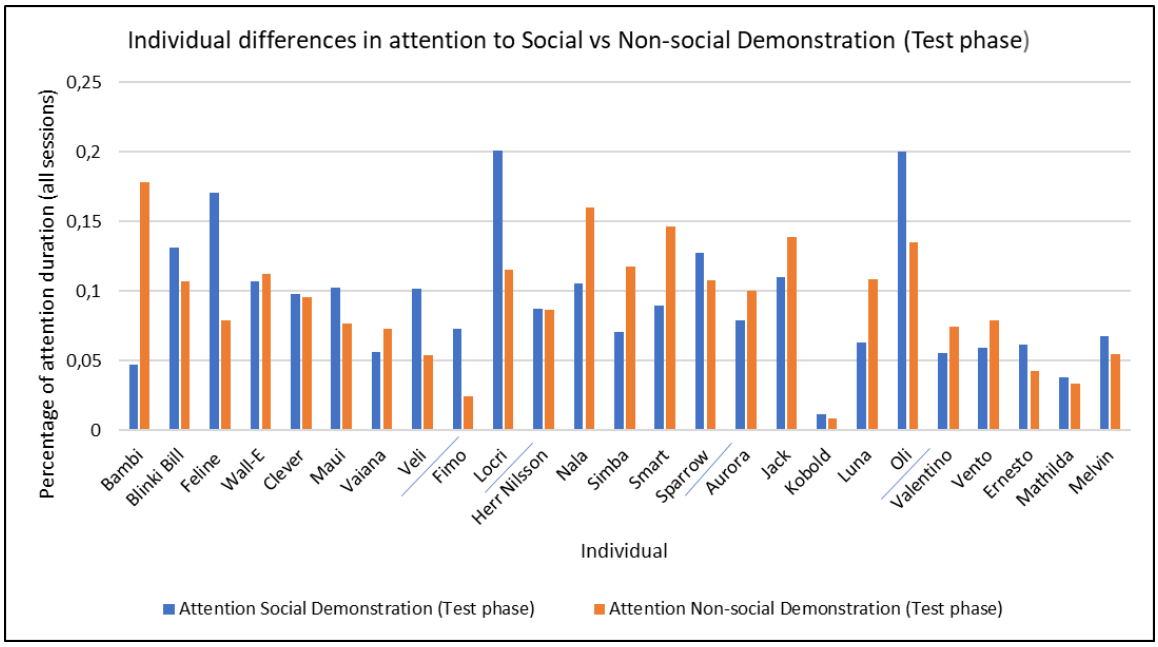

Figure 18 Graph showing the individual differences in the percentage of attention to the social and non-social demonstration during the Test phase.

Finally, I used a GLM to determine if age, sex, and/or group had affected the monkeys' choice to manipulate demonstrated or non-demonstrated containers on the social and non-social sides. The percentage of manipulation I got by dividing the duration of manipulation with the duration of the test (i.e., different for every individual). I summarized the values and divided the number with the total number of test sessions (i.e., which was 10). Using the Generalized Linear Model, I compared the full to the null model, and if the full model was better than the null model, I continued performing a stepwise model selection (reducing factors from a full model) using Akaike's Information Criterion (AIC) to select the best model. The best model predicting manipulation of demonstrated containers on both social and non-social sides was the one with a group as a predictor ($B = 0.144$, $p < 0.001$), Figure 19).

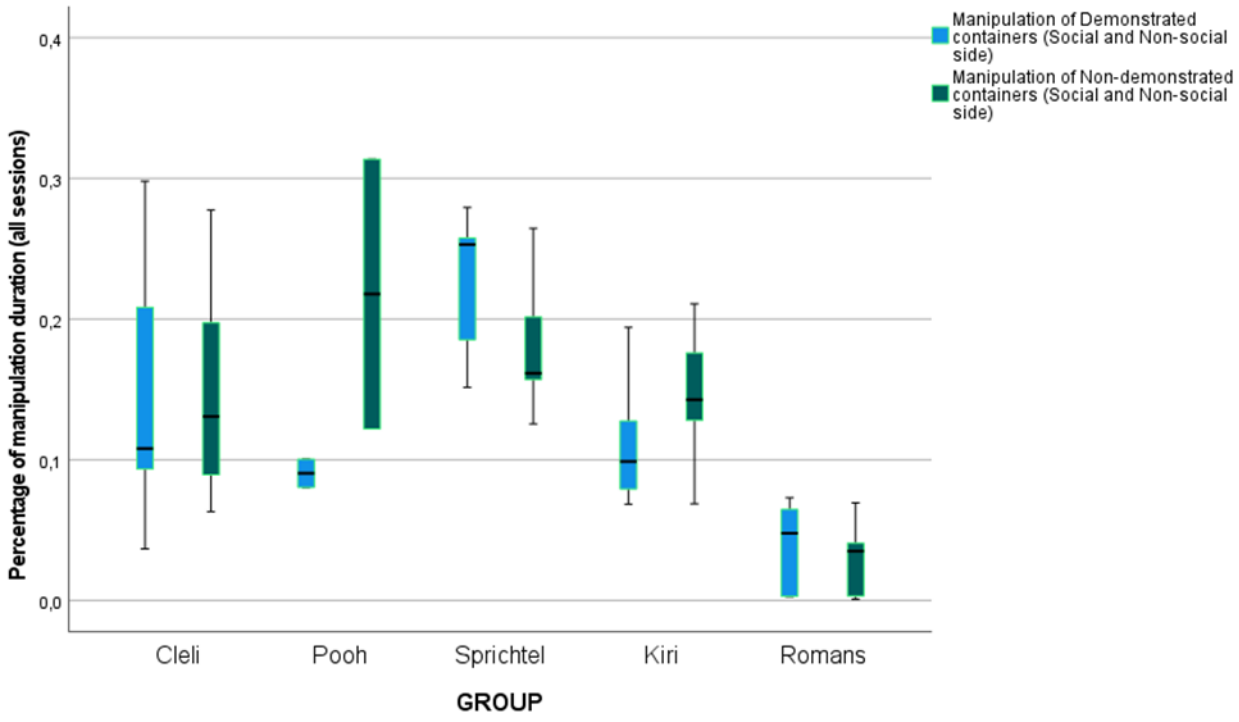

Figure 19 Boxplots showing group-level differences in the manipulation of demonstrated and non-demonstrated containers on the social and non-social sides.

5 DISCUSSION

Given the vast literature on social learning in marmosets (Chapter 1.1 and 1.4), we expected that monkeys spend more time watching the social video demonstration as compared to the non-social video demonstration. In contrast to our prediction, we found no significant difference in the proportion of time the subjects spent in front of the social compared to the non-social videos across all sessions in the demonstration and test phase. These findings suggest that the monkeys were interested in the video demonstration in general, which supports findings from previous studies (Gunhold, Range, Huber, & Bugnyar, 2015; Oh, Šlipogor, & Fitch, 2019), but that the social demonstration was not more attractive to them. Also, it could mean that monkeys do show a preference, but in our captive colony, there is a similar number of individuals who are interested either in social or non-social information. Finally, there is the possibility that the monkeys had difficulties in recognizing a virtual conspecific and thus failed to discriminate between social and non-social video demonstrations. This explanation is unlikely, however, as common marmosets successfully learned how to manipulate boxes after they watched a video demonstration clip in the study by Gunhold et al. (2014). Video clips were also used in a study by Burkart and colleagues (2012), where marmosets were shown a short video clip of a conspecific, robot and a black box approaching and/or interacting with a target. Results from this study suggest that marmosets were able to distinguish between a conspecific, robot and a black box, as they showed a stronger preference for the object that was approached by a conspecific or a robot (J. Burkart, Kupferberg, Glasauer, & van Schaik, 2012). All these studies' results suggest that marmosets were able to recognize a conspecific in a video.

Following the studies by Burkart et al. (2012) and Gunhold et al. (2014), I tested if there was a correlation between attention to social demonstration and the subsequent opening of the demonstrated container. Although no significant correlation was found, a non-significant trend goes in the predicted direction. One of the possible explanations for this result could be the rather small sample size. Future studies should thus try to include more individuals.

Focusing on the monkeys' choices between containers, I could not find a clear preference for the demonstrated or non-demonstrated containers. Some of the individuals showed a preference for the demonstrated container, but on the population level, there was no significant preference. This result could be explained by personal experience gained in the course of the experiment: after subjects figured out that there is a reward in every container,

they did not prefer the demonstrated container anymore, but just opened the first container they approached (Appendix 3 and Appendix 4). Even if they chose the demonstrated container, it could happen that they faced problems in opening it, so they moved on to open the other container.

To answer the question if the monkeys' attention to video demonstration is influenced by age, sex, or group, I used Generalized Linear Models. The best model for my data was the one containing only a group as a factor. Hence, which family group monkeys belong to could explain their attention to the social demonstration in the demonstration phase, but also their attention to the non-social demonstration in the demonstration and test phase (Figure 15 and 16). These results are in line with my prediction, and fit the findings from a previous study on the same monkeys' preferences for coping with new and risky stimuli (Šlipogor, Gunhold-de Oliveira, Tadić, Massen, & Bugnyar, 2016). Our captive family groups typically consist of an unrelated male and female, together with their offspring. Hence, the finding of a group similarity could be due to a combination of genetics and the social environment that individuals of the same family share (compare Šlipogor *et al.*, 2016; Koski and Burkart, 2015).

Focusing on the individual level, visual inspection of the data shows that some monkeys consistently prefer social over non-social demonstrations or the other way around The results indicate that, as predicted, there are individual differences within the colony, and within the family groups. These results are consistent with the finding in personality study (Šlipogor, Burkart, Martin, Bugnyar, & Koski, 2020; Šlipogor et al., 2016; Šlipogor, Massen, Schiel, Souto, & Bugnyar, 2021), that showed individual personality differences, and differences within the same family group, in the same colony of common marmosets. What is yet an open question is whether individuals of a particular personality type prefer social over non-social information.

Concerning the question of whether the monkeys' choice to manipulate the demonstrated or non-demonstrated containers is influenced by sex, age, or group, the results again showed a clear difference between family groups (Figure 19) but no effect of sex or age. The captive colony used for this study consists of a number of young individuals, especially in the 'Cleli' group, who are very explorative and playful. This could be a reason why some monkeys spent a similar amount of time in front of both demonstrations and did not have a clear preference for one of them. Furthermore, there are family groups like the 'Romans', who hardly had any interest in the video demonstration and the containers. This kind of difference within

and between the family groups perhaps explains why I found a difference in attention and manipulation on a group level, and why there was not a significant difference on a group level when it comes to attention to the social and non-social demonstration

The study of animal personality, which could be defined as "consistent inter-individual differences in correlated behavioral traits stable throughout time and/or context" (Gosling, 2001; Réale, Dingemanse, Kazem, Wright, & B, 2010), has received a lot of attention in recent years. Ever since scientists noticed the importance of personality variation for biological diversity and evolution, they have been studying it in a variety of species across the animal kingdom, from invertebrates to apes (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007; Réale et al., 2010; Wat, Banks, & Mcarthur, 2020; Watson et al., 2018). What these studies are aiming to answer is how different types of personality can influence individuals' behavior within the population. Researchers are trying to broaden our knowledge of animal personalities by observing them from an evolutionary and ecological point of view (Réale et al., 2010). A lot of personality traits are expressed inside of a social group and are of importance in the formation and functioning of cooperative social groups (Rothenberger, Heg, & Schu, 2010), such as we can observe in marmosets. Animal personalities are used to explain often variations in individual performance in a problem-solving task because they can affect how they discern and interact with the environment. This kind of personality effect on a successful problem-solving performance was observed in urban common brushtail possums (*Trichosurus vulpecula*) (Wat et al., 2020). Specifically, they found that personality traits (i.e., boldness, docility, exploration, activity, mobility, vigilance) affected problem-solving capability. Exploratory, more active, and vigilant individuals were more likely to succeed in their tasks, but only highly explorative individuals were able to solve difficult tasks. Even though my experiment was not focused on personality differences in our marmosets, it turned out to have a strong influence on the marmosets' decision making when it comes to watching video demonstrations or manipulating demonstrated or non-demonstrated container. Accordingly, it could be argued that, as proposed by Wat and colleagues, more active and more exploratory animals were more likely to open a container, and that experience and learning increased the probability of success in the experiment. Whether more inactive and shy subjects would particularly benefit from social demonstrations would be an interesting question fur further studies.

To my knowledge, this is the first study that provides monkeys with a choice between a social and non-social demonstration at the same time. Although no clear preferences for social

and non-social demonstration and demonstrated or non-demonstrated containers were found on the population level, I found strong hints for preferences in seeking and picking up on social or non-social information on the individual and/or family level. This experiment may thus provide a good basis for future studies. For those, I would suggest using additional social learning tasks with a multiple-choice set-up, combined with a battery of personality tests.

6 CONCLUSION

In this study, the preference for social learning was tested in 26 common marmosets using a choice set-up, in which they could decide to watch either a social or non-social video demonstration (a conspecific opening a container vs. an opened container) before they were confronted with the respective containers. I did not find a preference for social or non-social demonstration, nor a preference for demonstrated or non-demonstrated containers on the colony level. However, both the monkeys' attention for a video demonstration and their choice to manipulate demonstrated or non-demonstrated containers have been influenced by their origin/social environment, i.e. what family group they come from. Furthermore, large inter-individual differences in attention to video demonstrations were found in the demonstration and test phases.

Understanding how animals are using the information that they are provided with is an important step in understanding animal cognition. This experiment could be used as a good basis for future studies of social learning with a multiple-choice setup, as well as studies using video demonstrations. One of the next steps could be connecting individuals' choices with their personality, which might give us a clearer picture of who is preferring to get what kind of information.

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8 APPENDICES

Appendix 1 The schedule of the experiment. After each testing day, there was a one-day break. The first test subgroup (“right groups”) is marked orange and the second test subgroup (“left groups”) is marked green.

	Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
June	8	9	10	11	12	13	14
	15	16	17	18	19	20	21
	22	23	24	25	26	27	28
	29	30	1	2	3	4	5
July	6	7	8	9	10	11	12
	13	14	15	16	17	18	19
	20	21	22	23	24	25	26
	27	28	29	30	31	1	2
August	3	4	5	6	7	8	9

Appendix 2 The monkeys were assigned one video demonstration alternative before the experiment (green or right). Here is shown subgroup division (right or left) and which video demonstration was assigned to which subject.

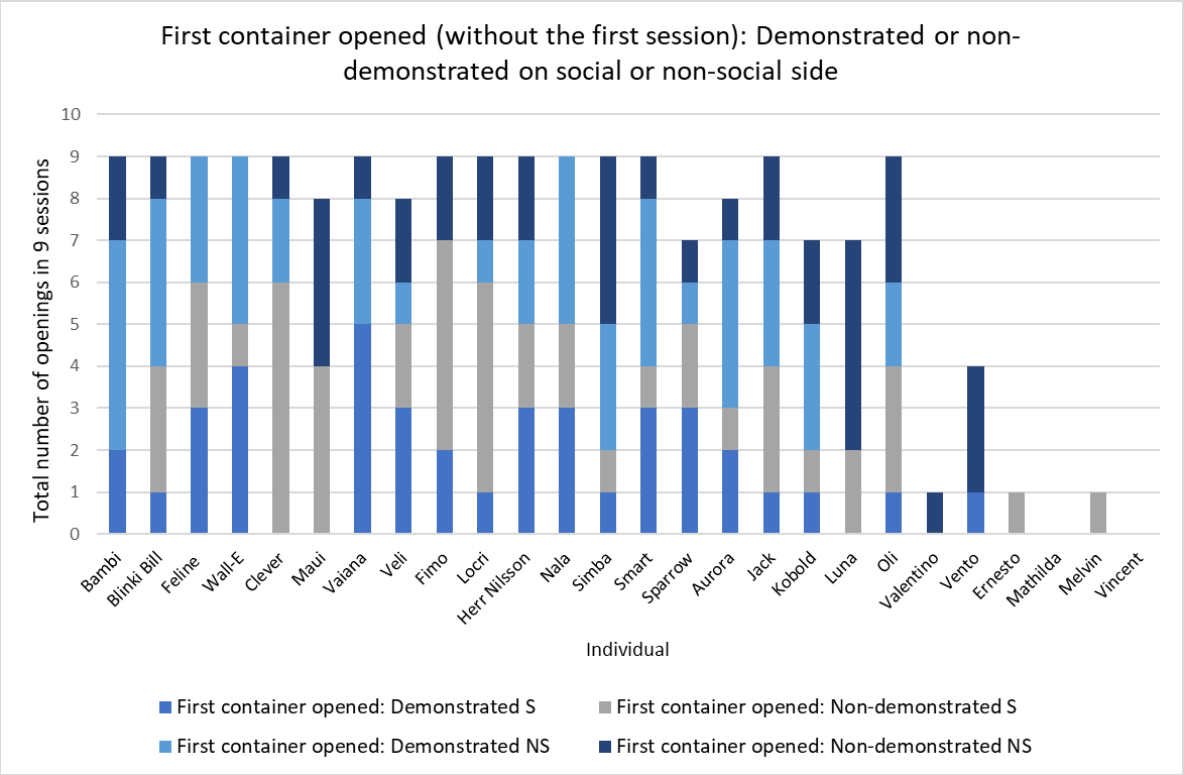
Family group	Individual	Subgroup	Video demonstration
Double V's	Vento	Right	Blue
	Valentino		Green
Kiri (Aurora)	Jack	Right	Green
	Aurora		Blue
Romans	Ernesto	Right	Green
	Mathilda		Green
	Melvin		Blue
	Vincent		Blue
Kiri (Kobold)	Luna	Right	Blue
	Kobold		Blue
	Oli		Green
Pooh	Fimo	Left	Green
	Locri		Blue
Sprichtel	Herr Nilsson	Left	Blue
	Nala		Green
	Simba		Blue
	Smart		Green
	Sparrow		Blue
Cleli 1	Bambi	Left	Green

	Blinky Bill		Blue
	Feline		Green
	Wall-E		Blue
Cleli 2	Clever	Left	Blue
	Maui		Green
	Vaiana		Blue
	Veli		Green

Appendix 3 Table showing the first container opened in Session 3 – the first session in which monkeys could manipulate the containers.

Individual	First session-first container opened		Individual	First session-first container opened		Individual	First session-first container opened
Bambi	Non-demonstrated NS		Locri	Non-demonstrated NS		Luna	Non-demonstrated NS
Blinki Bill	Non-demonstrated NS		Herr Nilsson	Demonstrated S		Oli	Non-demonstrated S
Feline	Non-demonstrated NS		Nala	Demonstrated NS		Valentino	Non-demonstrated S
Wall-E	Non-demonstrated S		Simba	Non-demonstrated NS		Vento	Demonstrated S
Clever	Demonstrated NS		Smart	Non-demonstrated NS		Ernesto	NONE
Maui	Demonstrated S		Sparrow	Demonstrated NS		Mathilda	NONE
Vaiana	Demonstrated S		Aurora	Non-demonstrated NS		Melvin	Demonstrated NS
Veli	Non-demonstrated NS		Jack	Non-demonstrated S		Vincent	NONE
Fimo	Non-demonstrated S		Kobold	Demonstrated S			

Appendix 4 Graph showing the first container opened in the remaining 9 sessions.



RESUME

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