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"Monkey see, monkey do… or do they?

Social learning in common marmosets and the influence of present conspecifics on learned preference"

verfasst von / submitted by

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Abstract

One advantage of living in social groups is the opportunity to learn from other group members. Social learning has been extensively studied and is usually explored either in a dyadic demonstrator-observer setting, or in a group setting. This study aimed to explore social learning of colour preferences in 28 common marmosets (*Callithrix jacchus*) in both, dyadic and group settings. The test-subjects first observed a conspecific demonstrator eating out of a specifically coloured box, and then had the choice between the previously demonstrated box and a novel one. Control-subjects received no social demonstration. I examined whether subjects choose the demonstrated box when given a choice between two differently coloured boxes, and if so, whether the learned preference perseveres in a social context, including their group members. Contrary to my predictions, social demonstrations did not lead to increased manipulation of the demonstrated box. Perhaps this was due to the test design, where both boxes were rewarded equally, and thus subjects did not *need* to pick one box over the other. In the subsequent group sessions, the marmosets altered their behaviour significantly adjusting to the group dynamics. In comparison to the dyadic sessions, they needed longer to touch and eat from the boxes, and ate for a shorter amount of time, likely due to within-group monopolization of the boxes by certain individuals. With slight alterations of the current experimental design, future studies could provide more knowledge on the information transmission in common marmosets and the mechanisms behind the conformity in a group.

Keywords

stimulus enhancement, social facilitation, conspecific demonstrator, *Callithrix jacchus*

Zusammenfassung

Das Leben in Gruppen bietet die Gelegenheit, von anderen Gruppenmitgliedern zu lernen. Soziales Lernen wird schon lange ausführlich erforscht, meist unter kontrollierten sozialen Bedingungen auf dyadischer Ebene oder auf Gruppenebene, um die Auswirkungen der Anwesenheit anderer Gruppenmitglieder zu untersuchen. Ziel dieser Studie war es, soziales Lernen von Farbpräferenzen bei 28 Weißbüschelaffen (*Callithrix jacchus*) sowohl auf dyadischer- als auch auf Gruppenebene zu untersuchen. Die Affen der Testgruppe beobachteten zunächst einen Artgenossen beim Fressen aus einer spezifisch gefärbten Box und hatten anschließend die Wahl zwischen der zuvor vorgeführten und einer unbekannten, andersfarbigen Box. Affen der Kontrollgruppe erhielten keine soziale Demonstration. Ich untersuchte, ob Affen aus der Testgruppe die vorher demonstrierte Box wählen, wenn sie die Auswahlmöglichkeit haben, und wenn ja, ob die erlernte Präferenz in einem sozialen Kontext, einschließlich Gruppenmitgliedern, bestehen bleibt. Eine soziale Demonstration zu erleben, führte nicht zu einer verstärkten Manipulation der demonstrierten Box. Eventuell lag dies am Testdesign, bei dem beide Boxen gleich belohnt wurden und die Probanden somit nicht eine vorzuziehen brauchten. In den anschließenden Versuchen mit der kompletten Gruppe anwesend, änderten die Weißbüschelaffen ihr Verhalten deutlich, um sich an die Gruppendynamik anzupassen. Im Vergleich zu den dyadischen Sitzungen brauchten sie länger, um die Boxen zu berühren und daraus zu essen, und aßen kürzer, wahrscheinlich aufgrund der Monopolisierung der Kisten innerhalb der Gruppe durch bestimmte Individuen. Mit kleinen Änderungen des hier ausgeführten Versuchsdesigns könnten zukünftige Studien mehr Wissen über die Informationsübertragung bei Weißbüschelaffen und die Mechanismen hinter der Konformität in einer Gruppe liefern.

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Introduction

Social learning

Using innovative solutions to retrieve a novel food source from its location, break it down to its edible parts, or even recognize if it is edible in the first place, may be functional. However, systematically observing conspecifics and copying their behaviour, in many cases may reduce the risk and time taken with the unknown food source to achieve the same outcome.

Thus, social learning, defined as ‘‘learning that is influenced by observation of, or interaction with, a conspecific, or its products’’ (Heyes, 1994) is assumed to be less costly than individual innovation or asocial learning, that occurs through trial and error (Laska and Metzker 1998; Laland, 2004; van Schaik and Burkart, 2011; Whiten and van de Waal, 2017). Acquiring information that has been previously sampled by conspecifics and adjusting the own behaviour accordingly when deciding what to feed on, where to forage, or whom to run from (Heyes, 1994; Danchin et al., 2004; Laland, 2004; Galef and Laland, 2005; Dall et al., 2005; Leadbeater and Chittka, 2007; Hoppit and Laland, 2008; Grüter et al., 2010), is evolutionarily advantageous. The observer's attention and interest in a specific stimulus can be particularly enhanced by a conspecific demonstrator, and it can increase the observer’s propensity to copy the shown behaviour, as well as the probability of interaction with similar stimuli in the future (Zentall, and Galef, 1988).

This is not a new phenomenon. Since the very beginning of the 1900s (Morgan, 1900) scientists have been observing and defining the different mechanisms and levels of social learning, starting at the motivational level (e.g., contagious behaviour; Massen et al., 2016) and response facilitation (Byrne, 1994). Zentall (2004) described the process of attention shifting towards a location or object associated with a reward as stimulus enhancement. This mechanism has been shown in many species (British blue tits, *Cyanistes caeruleus*: Fisher and Hinde, 1949; Sherry and Galef, 1991; grayleg geese, *Anser anser*: Fritz et al., 2000; long tailed macaques, *Macaca fascicularis*: Zuberbühler et at., 1996). Stimulus and local enhancement can be classified as social learning on a perceptional level. Observational conditioning, the process of learning an association between a given object and a subsequent event by observation (Heyes, 1994; Curio,

1988) can be categorized as social learning on the associative level. The cognitive level of social learning includes advanced forms of imitation and emulation. Imitation (Morgan, 1900) can be defined as the copying of behaviour (or vocalizations), and emulation (Custance et al., 1999) is defined as learning about consequences of a specific behaviour (Tomasello, 1996), and entails not only *reproducing* the behaviour, but also *understanding* the connection between the action and its outcome.

If social learning occurs repeatedly among individuals within a population as well as across generations, it can have long-term effects on the entire population and its offspring, and potentially lead to the evolution of culture. In this sense, culture acts as nature's 'second inheritance system' (Whiten, 2005). The degree to which social learning and culture are present in primates and other animals, has received much attention in the scientific community (Zentall and Galef, 1988; Hoppitt and Laland, 2008; Kendal et al., 2010; Whiten et al., 2011). Social learning is widespread and can be found in most (social) species all through the animal kingdom, from insects to mammals (Freeberg, 2000; Galef and Giraldeau, 2001; Brown and Laland, 2003; Leadbeater and Chittka, 2007; Thornton, 2008).

Even though social learning has also been observed in some solitary species (Coolen et al., 2005**;** Wilkinson et al., 2010), it is much more common in the socially more complex species (Reader and Laland, 2002). Aspects of social life, for instance the number of individuals in a group, keeping track of the hierarchical order, and maintaining social relationships with groupmates, as well as the ecological challenges like, for example, the group effort to avoid predators, can all contribute to the necessity and thus evolutionary advantage of individuals learning socially. These aspects have led to an array of hypotheses surfacing over the past few decades. The social complexity hypothesis (Jolly, 1966; Humphrey, 1976; Connor et al., 1992), the social brain hypothesis (Dunbar, 1998), the social intelligence hypothesis (Kummer at al., 1997) and the Machiavellian intelligence hypothesis (Whiten and Byrne, 1988) all, in their own way, link the aspects of sociality with cognition, which make social learning possible.

In primates, who are mostly social species, social learning has been observed to play a huge role in the information transmission within a population and across generations (Mineka and Cook, 1988; Call and Tomasello, 1994; Perry, 2011; Watson et al., 2018). New World monkeys have been shown to socially learn what to feed on and how to access the food (Prescott and Buchanan-Smith, 1999; Rapaport and Brown, 2008), in what context to use which vocalization (Lemasson et al., 2011; Snowdon, 2013), who to run from (Kemp and Kaplan, 2011) and how to access desired resources (Bugnyar and Huber, 1997; Perry, 2011).

Demonstrator choice

Laland (2004) studied the various social learning strategies: copying when uncertain, copying the majority, and copying if the other individual is better than you. In all these strategies, it is important to be selective in the choice of demonstrator (de Waal 2001; Henrich and Gil-White 2001; Giraldeau et al., 2002; Laland 2004; Galef and Laland, 2005; Mesoudi 2008; Rendell et al., 2010). The influence of the demonstrator on the observer often determines the extent to which the observer will pay attention to, copy, and adopt the demonstrated methods (Bandura, 1977; Nicol and Pope, 1994; Coussi-Korbel and Fragaszy, 1995; Valsecchi et al., 1996; Choleris et al., 1997; Choleris and Kavaliers, 1999; Laland, 2004; Range and Huber, 2007; Schwab et al., 2008; van de Waal et al., 2013). Proximity in social interactions (e.g., play and antagonism) can lead to transmission of social skills (Coussi-Korbel and Fragaszy, 1995; van Schaik and Burkart, 2011). Kinship and relationships between animals seem to have an influence on the acquisition and transmission pattern of behaviours, preferences, and skills in different species, like for example in hens, *Gallus gallus domesticus* (Nicol and Pope, 1994), sheep, *Ovis aries* (Thorhallsdottir et al., 1987), and chimpanzees, *Pan troglodytes* (Menzel, 1973; 1974). Especially primates, living in structured social family groups, are most likely to learn from models that are more knowledgeable, older, or higher-ranking than them (for review see Custance et al., 2002). This behaviour might be linked to conformity, so that the young subordinate individuals adjust their behaviour to the behaviour of the older and/or more dominant group members (de Waal 2001; van de Waal et al., 2013).

The common marmoset (*Callithrix jacchus*)

Common marmosets are routinely used as a model organism in many fields of biology like genetics (Nievergelt et al., 2000), neuroscience (Okano et al., 2012), and cognition (Ash et al., 2020) due to their quick development of the offspring (Vitale and Queyras, 1997; Dell'mour et al., 2009; Schiel and Souto, 2017), as well as the ease of maintenance in a laboratory due to their small size, relatively easy handling and close phylogenetic relation to humans (Abbott et al., 2003; Kishi et al., 2014), as well as their cooperative breeding system that is similar to that of humans (Digby et al., 2006; Burkart et al., 2009). The body size of a marmoset rarely exceeds 20cm (excluding the tail), and its average body weight is approximately 300g (Stevenson and Poole, 1976). Sexual maturity is reached at around 18 months of age, and the average lifespan in captivity is about 13 years (Chandolia et al., 2006; Nishijima et al., 2012). Their nutrition consists of fruits, flowers, small animals such as insects, frogs, and spiders, as well as gums and sap obtained from trees (Caton et al., 1996; Abreu et al., 2016), which they recognize and distinguish very easily by smell (Laska and Metzker, 1998).

Because of the X-chromosomal opsin gene, which is coding for colour vision, marmosets exhibit a polymorphism in their visual pigments. Even though the rods and short-wave receptors seem to be the same in both sexes, they can differ in number and spectral positions in the spectral region representing green and yellow colours. While female monkeys can draw one or two pigments of the ones on the green-yellow spectrum and can thus be trichromatic because of the two X chromosomal alleles they carry, males only draw one, which leads to a red-green colour blindness (Travis et al., 1988; Tovée et al., 1992**;** Williams et al., 1992; Hunt et al., 1993; Shyue et al., 1995; Jacobs, 2008).

Marmosets stay in their social group until adulthood and are typically characterized as cooperative breeders (Abbott et al., 1997; Schaffner and French, 1997). The dominant female in an extended family unit is usually the only one to reproduce, and the male parent(s) as well as older siblings assist with rearing the young (Mansfield, 2003). The breeding pair is usually dominant, and the breeding female is dominant over all others (Stevenson et al., 1988; Digby, 1995). For non-breeding individuals, the dominance hierarchy is age-graded, whereas sex is not a factor (Stevenson et al., 1988; Digby, 1995).

Social learning in common marmosets (*Callithrix jacchus*)

Due to their cooperative breeding system, marmosets make a good model for studying social learning mechanisms. For instance, young marmosets show social facilitation (Vitale and Queyras, 1997), and food transfers from parent to infant marmoset function as transmission of information (Voelkl et al., 2006). In problem-solving tasks marmoset infants were successful if they had previously received a demonstration from their mothers (Dell'mour et al., 2009) and adult marmosets needed less time to solve a push or pull paradigm if they received a demonstration prior to the test (Bugnyar and Huber, 1997).

Schiel and Huber (2006) found that while older infants were not more attentive than young infants, they were the most socially influenced foragers, while juveniles tended to not forage as much as infants. Moreover, the authors showed that female demonstrators most effectively transmitted information to their conspecifics. In terms of the vocal development, when separated from parents and with limited degree of social contact to conspecifics, marmoset food calls are limited (Gultekin and Hage, 2017; 2018; Vitale et al., 2003). This indicates that social learning is necessary for the full development of the already innately available vocal repertoire, as well as the development of the population-specific dialect. It has been shown that common marmosets' exploratory and foraging behaviour is influenced by social learning both in captive and in wild populations. Bugnyar and Huber (1997) observed that captive monkeys that received a demonstration of a push and pull paradigm showed less exploratory behaviour than monkeys who did not receive it, even though this difference disappeared after a few sessions and there was no significant effect overall. Follow-up studies showed marmosets imitate a demonstrator in a different experimental setup. Voelkl and Huber (2000) explored the ability of marmosets to imitate a demonstrator's method of removing a lid and found the monkeys adjusted to the demonstrated methodology. Later they also showed that marmosets match the demonstrators' movements in opening a box, which indicated their neural capacity of imitation (Voelkl and Huber, 2007). In wild populations, naïve marmosets learned to open an apparatus from a conspecific demonstrator and retained this knowledge even after several years (Pesendorfer et al., 2009; Gunhold et al., 2014a). In another study, wild common marmosets were shown to learn socially from a virtual unfamiliar conspecific how to open an artificial fruit box (Gunhold et al., 2014b).

Learning in a social context

In essence, social environment can have a large influence on the behaviour of individuals (Kralj-Fišer et al., 2007; Sih and Bell, 2008), by restricting or enhancing the behavioural expression through conformity or facilitation, respectively (Webster and Ward, 2011). Furthermore, the position in the group hierarchy or intragroup relationships could affect the behaviour of each member (Wrangham, 1980; Isbell, 1991; Sterck et al., 1997; Korstjens et al., 2002). In a recent study, common marmosets were shown to modify their boldness personality traits across social and solitary conditions (Koski and Burkart, 2015). Koski and Burkart (2015) called this effect "group personality" and hypothesized that the social facilitation by group members might be the mechanism that influences exploratory behaviour and leads to social facilitation and increase in group coordination and cooperation. This behaviour might have been evolutionary crucial for group-living species, for example, in confrontation with predators (Landeau and Terborgh, 1986). Recent research in marmoset personality corroborates the importance of social effects in this species: personality structure differs when monkeys are tested in social versus individual settings (see e.g., Šlipogor et al. 2021; Koski and Burkart, 2015).

Aims and Predictions

In this study, I first tested in a dyadic set-up whether captive common marmosets can learn from a conspecific demonstrator to prefer a particularly coloured food source. In the second part of the study, I explored whether any preference learned in the dyadic set-up is retained when tested in the social group. To my knowledge, this has not been done before.

Thus, my aim was twofold: to explore i) whether common marmosets show a preference towards the demonstrated vs. the non-demonstrated box, and ii) whether the presence of the entire family group, as well as the (hierarchical) relationships and interactions within the group influence previously learned individual preferences. In the first experiment, I predicted that the test-subjects would approach the demonstrated box first, would open and eat from it sooner, and/or would manipulate it for a longer period than the control-monkeys. Thereafter, with the entire group in the same setting, I predicted an adjustment of the monkeys' behaviour by conforming to the behaviour of other group members.

Methods

Subjects

In this study, I tested 28 common marmosets (*Callithrix jacchus*) (18 males, 10 females) belonging to five family groups that were all born in captivity and housed either as whole family groups (i.e., Pooh, Sprichtel) or as sub-groups of the family groups (i.e., 2 Vs and V-group, which both belonged to V-group; and Aurora and Kobold sub-group, which both belonged to Kiri group) (see Appendix Table 1 for details). The family groups were housed in two keeping rooms in the Animal Care Facility of the Department of Behavioral and Cognitive Biology, University of Vienna. Three family-groups were housed in one room (i.e., Pooh, Sprichtel, V-group) and two family-groups, divided into four sub-groups, in the other room (i.e., Cleli, Kiri). The family group size was variable, ranging from two (i.e., Pooh) to eight animals (i.e., Cleli), although during the testing time, one individual of the Cleli group (i.e., Maui) was temporarily separated from his group due to facility management. Each family group was kept in an indoor compartment (approx. 250 × 250 × 250cm) of wire mesh connected via a passageway tunnel system with moveable doors to an outdoor compartment (approx. 250 × 250 × 250cm), and additionally connected to an extra testing room with an experimental cage with three successive experimental compartments (100 x 100 x 200cm each). Each home enclosure contained coniferous wood pellets as floor bedding material, and had plenty of enrichment objects (branches, ropes, hammocks, platforms, blankets, sleeping boxes, tunnels). Visual contact between the family groups was prevented by an opaque barrier between the compartments, as this species shows a highly territorial character, and thus visually separating different family groups alleviated the stress level. A wire-mesh as physical barrier was introduced between sub-groups of one family group, if there had been extensive conflicts in the family. To give an example, between the groups Pooh and Sprichtel there was an opaque barrier as they belonged to different family groups, but between the 2V and V group there was only a wire mesh partition, without an opaque barrier, because they were a part of the same family group. This arrangement allows for potential future merging back into the same family group once the social tensions are reduced. Acoustic and olfactory contact was always possible. Temperature was maintained at 21-29°C, and humidity was kept at 30-60%. Daylight was the main source of lighting, and lamps were placed above the enclosures to provide additional light to the animals. They were kept on a stable 12:12 hour light: dark cycle. A few heating lamps were installed above each enclosure. During the testing days, the animals were fed with a mix of New World monkey pellets for breakfast, and a selection of different fruits, vegetables, grains, milk products, pellets, marmoset gum, protein as well as vitamin supplements, and insects for lunch. Water was available *ad libitum*.

Experimental design

This study consistent of two experiments: the first one was conducted in a dyadic model/observer setting and the other one was done in a social (i.e., family sub-group) setting. In the first experiment, I wanted to investigate whether the marmosets develop a preference for a coloured box based on the demonstration they receive from a breeding male of each group, in the observation phase. In particular, I was interested to see whether observing the demonstrator eat from either a blue- or a pink-coloured box would lead to the observer marmoset developing a preference for the demonstrated box in the subsequent experimental phase. To control for the effect of the demonstrator, seven monkeys belonging to three groups (i.e., Pooh, 2Vs and Aurora) did not get a conspecific demonstration during the observation phase. Instead, they individually observed either a blue- or a pink-coloured box in the experimental compartment.

If the monkeys developed a preference for one box in the first experiment, I was going to look into whether their preference would change when set in a bigger social context. Therefore, in the second experiment, I tested the observer monkeys in a group setting. Here, the observation phase consisted of the presentation of both coloured boxes, however, without a demonstrator monkey present, neither in the experimental groups, nor in the control groups. The entire family group or its sub-group (excluding the previous demonstrator) served as observers. In the subsequent experimental phase, the whole family group or its sub-group was let into the demonstration compartment. Here, I looked whether the monkeys chose the box they had been observing during the dyadic sessions or if they changed their preference and adjusted their behaviour due to the presence of their groupmates.

Experimental setup

Experiments took place in the experimental room with a large experimental cage consisting of three compartments (labelled C1, C2 and C3 hereafter; see Figure 1). Except for a small (20 x 20cm) window between C1 and C2 compartments, the three cages were visually separated by two opaque walls to prevent visual contact between monkeys, but auditory and olfactory contact was always possible. The tunnel system with moveable doors between compartments ensured the transition of the monkeys from one compartment into the other (see Figure 1). C3 was the compartment closest to the experimental room's entrance door and therefore to the home compartments in neighbouring rooms. Thus, it was used as the "waiting" compartment for the rest of the group when other members were tested in the adjacent compartments (Figure 1). C2 was the middle, "observation" compartment in which the observer monkey was able to look through the window into C1. In C1, the "experimental" compartment, the demonstration, as well as the experimental phases took place (Figure 1). The "experimental" compartment was subdivided into two sub-compartments (100 x 100 x 100cm). The monkeys had access only to the upper sub-compartment that had a white plastic plate floor, at the height of approximately 100cm. A plasticized wooden platform was placed against the wire mesh opposite to the window in C1, so that it was clearly visible through the window from C2 for the observer (Figure 1). Four plasticized wooden platforms with different combinations of small plastic boxes with lids fixed with double-sided adhesive tape (Figure 2) were pre-prepared. There were two wooden platforms with one box, either blue (Figure 2.a) or pink (Figure 2.b) and two platforms with both blue and pink boxes symmetrically fixed on them, in both combinations; the blue one being on the left side of the wooden platform (condition 1; Figure 2.c) or the pink one being on the left side of the wooden platform (condition 2; Figure 2.d).

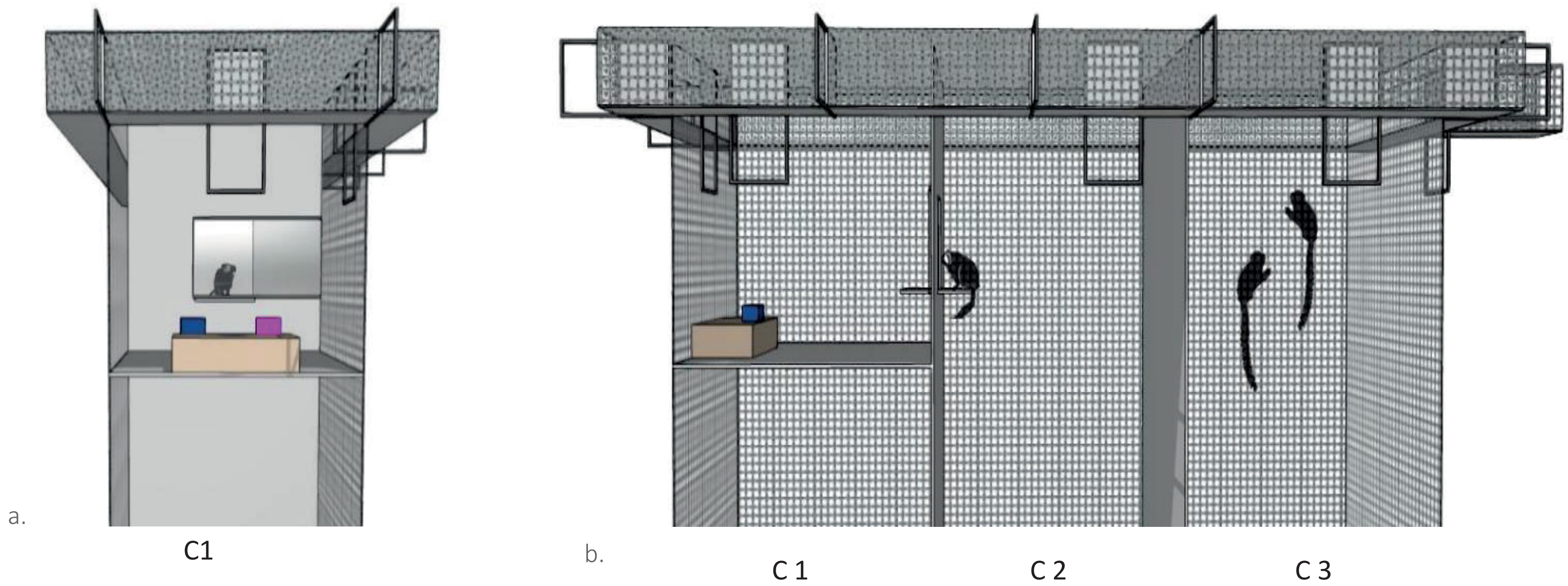

Figure 1. Experimental setup showing the compartments in the experimental room: a) frontal view showing C1, viewpoint of camera 1, b) side view showing compartments C1-C3, viewpoint of camera 2.

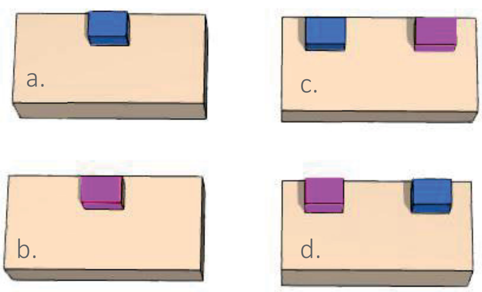

Figure 2. a) Blue- and b) pink-coloured box shown in the observation phase of the first experiment; c) condition 1: both boxes present, blue on the left; d) condition 2: both boxes present, pink on the left.

All experimental sessions consisted of an observation and an experimental phase. The observation phase was characterized by the tested individual(s), i.e., “observer(s)”, being in C2 and looking through the window into C1. In the first experiment, during the observation phase, a demonstrator monkey was present in C1. In the second experiment, no demonstrator monkey was present during the observation phase. In both experiments, the experimental phase was characterized by the tested individual(s) being let through the window into C1.

The boxes were filled with freshly prepared, high-quality food as a reward for the subjects’ participation. Each box was filled with the same amount of food; namely, two approximately 0.5cm^2 pieces of boiled egg white, two 0.5cm thick slices of banana cut into quarters, a tip of a teaspoon of marmoset gum and one halved millet waffle of 0.5cm in diameter in each box. Handling of different platforms and preparing the food was always concealed to the monkeys behind an opaque curtain. Between the observation and the experimental phase, while putting the wooden platforms back into C1, the observers were able to see the boxes, and at these times the experimenters made sure to, if necessary, touch both boxes at the same time to prevent any possible effect of different handling.

In between the observation and experimental phases of both experiments, the compartments were cleaned with a vinegar-water solution to prevent any olfactory cues between monkeys.

Two cameras (Canon Legria HF R806 and Canon Legria HFG25) were placed in front of the C1 and C2 (i.e., as shown in Figure 1), to cover movement of the subject(s) in the C1 and the upper half of C2. Two experimenters were always present during experiments of the dyadic model/observer sessions and one experimenter was present during the experiments of the group sessions. Apart from the video information, I also kept written notes and comments on each monkey, in case of unexpected technical problem (e.g., a camera malfunction) or peculiar behaviour during the testing.

Group allocation

The subjects were allocated to four test groups (dyadic model/observer sessions: 17 observers (nine females, eight males and four male demonstrators); group sessions: 16 observers (nine females, seven males, no demonstrators)) and three control groups (individual test sessions: seven observers (one female and six males); group sessions: six observers (one female and five males)). The test groups had a conspecific from their family group acting as a demonstrator for the task in the observation phases of the dyadic model/observer sessions, whereas the control groups had no conspecific present and was thus an individual test. The conspecific demonstrator was the breeding male of the group who, apart from the breeding female, had the highest status in the group hierarchy (Bandura, 1977; Nicol and Pope, 1994; Coussi-Korbel and Fragaszy, 1995; Valsecchi et al., 1996; Choleris et al., 1997; Choleris and Kavaliers, 1999; Laland, 2004; Schwab et al., 2008; van de Waal et al., 2013).

Pre-training

The monkeys were accustomed to the experimental procedure and the setting in a pre-testing phase.

For the control groups, one monkey from the group was let in C1, once, and the other monkey was in C2 acting as the observer for five minutes. That way, the observers learned that they were able to look through the window into the experimental compartment C1. To not pre-bias the monkeys for any boxes, the monkeys of the control group were only able to observe a metallic bowl with food being handled by the other group members.

For the test groups, the assigned demonstrator of the experimental groups was let in C1 for ten times. The demonstrators were trained with two boxes, one pink and one blue, and were allowed to interact with them freely for five minutes, to be able understand that there was food inside and to practice opening the boxes and accessing the food. There were no observers present during the pre-training phase of the experimental groups.

Preparation for testing

Before the start of the experiments, I prepared spreadsheets with a counterbalanced allocation of subjects to demonstrated boxes (i.e., blue, or pink), which was always the same throughout the ten sessions. As far as possible, I made sure that their sex, age, and dominance status was distributed equally for the two boxes, to control for any sex, age, or status effect. Both experiments in this study consisted of ten sessions. To control for the possible side preferences, I used two different set ups of boxes on the wooden platform (i.e., as conditions 1 and 2, respectively; see Figure 2.c and 2.d). These were assigned for each session and monkey in advance so that five sessions consisted of condition 1 and five consisted of condition 2.

Furthermore, the order of subjects was semi-randomized (each testing day had a rotating order of groups and the monkey order within the groups was randomized to control for the order effect within the group or due to the time of the day). Tests were always conducted in the mornings between 8:00-12:00. The testing was done from April to September 2019.

Experiment 1: Dyadic demonstrator-observer setting

The goal of this experiment was to determine whether the marmosets would follow a conspecific demonstrator's choice of a box, i.e., if the observers would choose the same box as the demonstrator, and thus approach it, touch it, and open it sooner than the non-demonstrated one, and whether the observers would also manipulate and spend more time eating from the demonstrated than the non-demonstrated box. The boxes on the wooden platforms were slightly opened at the beginning of each trial, to make it easier for the monkeys to grab the lid, open the box and access the food.

The dyadic sessions consisted of two phases: the observation phase which was immediately followed by the experimental phase. There were ten demonstration-observation sessions in total, and they were always conducted by two out of five experimenters on a rotating basis. Four of them conducted the first half of the dyadic sessions, semi-randomly distributing the working hours (i.e., so that all possible experimenter dyads were testing all monkeys of all groups the same number of times). Two of the five experimenters continued the tests for the next five sessions. All ten dyadic sessions were conducted between June 17th and August 18th 2019.

Observation phase

In the five-minute observation phase, the focal marmoset could watch the demonstrating conspecific eat from one box of a particular colour.

At the start of the observation phase, the wooden platform with one of two (i.e., blue, or pink) coloured plastic boxes, filled with food rewards, was put into C1. Before the start of the test, the demonstrator monkey was situated in the tunnel, on top of C1 (i.e., "experimental compartment"), and the observer monkey was in the tunnel system above C2 (i.e., "observation compartment") (see Figure 3). Two pieces of banana were placed onto the window platform of C2, before the monkey entered that compartment, for extra motivation to approach the window plate since the demonstrator was best visible from this position.

First, the door to C2 was opened. As soon as the observer monkey entered C2, the experimenter said "inside" and closed the door. This was a cue to the other experimenter to open the door to C1. Once the demonstrator monkey entered C1 with the full body without tail, the second experimenter said "Start" and closed the door, which indicated the start of the observation phase. Both experimenters then started a stopwatch. The demonstrator was allowed a maximum of five minutes in C1, to open the box and eat the food inside, as well as to explore the compartment. The observer was able to follow the demonstration through the window. The observation phase was considered as successfully completed if the observer indeed watched the demonstrator eat, for at least six seconds, which was suggested as the mean marmoset attention span and thus deemed as sufficient for gathering the needed information from the demonstrator (Range and Huber, 2007). In case the five minutes passed, but the observer had not met this criterium, the trial was repeated. The observation phase could be prematurely ended as soon as the demonstrator ate all food from the box, but only if a minimum of three minutes had passed. Maximum observation time was five minutes. As soon as the time was over, one experimenter said, "five minutes" and the door of C1 was opened for the demonstrator to exit the compartment into the tunnel system where he would await the next demonstration trial. As soon as the demonstrator was out of C1, the wooden platform with the single box was removed, and the compartment cleaned with the water-vinegar solution.

Experimental phase

In the five-minute experimental phase, the observer now had a choice to eat from two differently coloured boxes (i.e., pink, or blue), one of which was the previously demonstrated one.

The platform with the two boxes was put into C1 (see Figure 2.c and 2.d). While the baiting of the boxes was done behind the opaque curtain and outside of view to the observer monkey, the handling of the wooden platform in C1 was visible to the observer monkey through the window, so the experimenters made sure to always touch both boxes at the same time, to avoid any possible biases. The trial started with the experimenter opening the transparent window between C1 and C2 and the marmoset entering C1, with the entire body (without tail). The experimenter then closed the window, said "start" and the stopwatches were started. The monkey was given five minutes to explore the compartment and eat out of the two boxes. After this time, the trial ended and the door was opened for the monkey to exit and get back to its group through the tunnel system into C3, where the next monkey was awaiting its turn.

Control

To control for the effect of the demonstrator on the demonstration, seven subjects were exposed to the entire procedure, without having a demonstrator in the observation phase. The controls were conducted in the same manner as the tests, to ensure that there were no procedural differences (e.g., the boxes with rewards were placed in C1 in the same way, the doors opened and closed in the same way even if not necessary, and “waiting times”, during which under the experimental group conditions the demonstrated would have entered for example, stayed the same). The observer was let into C2, the demonstrators’ door was opened and closed, and the focal animal was able to see his/her assigned coloured box for five minutes and afterwards the “imaginary” demonstrator was let out by opening and closing his doors, the boxes were taken out, the compartment cleaned and the platform with the two boxes was put in. Then, the observer was let in through the window and was able to explore the compartment and the baited boxes for five minutes. Afterwards the trial was ended, and the subject was let back into the group in C3.

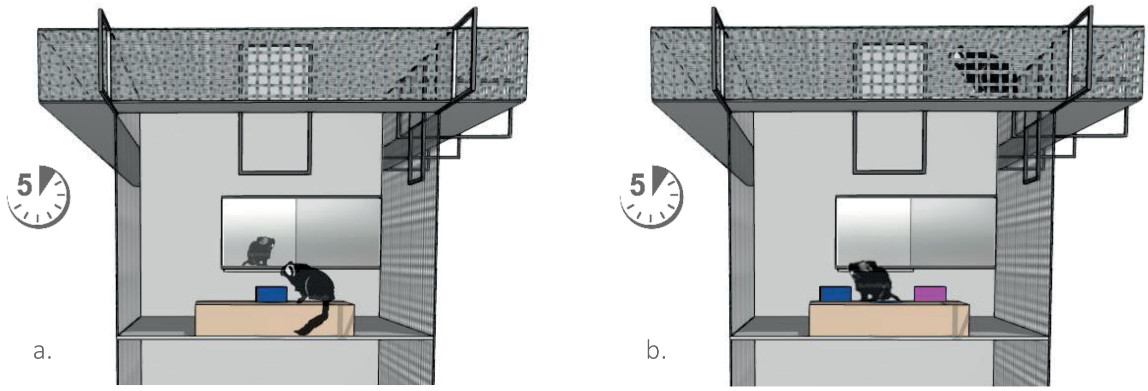

Figure 3. Dyadic session procedure, camera 1 view. a) Observation phase: observer watching a demonstrator interacting with the box, and b) Experimental phase: observer interacting with boxes, demonstrator waiting for his next demonstration in the tunnel system.

Experiment 2: Social group setting

The goal of the group sessions was to determine whether the marmosets would change a previously acquired preference of the box (i.e., if acquired, as described in Experiment 1) depending on the social setting, with their family group (or sub-group) members.

Experiment 2 consisted of ten sessions, of two phases each (i.e., the observation phase, and the experimental phase). All ten group sessions were conducted by one experimenter and happened with a fixed two-day gap between sessions, between September 2nd and October 5th in 2019. For two sub-groups (Sprichtel and Pooh), the first testing day was disregarded because of technical difficulties with the video recordings, and the first session was thus repeated. During the observation phase in group sessions, both boxes were displayed in C1, as different monkeys of the group previously received different demonstrations. The boxes on the wooden platforms were entirely closed in contrast to the dyadic sessions above, to make their opening slightly more difficult in the testing session, especially since more individuals were present in the group sessions.

In this experiment, the demonstrators were not present. Two monkeys were excluded from this experiment in the social setting, but they participated in the dyadic/ individual test setting: one from a test group (i.e., Maui) due to aggression problems with another group member, and one from a control group, due to health problems caused by old age (i.e., Mink) (see Appendix Table A1 for an information overview of the individuals).

Observation phase

This phase lasted for five minutes. Here, the entire group was able to observe the two boxes in C1 through the window from C2. The boxes were later manipulable in the experimental phase.

Before the start of the observation phase, all monkeys of a group (i.e., except for the demonstrator monkey who stayed in C3 during the testing of the group) were waiting in the tunnel system above the C2. Two pieces of banana per monkey were put onto the C2 window platform to motivate subjects to enter the compartment and approach the window from where the boxes were best visible. Then, I opened the door to C2. As soon as the last subject entered the C2 with the entire body, I closed the door and said "inside" to indicate the start of the phase and started the stopwatch. The entire group was able to observe the two boxes (i.e., blue, and pink) in C1 through the window for five minutes. The two boxes were filled with food and placed on wooden box. As soon as the time was over, I said, "five minutes", took the platform out of C1, cleaned the compartment with the vinegar-water solution, and put the platform with boxes back in. This was done to keep the procedure between the dyadic demonstration sessions and the group sessions as similar as possible.

Experimental phase

In the experimental phase, the marmoset group was able to enter C1 and eat out of the two differently coloured boxes. This phase started by my opening of the window between C1 and C2. The moment the last member of the group entered C1 with the entire body (without tail), said "start", started the stopwatch, and closed the window. The monkeys were then given five minutes to eat out of the two boxes and explore the compartment.

After the end of each trial, the door was opened for the monkeys to exit through the tunnel system and back to their home enclosures. The next group was then led into the experimental room.

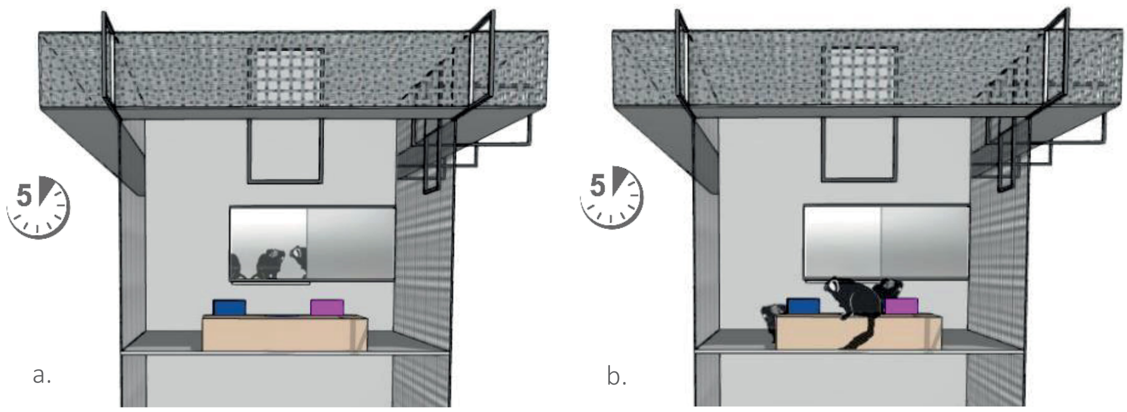

Figure 4. Group session procedure, camera 1 view: a) Observation phase, all monkeys of one group (except for the breeding male who acted as demonstrator in the dyadic sessions) observing the boxes, b) Experimental phase, all monkeys of one group could interact with the boxes filled with food rewards.

Table 2. Ethogram of behaviours coded and analysed in this experiment. M=markers, D=duration, F=frequency, L=latency, P=proportion. For the entire ethogram see Appendix Table A4.

Observation phase	
Start demo ^{M}	The moment the monkey was inside the observation cage, with full body (without tail).
End demo ^{M}	The moment when 299.9 seconds elapsed.
Attention ^{DF}	The focal individual looking in the direction of the two coloured boxes though the window, clearly visible in camera 1.
Experimental phase	
Touch demonstrated^{LF} /Touch non-demonstrated^{LF}	Every attempt and time needed to touch the positive/demonstrated or negative/non-demonstrated box. Touch is defined as any non-accidental touch (brushing the box while passing by would not be coded). As soon as the box was opened by the monkey it was not coded anymore. In the social sessions, in case another monkey opened the box beforehand, the first touch was still coded, but only once.
Open demonstrated^{L} /Open non-demonstrated^{L}	The time needed to open the positive/demonstrated or negative/non-demonstrated box.
Eat out of demonstrated^{L} /eat out of non-demonstrated^{L}	The time needed to start eating from the positive/demonstrated or negative/non-demonstrated box for the first time.
Eat out of demonstrated^{D} /Eat out of non-demonstrated^{D}	Time spent eating out of the demonstrated/non-demonstrated box. The coding started the moment the head or hand of the monkey was in the box and stopped as soon as the monkey stopped chewing.
First touch demo^{P}	The proportion of times the focal monkey touched the demonstrated box first to the total number of touching.
First open demo^{P}	The proportion of times the focal monkey opened the demonstrated box first to the total number of opening.
First eat demo^{P}	The proportion of times the focal monkey ate from the demonstrated box first to the total times eating from both boxes.
Eat demo ^{DP}	The proportion of time the focal monkey ate out of the demonstrated box to the total time spent eating.

Data analysis

The two original videos were merged into one video, containing both camera angles, with the video editing program Shotcut (Version 20.04.12). For further details, please see Appendix (Figures A1 and A2 for information on the proportional screen sizes in Shotcut).

I coded the videos in the video coding program Solomon coder (Version: beta 19.08.02). Each animals' behaviour was coded individually in both, the dyadic and group sessions, using focal sampling on the continuous recording (Table 2). The observation phase of the dyadic sessions was marked as the moment that the monkey entered the observation compartment C2 and ended a maximum of five minutes later. The experimental phase started with the focal monkey entering the experimental compartment C1 and ended after five minutes. The observation phase of the group sessions started when the first monkey entered C2 and ended five minutes after the last monkey had also entered C2. The experimental phase started with the opening of the window and ended five minutes after the moment the last monkey of the group had entered C1. For coding and comparable statistical analysis purposes, due to big differences between groups and session durations, however, I marked the end of the experimental phase five minutes after the first monkey entered the C1.

During the observation phases, the duration and frequency of attention to the coloured boxes was coded. During the experimental phases, I coded other behaviour such as latency to approach and interact with the boxes (see Table 2). Additionally, the position, locomotion, self-directed behaviours, interactions with the boxes and the food rewards were coded in both dyadic and social group sessions, as well as the socio-positive and -negative behaviour in the group sessions (see full Ethogram in the Appendix for more information). For the statistical analysis in this study, I focused, however, mostly on the subjects' interaction with the boxes.

Data were organised in Microsoft Excel (Windows 10) and analysed in IBM SPSS (Version 27 for Windows). For the data analysis, I looked at different types of behaviour (latency, frequency, and duration), their sums and means. Moreover, I calculated proportions of the monkeys' frequencies to touch, open and eat out of their previously demonstrated box first to the total amount of times interacting in these ways with either box, as well as the duration of eating out of the demonstrated box in proportion to the total time spent eating out of either box. For that I created a variable to see which box was, for example, touched first according to the coded latencies which I divided by the total number of sessions where they touched a box (i.e., usually ten for the dyadic and ten for the group sessions, except if a monkey did not participate in a trial at all and did not touch any box). Accordingly, the proportion of time spent eating from the demonstrated box was calculated by dividing the seconds of eating from the demonstrated box by the total time the monkey spent eating out of both boxes.

As the variables used were continuous, but not normally distributed, I used Mann-Whitney U-tests to test whether two variables/groups differ (e.g., difference in the latency to touch the demonstrated box for the first time in comparison to the non-demonstrated one).

As variables between the two different groups (i.e., experimental and control) and across session types (i.e., dyadic and group sessions) were paired and not normally distributed, I applied Wilcoxon singed rank tests (e.g., latency a marmoset needed to touch the demonstrated box for the first time, between the dyadic sessions and the group sessions according to whether they were a control or experimental group).

Results

Social learning in a dyadic setting: attention and the effect of the demonstration

Marmosets from the experimental group (EG) and the control group (CG) significantly differed in their attention during the observation phase across sessions (Figure 5). A one-way ANOVA revealed that having a conspecific demonstrator opening and eating from the demonstrated box motivated the subjects (N=17) to look in the direction of the box more often (F=40.835, P<0.001), faster (F=3.896, P=0.022) and for a longer overall time (F=62.853, P<0.001) than those subjects that received a non-social demonstration (N=7) (Figure 5; see also Appendix, Figures A3-5).

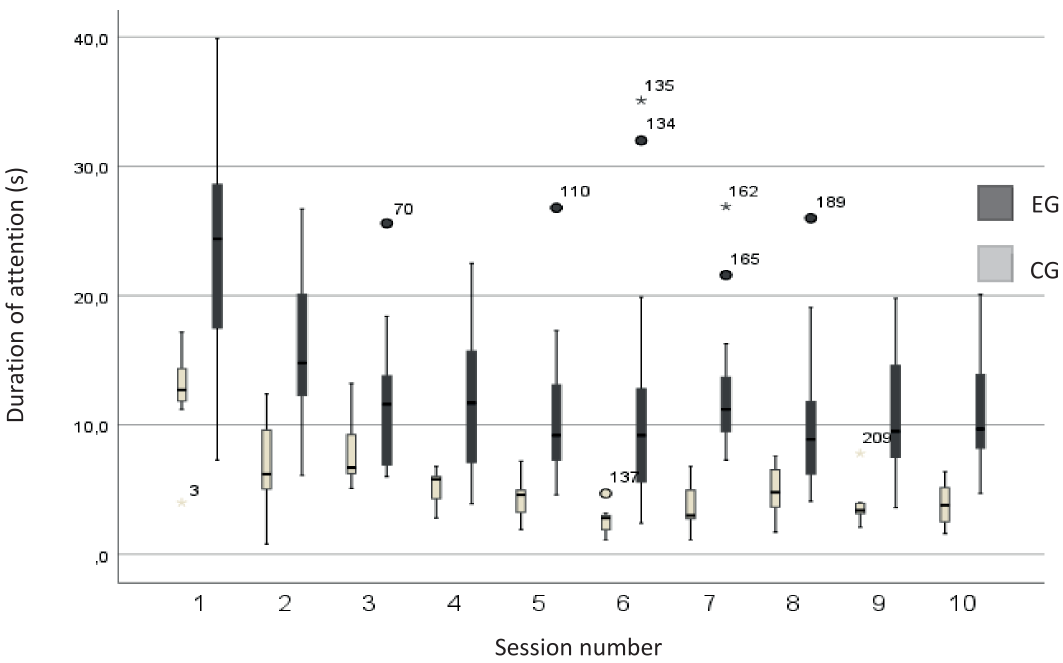

Figure 5. Mean amount of time (±SD) the observer monkey paid attention to the demonstration throughout the sessions (1-10). Experimental group (EG): subjects that received a social demonstration; control group (CG): subjects that received a non-social demonstration. The boxplot outlines indicate the first (25%) and third (75%) quartile, whiskers extend 1.5 times the interquartile range between the first and third quartile. Outliers are indicated as dots.

Overall, the marmosets did not approach the demonstrated box sooner than the non-demonstrated one (Mann-Whitney U test: U=58.0, Z=-0.095, P=0.924), nor were they manipulating it more often or for the longer amount of time (for a summary on further comparisons across all sessions, and in the first session; see Table 3). Marmosets did not develop a preference for the demonstrated box in the dyadic model/observer setting, regardless of whether the monkeys received a social demonstration beforehand (EG) or not (CG). However, the subjects showed a trend in their preference to approach the demonstrated box first if they had previously received a conspecific demonstration during the observation phase (Mann-Whitney U test; U=32.5, Z=-1.792, P=0.073; Figure 6),

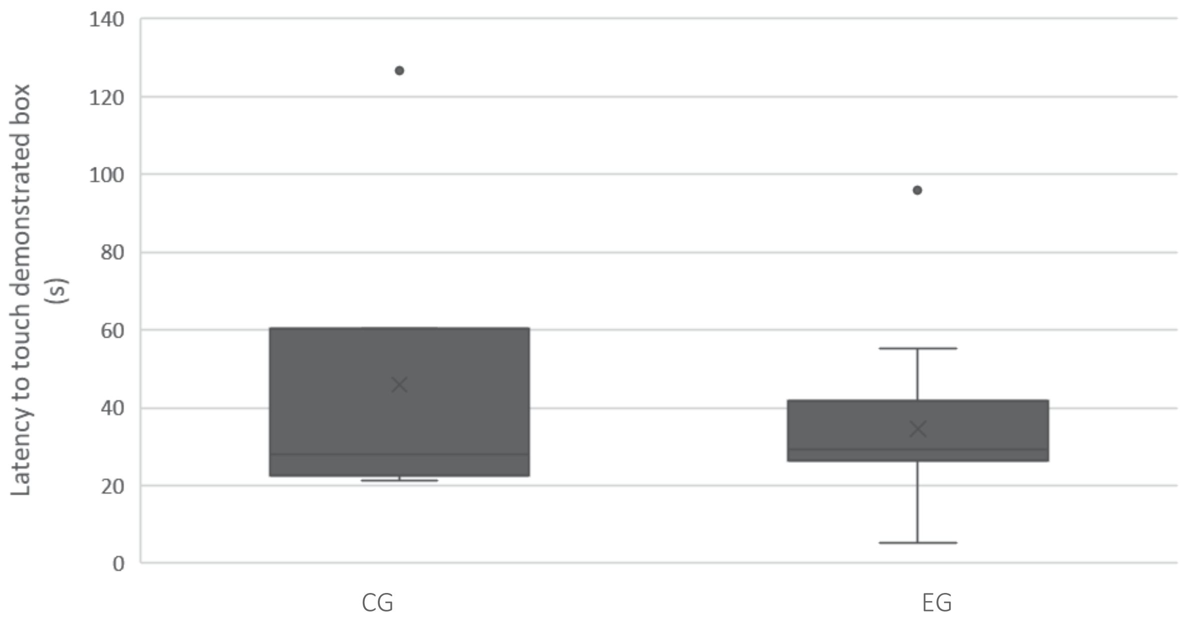

Figure 6. Mean latency ±SD to touch the demonstrated box for the first time, across all sessions in the dyadic setting. Experimental group (EG); subjects that received a social demonstration; control group (CG): subjects that received a non-social demonstration. The boxplot outlines indicate the first (25%) and third (75%) quartile, whiskers extend 1.5 times the interquartile range between the first and third quartile. Outliers are indicated as dots.

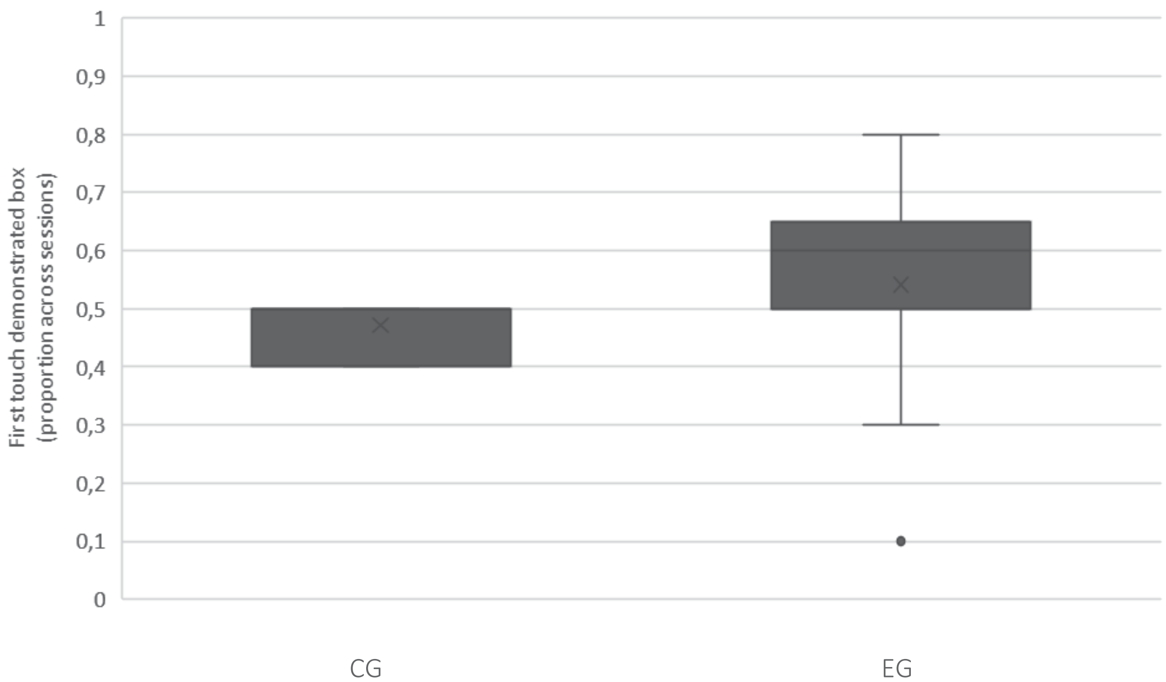

Figure 7. Mean proportion ±SD of times marmosets touched the demonstrated box first to the total amount of times touching either box. Comparison between the individuals of the control group (CG) and the individuals of the experimental group (EG) across all dyadic model/observer sessions. The boxplot outlines indicate the first (25%) and third (75%) quartile, whiskers extend 1.5 times the interquartile range between the first and third quartile. Outliers are indicated as dots.

Overall, the experimental group and the control group did not significantly differ in the latencies of first touches, openings, eating or duration of eating from either box in the dyadic model/observer setting (Table 3; Figure 6-8; Appendix Figures A6-A9). I wanted to see whether the monkeys got faster in eating out of the demonstrated box; ate out of it for a longer amount of time or manipulated it first more often than the non-demonstrated one, over the ten sessions. I also wanted to know whether the monkeys receiving social demonstrations (EG) prior to every session had a higher tendency towards the demonstrated box in comparison to the ones who did not receive a social demonstration (CG). Therefore, I looked at graphical representations of the sessions comparing the latencies, durations and proportions of the behavioural variables coded between EG and CG (Figure 8; Appendix Figures A9. a-h).

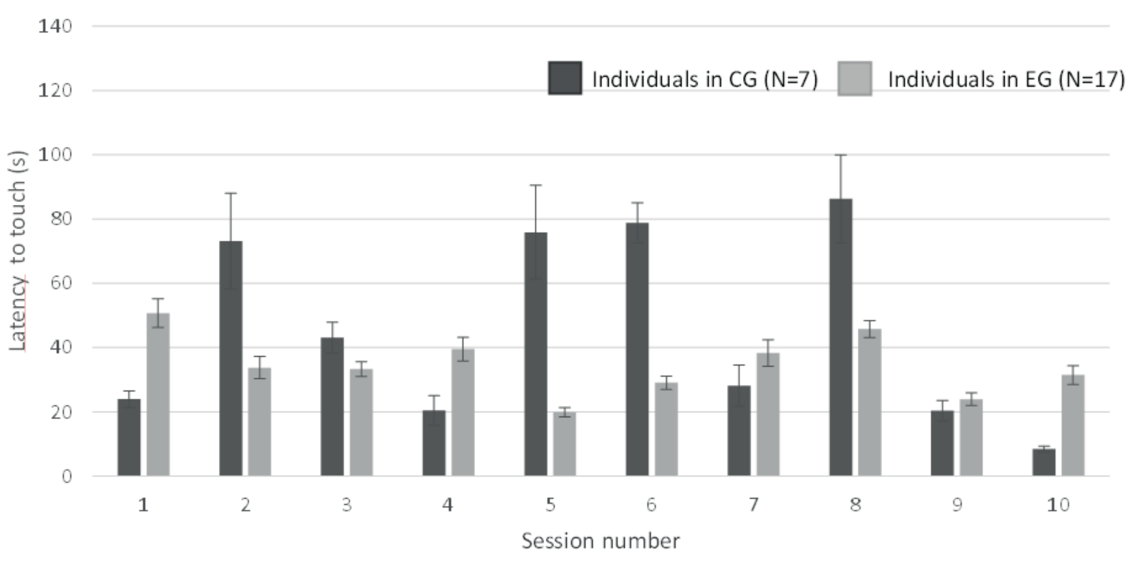

Figure 8. Comparison of the mean latency (±SD) to touch the demonstrated box for the first time, between the CG and the EG individuals in each session.

There was no visible preference pattern of the monkeys, in neither the proportions of times they chose the demonstrated box first compared to the total amount of times they chose a box, nor in the latencies of first interactions with the boxes, in each session. The monkeys seemed to get faster over the ten sessions in touching, opening, and eating out of the two boxes, regardless of which box was the demonstrated one (Appendix, Figures A9. a-f). Duration of eating out of the boxes did not differ depending on the breeding status of the marmoset (Appendix Figures A9. g-h).

Table 3. The differences between experimental and control groups across all sessions and in the first session. Mann-Whitney U tests. Variables showing a trend are shown in italic.

Variable	over all sessions			1st session		
	U-value	Z-value	P-value	U-value	Z-value	P-value
First touch^{PL}	32.5	-1.792	*0.073*	56	-0.217	0.828
First open^{PL}	44.5	-0.983	0.326	47.5	-0.863	0.388
First eat^{PL}	45	-0.941	0.347	45	-1.066	0.286
Longest eat^{PD}	54	-0.349	0.727	40	-1.249	0.212
Touch demo^{L}	58	-0.095	0.924	59	-0.032	0.975
Touch non-demo^{L}	49	-0.667	0.505	56	-0.222	0.824
Open demo^{L}	48	-0.730	0.465	37	-1.432	0.152
Open non-demo^{L}	45	-0.921	0.357	51	-0.544	0.586
Eat demo^{L}	43	-1.048	0.295	34	-1.627	0.104
Eat non-demo^{L}	45	-0.921	0.357	52	-0.480	0.725
Eat demo ^{D}	48	-0.730	0.465	50	-0.606	0.545
Eat non-demo^{D}	52	-0.476	0.634	54	-0.352	0.725

Individuals receiving a conspecific demonstration showed no preference between a demonstrated versus the non-demonstrated box, and they showed no significant differences in the latencies to touch the demonstrated versus the non-demonstrated box (Wilcoxon signed rank test: T=75, Z=-0.362, P=0.717), to open the demonstrated versus the non-demonstrated box (Wilcoxon signed rank test: T=59, Z=-0.465, P=0.642) and to eat out of the demonstrated versus the non-demonstrated box (Wilcoxon signed rank test: T=55, Z=-0.672, P=0.501). They also did not eat longer from the demonstrated versus the non-demonstrated box (Wilcoxon signed rank test: T=87, Z=-0.982, P=0.326).

I further checked whether subjects' status, sex, and age, as well as the colour of the demonstrated box prompted subjects to differentiate between the boxes by interacting with one more often than with the other depending on whether the individuals had previously received a social demonstration (EG) or not (CG) (Table 4). The individuals receiving no social demonstration (CG) during the dyadic sessions, tended to prefer the blue-coloured box. The individuals were significantly faster to open the blue-coloured box than the pink one ("Open demo^{L}", Mann-Whitney U test: U=413, Z=-2.22, P=0.026). If the marmosets had been demonstrated the pink box previously, they spend significantly more time to eat out of that one than the blue one ("Eat demo^{PD}", Mann-Whitney U test: U=370, Z=-2.731, P=0.006; Table 4) Visual inspection of the data however, showed that these results were driven by one individual, Mink, whose latencies were very long due to age-related locomotion constrictions.

Table 4. The effects the sex, ageclass, breeding status, and the demonstrated colour on the monkeys' latencies, durations, and proportions of interacting with the boxes during the experimental conditions of both the dyadic and the group sessions. P-values in italics indicate a significant difference between the compared groups.

Effects of sex, ageclass, status and colour preference on the behaviour of the marmosets

		significance levels:	Touch demo[L]			First touch[PL]			Open demo[L 3]			First open[PL 3]			Eat demo[L]			First eat[PL]			Eat demo[PD]		
			U-value	Z-value	P-value	U-value	Z-value	P-value	U-value	Z-value	P-value	U-value	Z-value	P-value	U-value	Z-value	P-value	U-value	Z-value	P-value	U-value	Z-value	P-value
Dyadic sessions	EG (n=17)	sex (male; female)	3549.5	-0.158	0.875	3392	-0.749	0.454	3532	-0.212	0.832	3465.5	-0.486	0.627	3559.5	-0.126	0.899	3575	-0.091	0.928	3400.5	-0.623	0.533
		ageclass (young 0-8; old >9)	2476.5	-0.454	0.650	2554.5	-0.193	0.847	2579.5	-0.075	0.940	2390	-0.894	0.371	2525	-0.276	0.783	2485	-0.491	0.623	2346	-0.933	0.351
		Status in the group (breeder; non-breeder)	1144.5	-1.719	0.086	1311.5	-1.052	0.293	1342	-0.764	0.445	1267	-1.306	0.192	1324	-0.851	0.395	1260	-1.350	0.177	1117	-1.853	0.064
		demonstrated colour (blue; pink)	3253.5	-2.128	0.279	3215.5	-1.381	0.167	3437.5	-0.507	0.612	3565.5	-0.125	0.901	3367	-0.728	0.467	3540	-0.218	0.828	3575.5	-0.077	0.939
	CG (n=7)	sex (male; female) [1]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		ageclass (young 0-8; old >9)	460.5	-0.514	0.608	485	-0.226	0.822	406.5	-1.216	0.224	470.5	-0.440	0.660	448	-0.676	0.499	500	0.000	1.000	417	-1.080	0.280
		Status in the group (breeder; non-breeder) [2]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		demonstrated colour (blue; pink)	529	-0.843	0.399	595	-0.069	0.945	413	-2.220	*0.026*	575.5	-0.333	0.739	446	-1.829	0.067	565	-0.480	0.632	370	-2.731	*0.006*
Group sessions	EG (n=16)	sex (male; female)	3034	-0.400	0.690	2840.5	-1.198	0.231	-	-	-	-	-	-	2498.5	-2.257	*0.024*	3067	-0.321	0.748	2483	-2.313	*0.021*
		ageclass (young 0-8; old >9)	2286	-0.450	0.653	2252.5	-0.654	0.513	-	-	-	-	-	-	1866	-2.120	*0.034*	2321	-0.726	0.726	2148	-1.001	0.317
		Status in the group (breeder; non-breeder)	834	-2.924	*0.003*	1301.5	-0.572	0.567	-	-	-	-	-	-	1163	-1.232	0.218	1377	-0.134	0.894	1245.5	-0.804	0.422
		demonstrated colour (blue; pink)	2412.5	-2.540	*0.011*	2591	-2.164	*0.030*	-	-	-	-	-	-	2906.5	-0.844	0.399	1836	-5.086	*0.000*	2931	-0.760	0.448
	CG (n=6)	sex (male; female) [1]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		ageclass (young 0-8; old >9)	222.5	-2.786	*0.005*	345.5	-0.980	0.327	-	-	-	-	-	-	241.5	-2.495	*0.013*	326	-1.333	0.182	282.5	-1.850	0.064
		Status in the group (breeder; non-breeder) [2]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		demonstrated colour (blue; pink)	321.5	-1.232	0.218	375	-0.449	0.653	-	-	-	-	-	-	396	-0.063	0.950	326	-1.333	0.182	393	-0.110	0.912

1. The control groups consisted of six individuals in total of which five were males, so the sex effect cannot be tested.
2. The control group did not include any breeders, thus the effect of the status in the group cannot be tested.
3. During the group sessions multiple marmosets had the opportunity to open both boxes at once, so this variable was excluded from the analysis in the group sessions.

Social learning in the social setting: The effect of the group

The individuals of the experimental group were significantly slower in the group sessions than they were in the dyadic model/observer sessions to touch (Wilcoxon signed rank test: demonstrated box: T=-2.379, Z=114, P=0.017; non-demonstrated box: T=-2.430, Z=115, P=0.015) and eat out of each box (Wilcoxon signed rank test: demonstrated box: T=-2.947 Z=125 P=0.003; non-demonstrated box: T=-2.045, Z=96, P=0.041), and they spent less time eating out of both boxes in the group than in the dyadic sessions (Table 5; Appendix Figure A13). They did not touch (Wilcoxon signed rank test: T=-0.539, Z=53, P=0.590) or eat out of the demonstrated box first (Wilcoxon signed rank test: T=-0.114, Z=62, P=0.909) or ate the longest out of the demonstrated box over the non-demonstrated (Wilcoxon signed rank test: T=-0.776, Z=53, P=0.438; Table 5).

The latencies for the monkeys in control group were significantly different between individual testing and group sessions to touch (Wilcoxon signed rank test: T=-1.992, Z=20, P=0.046; Figure 9; Table 5) and eat out of the demonstrated box (Wilcoxon signed rank test: T=-1.992, Z=20, P=0.046; Table 5; Appendix Figure A13.b.), as well as the duration of eating from the demonstrated box (Wilcoxon signed rank test: T=-1.992, Z=1, P=0.046; Table 5; Appendix Figure A13.d). They needed longer to touch and to eat from the demonstrated box in the group than in the individual test sessions, and they ate for a shorter time from the demonstrated box in the group than in the individual test sessions. Moreover, they ate more often first out of the demonstrated box than the non-demonstrated box (Wilcoxon signed rank test: T=-2.201, Z=0, P=0.028; Figure 10; Table 5). Consistent with their behaviour in the individual test sessions, they did not show a preference to touch (Wilcoxon signed rank test: T=-1.342, Z=3, P=0.180) or eat out of the demonstrated box first (Wilcoxon signed rank test: T=-0.136, Z=7, P=0.892).

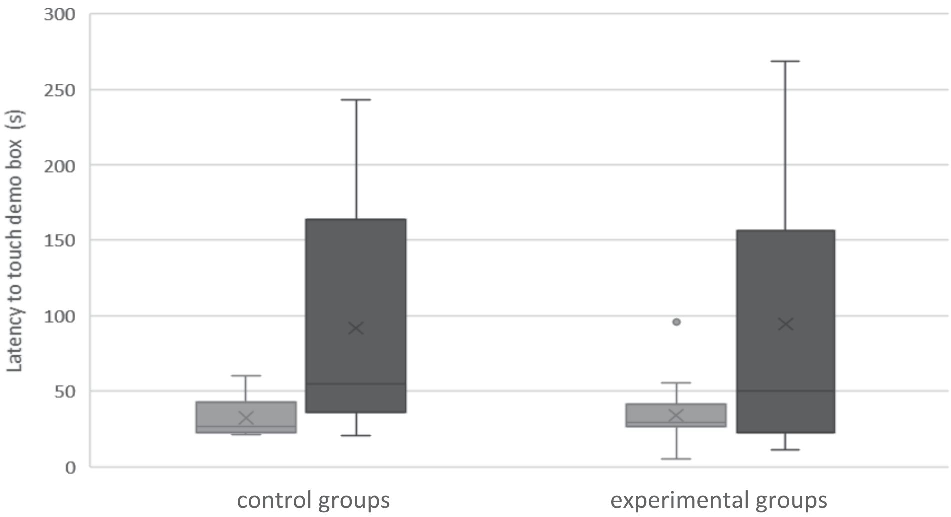

Figure 9. Mean latency ±SD a marmoset needed to touch the demonstrated box for the first time, for control groups and experimental groups. Dyadic model/observer sessions and their controls of individual testing sessions are shown in light grey, whereas the group sessions are shown in dark grey. The boxplot outlines indicate the first (25%) and third (75%) quartile, whiskers extend 1.5 times the interquartile range between the first and third quartile. Outliers are indicated as dots.

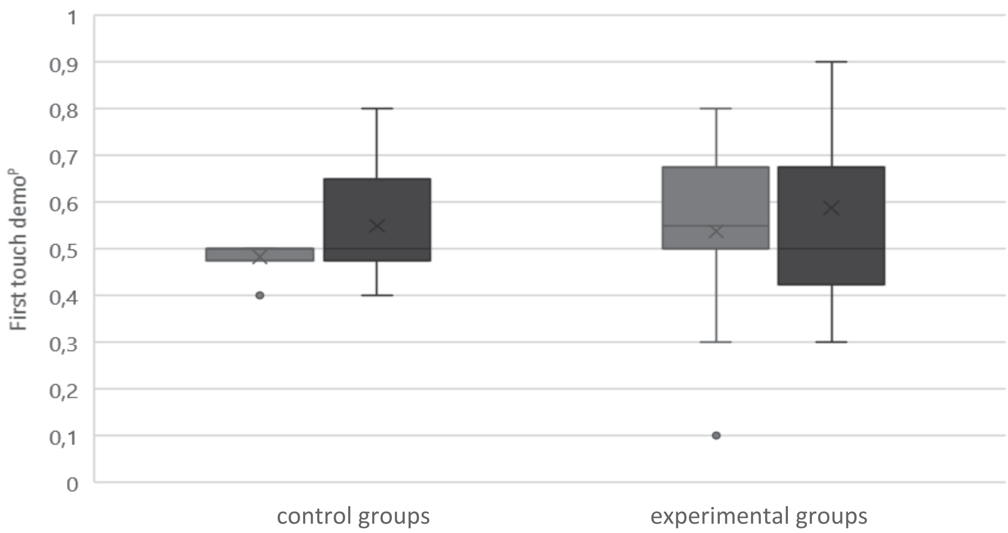

Figure 10. Proportion ±SD of touching the demonstrated box first of the total times touching either box for the first time during a session, for control and experimental groups. Dyadic model/observer sessions and their controls of individual testing sessions are shown in light grey, whereas the group sessions are shown in dark grey. The box outlines indicate the first (25%) and third (75%) quartile, whiskers extend 1.5 times the interquartile range between the first and third quartile. Outliers are indicated as dots.

Table 5. Statistical comparison of the marmosets' interactions with the boxes during the experimental phase in the IS and GS for the individuals of the experimental and the control group. Significant P-values are highlighted in italics.

		Z-value	T-value	P-value
Experimental groups (N=16)	First touch^{PL}	-0.539	53	0.590
	First eat^{PL}	-0.114	62	0.909
	Eat demo^{PD}	-0.776	53	0.438
	Touch demo^{L}	-2.379	114	*0.017*
	Touch non-demo^{L}	-2.430	115	*0.015*
	Eat demo^{L}	-2.947	125	*0.003*
	Eat non-demo^{L}	-2.045	96	*0.041*
	Eat demo ^{D}	-2.947	6	*0.001*
	Eat non-demo^{D}	-2.045	10	*0.003*
Control groups (N=6)	First touch^{PL}	-1.342	3	0.180
	First eat^{PL}	-0.136	7	0.892
	Eat demo^{PD}	-2.201	0	*0.028*
	Touch demo^{L}	-1.992	20	*0.046*
	Touch non-demo^{L}	-0.314	12	0.753
	Eat demo^{L}	-1.992	20	*0.046*
	Eat non-demo^{L}	-1.363	17	0.173
	Eat demo ^{D}	-1.992	1	*0.046*
	Eat non-demo^{D}	-0.943	6	0.345

The effect of status, sex, and age of the marmosets, as well as the colour of the demonstrated box was controlled for in the different types of sessions and between the groups (Table 3). In the GS, the demonstrated colour, i.e., whether the box was blue or pink, influenced the latency of EG marmosets (N=16) to touch the demonstrated (Mann-Whitney U test: U=7982.5, Z=-2.540, P=0.011) as well as the non-demonstrated box (Mann-Whitney U test: U=8237, Z=-3.415, P=0.001), the proportion of touching the demonstrated box first (Mann-Whitney U test: U=7804, Z=-2.164, P=0.03), the duration of eating out of the demonstrated (Mann-Whitney U test: U=6782, Z=-5.496, P=0.000), and the non-demonstrated box (Mann-Whitney U test: U=5634.5, Z=-5.574, P=0.000), and the proportion of eating out of the demonstrated box first (Mann-Whitney U test: U= Z=-5.086, P=0.000; Table 4). In all these cases the blue box seems to be preferable as it was approached and manipulated faster and for a longer amount of time. Visual inspection of the data however, showed that these results were driven by two individuals, Vincent, and Feline, and should thus be viewed with caution.

The sex had an effect on the latency to eat out of the demonstrated box (Mann-Whitney U test: U=6286.5, Z=-2.257, P=0.024), the duration of eating out of both the demonstrated box (Mann-Whitney U test: U=4276.5, Z=-4.707, P=0.000), and the non-demonstrated box (Mann-Whitney U test: U=4823, Z=-2.810, P=0.005), as well as on the proportion of the duration of eating out of the demonstrated box compared to the total time spent eating (Mann-Whitney U test: U=4968, Z=-2.313, P=0.021) for the experimental groups. Particularly, females were faster to eat out of the demonstrated box, and they ate longer out of both boxes than males. The age of the monkeys also influenced their latency to eat out of the demonstrated box, as the older individuals were faster to eat out of it than the younger ones (Mann-Whitney U test: U=2686, Z=-2.120, P=0.034).

In the control individuals, age class (divided in ‘young’: below the median value; i.e., eight years and ‘old’: above eight years), was the only factor affecting the latency to touch (Mann-Whitney U test: U=1397.5, Z=-2.786, P=0.005) and eat out of the demonstrated box (Mann-Whitney U test: U=1378.5, Z=-2.495, P=0.013), as well as the proportion of time eating out of the demonstrated box to the total duration of eating out of either box (Mann-Whitney U test: U=1102.5, Z=-1.850, P=0.064; Table 5) with the older individuals being faster and eating for a longer amount of time out of the demonstrated box than the younger marmosets.

Discussion

Overview

In the present study I investigated whether captive common marmosets would, by observing a conspecific demonstrator interacting with a box of a particular colour, develop a preference for that box, and preferentially choose it when given a choice of two differently coloured ones. I expected the marmosets to develop a preference for a demonstrated box, whereas the effect would not be present in the control monkeys that received no social demonstration. Additionally, I explored whether, if the monkeys developed a preference for a given box, this preference persists also in a social setting. I predicted that the group dynamics and increased competition in the social setting would make monkeys faster in choosing a box and interacting with it and that they would either change or maintain their preference depending on the choice of other individuals. Subjects receiving a social demonstration paid more attention to the box during the demonstration phase than the control individuals. However, I found that the subjects did not develop a preference for one of two boxes in the dyadic model/observer sessions: they did not first touch, open, or eat out of the demonstrated box, or eat out of it for a longer amount of time, than the non-demonstrated box. Individuals in the experimental group also did not touch, open, or eat out of the demonstrated box faster or for a longer amount of time than the individuals in the control group. Looking at the first sessions, to check for any immediate effect that disappeared over the course of ten sessions there was a trend in marmosets of the experimental group touching the demonstrated box first more often than the non-demonstrated one in comparison to the marmosets of the control group. In contrast to my expectations the social group sessions lead to the individuals getting overall slower in approaching either box and they eat out of the boxes for a shorter amount of time. Nevertheless, their behaviour was significantly altered to conform with the group dynamics and hierarchical structures of the group.

Attention and demonstrator choice

That individuals pay attention to a model is expected whenever social learning is occurring and the retrieval of food seems to be a good motivator for the marmosets to learn socially (Fragaszy and Visalberghi, 2004). How much attention an observer pays to the demonstration can play a crucial role in the outcome of an experiment (Range and Huber, 2007). Therefore, I checked whether the attention of observers in the observation phase changed throughout the sessions, both in experimental and control groups. I coded the observer's latency to first look through the window connecting the C1 and C2 compartments, as well as the number of looks and duration of looking. Marmosets receiving a social demonstration were consistently paying more attention to the demonstration than the individuals who didn't receive a social demonstration by a conspecific group member. They were faster to check out the experimental compartment, looked in the direction of the boxes more often and for a longer amount of time. This is likely to influence the amount and type of information that is extracted. Studies have shown that the duration of looking should be long enough so that the observer can perceive the act to be copied, particularly when demonstrated complicated and novel actions (Miklósi, 1999; Range and Huber, 2007). Different species have different patterns of attention (Caine and Marra, 1988; Day et al., 2003) and the individual variation is quite large in common marmosets (Range and Huber, 2007). Also, a demonstrator of the opposite sex is eliciting an increased attention in the observing marmosets. Factors like the age, sex, status in the group, and relationship to the demonstrator have been shown to influence the effectiveness of a demonstration (Nicol and Pope, 1994, Valsecchi et al., 1996, Choleris et al., 1997, Choleris and Kavaliers, 1999). In this study, I made sure that the monkeys paid attention at least six seconds, in accordance with Range and Huber (2007), for the trial to be counted as valid. If this criterium was not met, the trial was repeated. The demonstrator was always a breeding male of the group and they demonstrated for two to six other individuals of their respective family group. This may of course have affected the observers' attention, since the demonstrators were not always of the opposite sex than the observing monkey, they could not have had the same relationship with every observer, and the status of the observer in relation to the demonstrator was also varying. By always using individuals with the same social role as a demonstrator, it was ensured that there was as little variation in the hierarchical relationship to the demonstrator between observing individuals as possible.

Female and male observers may differ in their attention and social learning abilities (for review see Choleris and Kavaliers, 1999). Female chimpanzees were, for example, shown to peak in their socially learned performances earlier than their male counterparts (Lonsdorf, 2005). In the present study the observer’s learning was not significantly different between the two sexes, which is in accordance with the absence of sex differences in social learning tasks in common marmosets (Bugnyar and Huber, 1997), as well as squirrel monkeys (*Saimiri sciureus*) and tamarins (*Saguinus labiatus*) (Caine and Marra, 1988). The effect of the sex of the demonstrator could not be tested in my study, since I eliminated this variable by choosing all male demonstrators, but this might have also affected the outcome of the attentiveness levels of different observing individuals, as noted above (Range and Huber, 2007).

Most monkey studies have determined that the philopatric sex -the females- are often more followed in terms of food acquisition or object manipulation (van de Waal et al., 2010; 2012; 2013; Renevey et al., 2013; Bono et al., 2018; Grampp et al., 2019), so perhaps using a breeding female as a demonstrator would be important in future studies. In this study, they were not used because in one family group there was no breeding female available (i.e., V-group), whereas a breeding male always was. Further, breeding males in our group were very well socially integrated, which was not always the case for breeding females.

Additionally, it has been suggested that the biased attention towards females might be caused by their higher centrality in social networks, which leads to them being chosen as the preferred social partner (Cheney and Seyfarth, 1990). Thus, social relationships may be of importance when choosing whom to follow. Animals living in socially complex groups form social bonds with certain partners to whom they may mainly direct attention. Affiliative relationships monopolize the visual attention of individuals (Chance and Jolly, 1970), as confirmed in species like hens, *Gallus gallus domesticus* (Nicol and Pope, 1994), chimpanzees, *Pan troglodytes* (Menzel, 1973; Menzel,

1974) and Japanese macaques, *Macaca fuscata* (Nishida, 1987). These affiliative relationships are often formed between kin, especially in the beginning of one's life, and may be the focus of social visual attention in juveniles of several species (Jaeggi et al., 2010; Lonsdorf, 2005; Dindo et al., 2011**;** Schuppli et al., 2016; Grampp et al., 2019).

The age of the observer and the demonstrator may also play a role in attention. Most studies show that juveniles usually pay more attention, particularly to adult or older individuals. In the present study, only one juvenile was involved. Grampp and colleagues (2019) found that young, orphaned juveniles were more attentive compared to other age classes. Thus, older individuals that the observes find trustworthy might be considered as better demonstrators (Biro et al., 2003; Schiel and Huber, 2006). Younger observers have also been shown to be better and more active social learners (Matsuzawa et al., 2008; Schiel and Huber, 2006). Higher-ranking and older individuals might thus be better demonstrators than observers. Studies on the hierarchy and its effect on the social attention show that the highest-ranking conspecifics were indeed more frequently observed than low ranking conspecifics (Grampp et al., 2019; but also see Dindo et al., 2011; Kendal et al., 2015; Watson et al., 2018).

Any of these factors (sex, age, kinship, and breeding status) can alter the outcome of any social learning experiment and thus needs to be explored and discussed in possible follow up studies. Also, attention of the individuals seems to play a crucial role in common marmosets. By choosing a male breeding individual of each experimental group, the social status and sex of the demonstrator was kept the same in all groups. Since all individuals do not have the same affiliative bond with the demonstrator, it is possible that the relationship with the demonstrator affected whether individuals learned from them. Future studies should thus incorporate slight changes in design, to test for these effects as well as trying using a virtual demonstrator to control for relationship differences between demonstrator and observer.

Dyadic model/observer sessions

Dividing the tested groups in those with and those without social demonstrations previous to the dyadic sessions allowed me to study whether the monkeys socially learned on a perceptual level, that is, whether stimulus enhancement took place. In stimulus enhancement there is a heightened possibility of an individual interacting with an object because of a demonstrator's prior interaction with said object (Heyes, 1994; Zentall and Galef, 1988). The social sessions additionally tested effects of social facilitation or adjustment of behaviour of an individual to that of another social partner that often involves the synchronisation of behaviours like feeding or resting (Clayton, 1978; Zentall and Galef, 1988).

In the first experiment, the common marmosets in our lab did not touch, open, or eat out of the demonstrated box first, for a longer period, or more often than out of the non-demonstrated box. Also, the individuals that received a demonstration from a breeding male of their group did not touch, open, or eat out of the demonstrated box faster, more often, or for a longer amount of time than the individuals of the control group. Nevertheless, they seemed to be affected by repeated observations. The monkeys in the experimental group were touching and interacting with the demonstrated box above chance level in the first sessions in contrast to the control monkeys who did not make a differentiation between the two. Over the course of ten sessions, the differences in latencies to first touch, open and eat out of the demonstrated box in comparison with the non-demonstrated box reduced. This suggest that the repeated exposure to the demonstrated box, as well as the repeated interaction with the two boxes during the experimental condition, increased familiarity with the procedure and with the fact that both boxes contained the same quality and quantity of food. Thus, it was of less importance to choose the demonstrated one.

During the observation phase of experiment, the colours of the boxes were equally and semi-randomly assigned to the individuals to make sure that the same number of monkeys -balanced for age and sex- were observing a blue or a pink box, among others to avoid a possible colour preference due to the different visual capabilities of the two sexes (Travis et al., 1988; Tovée et al., 1992; Williams et al., 1992; Hunt et al., 1993; Shyue et al., 1995; Jacobs, 2008).

Developing a preference for one demonstrated stimulus over another is only given when there is a perceived biologically and ecologically relevant upside to this specific choice, or a downside to an alternative. Since the animals did not observe a negative or less desirable stimulus or encounter any time- or social-pressure during the dyadic sessions, they did not have a necessity to socially learn to prefer one over the other in this setup.

Van de Waal and colleagues (2013), for instance, investigated how wild vervet monkeys (*Chlorocebus pygerythrus*) socially learned and adjusted their foraging decisions. For training, they presented entire groups of vervet monkeys with coloured corn of which one color was highly distasteful and thus the other colour was more desirable for the monkeys. The colonies quickly developed a preference for the colour representing the tasty corn. However, when juveniles or males with a different colour preference immigrated from other groups, they adjusted their behaviour to the norm of the new group, which shows social learning but also how hierarchy and social conformity in vervet monkey groups work (also see Whiten et al., 2005; Whiten et al., 2007).

To ensure an ecologically realistic necessity to the learning process in this study, the second, less desirable / negative stimulus- box could have been added during the demonstration. The setup in the experimental phase could have stayed the same, with two boxes with equal quantity and quality of food in them. Adding a second box and training the demonstrator to prefer one box over the other (e.g., by making one less desirable than other by not baiting it with food, by using food of less quality/quantity or by making the box not usable by permanently closing it), would have made one box "negative" or less desirable for the observer, which could have resulted in a higher percentage of animals choosing the demonstrated box. However, many new variables would arise in these setups that would need to be controlled for, such as the need for training more demonstrators, for controlling the scent, or for controlling the individual food or colour preferences of monkeys, and were therefore not implemented in the present study.

Another way to increase the necessity to choose one box would be to add time pressure, or allowing only first choice (i.e., which would eliminate the possibility to go to the second box after choosing the first one). During the ten experimental phases of the dyadic sessions, the marmosets had five minutes to open and interact with the two boxes which was enough time for every marmoset to open and entirely eat up the contents of both boxes. By reducing the time to one minute for instance, the monkeys would not have had enough time to explore all options and would need to choose a box based on its perceived higher quality. Alternatively, allowing only one choice by disabling the second box, once the first choice has been made would also force the marmosets to choose one box. Lastly, to add a biologically and ecologically relevant necessity to decide and act fast, would be to increase the social (i.e., peer) pressure and thus create a competition for the available resources – the implementation of which is discussed below.

Group sessions

To see how the presence of the group affected every individual's behaviour towards the boxes, I compared the latency to touch, open, eat out of, and the duration of eating out of each box, as well as the proportions of first touching the demonstrated box over the total amount of times touching either box first, time spent eating, and the duration of eating out of the demonstrated box.

The analysis of the group sessions in comparison to the dyadic sessions showed that individuals of the control group, who had not received a social demonstration, needed more time to touch and to eat from the demonstrated box, and they ate for a shorter amount of time from the demonstrated box in the group sessions than in the dyadic sessions. Moreover, they ate more often out of the demonstrated than the non-demonstrated box first. The monkeys of the experimental groups which had received a social demonstration were significantly slower to touch and eat out of each box in the group sessions than they were in the dyadic sessions, and they spent less time eating out of both boxes in the group sessions than in the dyadic sessions.

Those differences between the dyadic and group sessions are expected because even though individuals experienced increased social pressure in the latter, only one individual was in a preferential starting position, but all other group members had to “await their turn” or fight to eat out of either box. So, the mean latency the monkeys needed to touch and eat out of the boxes was higher in the group setting. In the same way, they did not have the time to spend more time eating out of the boxes and might have been fought away by other group members more often, so that the duration of eating out of the boxes in the group sessions was shorter than in the dyadic sessions.

Advantages and limitations of this study

What needs to be considered is the small sample size, that, even though respectable for a study with marmosets in captivity, posits a considerable limitation as the groups were not equally divided into experimental ($N_{(IS)}$=17, and $N_{(GS)}$=16) and control groups ($N_{(IS)}$=7, $N_{(GS)}$=6). This could have influenced the possible dynamic between individuals in a competition for resources and adds proportionally more pressure to each marmoset, since the family groups in controls were only small groups of two individuals compared to the experimental family groups with up to six individuals. Additionally, the control groups consisted of only one female marmoset, which renders the control for sex effects impossible.

Recapitulation and conclusion

In sum, this study shows that captive common marmosets, even though showing a slight preference for a demonstrated choice, did not learn socially a colour preference from a breeding male conspecific, yet they have altered their behaviour when in a social setting to adjust to the group setting and possible “peer pressure”. Follow-up studies should include demonstrations with both boxes, where one is less desirable than the other, to see whether then the monkeys will learn to approach and interact with the one that was more desirable for the demonstrator. Moreover, the use of a virtual demonstrator could also lower the variation in nature or quality of relationship between demonstrator and observer that may heavily affect the outcome.

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The 3D visualizations of the compartments were designed and rendered by Patrick Hänel (with the invaluable help of my constant nagging).

Appendix

Methods

Table A1. Overview of the individual marmosets who participated in this study, with information on their sex, age, ageclass, family group affiliation, breeding status, testing versus control group affiliation and colour of demonstrated box during the observation phase of the ten dyadic model/observer sessions. Marked with asterisk (*) are the individuals who did not participate in the group sessions.

Name	Sex	Age	Ageclass (<8= young; >8=Old)	Group	Breeding status	Control (CG) vs. Experimental group (EG); (demonstrator in brackets)	Demonstrated colour
Valentino	M	6	Young	Romans (2Vs)	Helper	CG	Pink
Vento	M	9	Old	Romans (2Vs)	Helper	CG	Blue
Aurora	F	6	Young	Kiris (Aurora)	Helper	CG	Blue
Jack	M	13	Old	Kiris (Aurora)	Helper	CG	Blue
Mink*	M	13	Old	Kiris (Aurora)	Helper	CG	Pink
Bambi	M	2	Young	Cleli	Helper	EG (Clever)	Pink
Blinky Bill	M	3	Young	Cleli	Helper	EG (Clever)	Blue
Feline	F	2	Young	Cleli	Helper	EG (Clever)	Pink
Maui*	M	1	Young	Cleli	Helper	EG (Clever)	Blue
Vaiana	F	1	Young	Cleli	Helper	EG (Clever)	Pink
Veli	F	14	Old	Cleli	Breeder	EG (Clever)	Blue
WallE	M	3	Young	Cleli	Helper	EG (Clever)	Pink
Luna	F	5	Young	Kiris (Kobold)	Helper	EG (Kobold)	Blue
Nemo	F	14	Old	Kiris (Kobold)	Helper	EG (Kobold)	Blue
Oli	F	13	Old	Kiris (Kobold)	Helper	EG (Kobold)	Pink
Fimo	M	16	Old	Pooh	Helper	CG	Pink
Locri	M	15	Old	Pooh	Helper	CG	Blue
Mathilda	F	4	Young	Romans (Ernesto)	Helper	EG (Ernesto)	Pink
Melvin	M	4	Young	Romans (Ernesto)	Helper	EG (Ernesto)	Blue
Vincent	M	6	Young	Romans (Ernesto)	Helper	EG (Ernesto)	Pink
Herr Nilsson	M	0	Young	Sprichtel	Helper	EG (Smart)	Blue
Nala	F	3	Young	Sprichtel	Helper	EG (Smart)	Blue
Simba	M	3	Young	Sprichtel	Helper	EG (Smart)	Pink
Sparrow	F	13	Old	Sprichtel	Breeder	EG (Smart)	Pink

Table A2. Camera 1 was positioned in front of C1 opposite to the window to C2 (see Figure A1 for reference). Camera 2 was positioned on the side, recording both, C1 and C2 (see Figure A1 for reference). The recorded videos of each trial of the dyadic sessions were merged in Shotcut into one with the following sizes and positions to each other.

Dyadic session videos	Camera 1	Camera 2
Position (pixel)	0.0	1261.709
Size (pixel)	1533.866	659.371

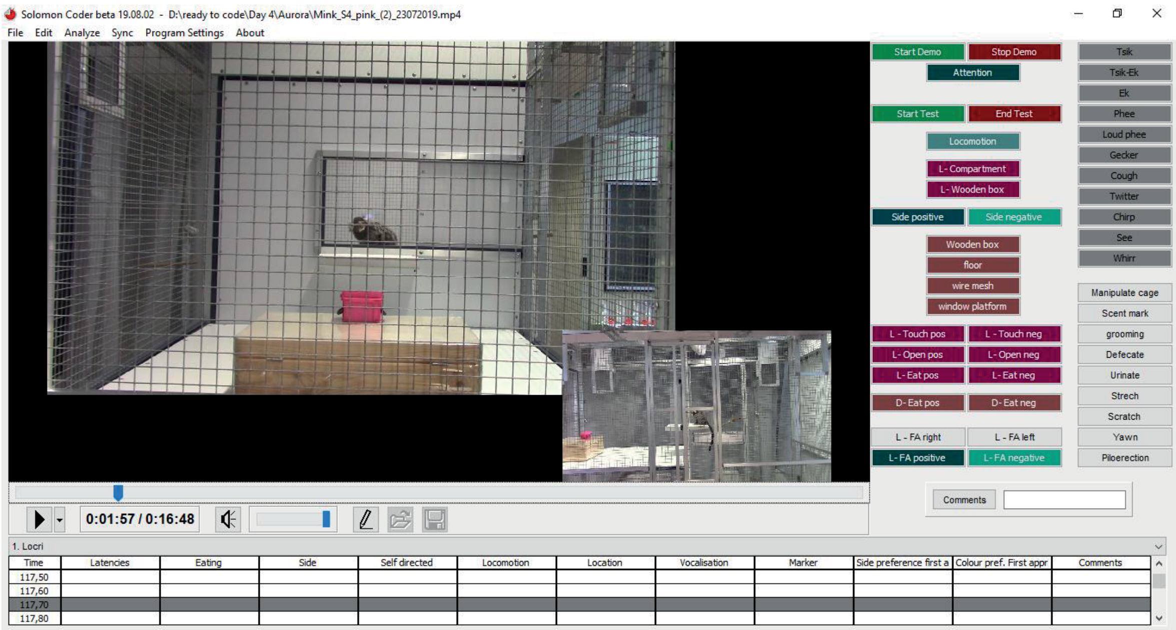


Figure A1. Screenshot of the Solomon coder coding sheet used for the behavioural coding of the dyadic sessions, with an imported merged video of the demonstration phase of a dyadic session.

Table A3. Camera 1 was positioned in front of the C1 opposite to the window to C2. Camera 2 was positioned so that it could record both, C1 and C2 (see Figure A2 for reference). The recorded videos of each trial of the group sessions were merged in Shotcut into one with the following sizes and positions to each other.

Group session videos	Camera 1	Camera 2
Position (pixel)	0.0	735.410
Size (pixel)	960.540	1185.670

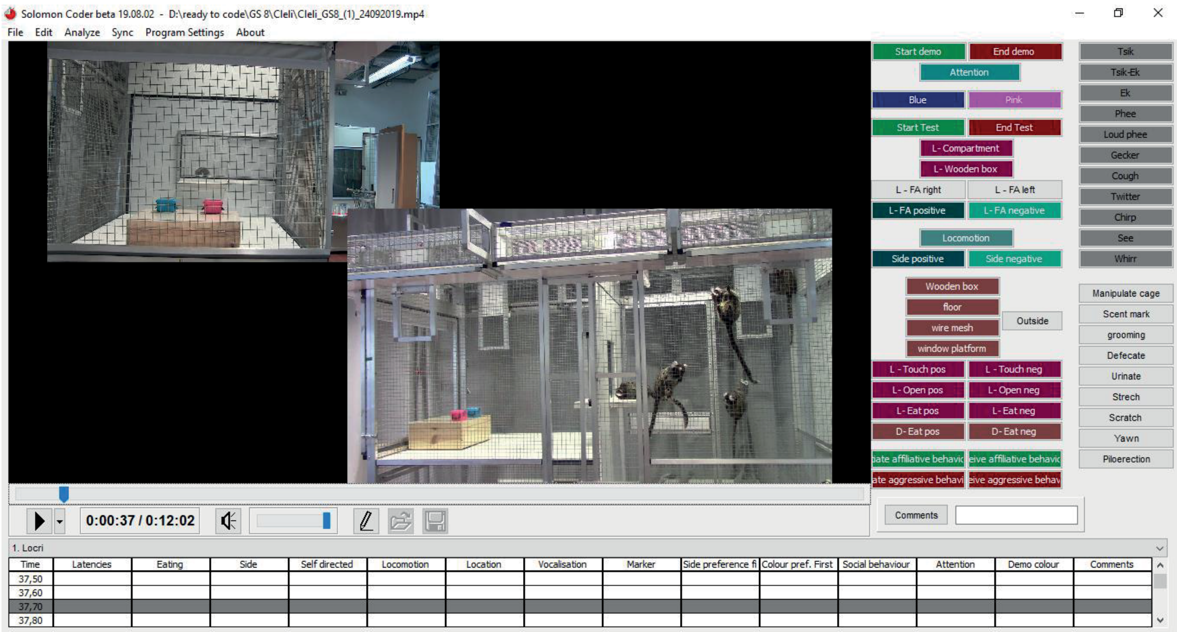


Figure A2. Screenshot of the Solomon coder coding sheet used for the behavioural coding of the demonstration phase of the group sessions, with an imported merged video.

Table A4. Ethogram of all the behavioural variables coded during these experiments, their category (i.e., frequency marked as superscript F, latency marked as superscript L, duration marked as superscript D and markers marked as superscript M), and description. “Positive” is always the colour of the box which was demonstrated during the observation phase of the dyadic sessions to each individual monkey. “Negative” is the box which was not demonstrated to the monkey.

Observation phase	
Start demo^{M}	The moment the focal fully enters the observation cage C2.
End demo^{M}	299.9 seconds after the focal enters C2.
Attention^{DF}	The focal individual looking in the direction of the wooden platform through the window, clearly visible in camera 1.

Experimental phase	-
Start test^{L}	Opening of the window.
End test^{L}	299,99 seconds after the focal enters C1.
FA right/FA left^{L}	First approach of the focal on the right/left side of the experimental compartment upon entering.
FA positive/FA negative^{L}	First approach of the monkey on the positive/negative side of the experimental compartment upon entering.
Locomotion^{LDF}	Focal is walking, climbing, jumping, running.
Compartment^{L}	Time needed to enter with the entire body (tail not included) into the experimental cage for the first time.
Wooden box^{L}	Time needed to intentionally touch the wooden box/platform for the first time.
Side positive/side negative^{LD}	Focal is situated on the positive/negative side of the experimental compartment.
Wooden box^{DF}	Focal is on the wooden box.
Floor^{DF}	Focal is on the floor.
Wire mesh^{DF}	Focal is on the wire mesh.
Window platform^{DF}	Focal is on the window platform.
Manipulate cage^{LDF}	Focal is manipulating parts of the cage other than the two coloured boxes (e.g., biting the wooden box).
Scent mark^{LDF}	Focal is rubbing genitals or snout on the floor, wire mesh or box.
Grooming^{LDF}	Focal is auto grooming.
Defecate^{LDF}	Focal is defecating.
Urinate^{LDF}	Focal is urinating.
Stretch^{LDF}	Focal is stretching.
Scratch^{LDF}	Focal is scratching themselves.
Yawn^{LDF}	Focal is yawning.
Piloerection^{LDF}	Focal has erected hair on tail or on entire body.
Geckering^{LDF}	Aggressive vocalization.

Touch demonstrated^{LF} /Touch non-demonstrated^{LF}	Every attempt and time needed to touch the positive/demonstrated or negative/non-demonstrated box. Touch is defined as any non-accidental touch. As soon as the box was opened by the focal it was not coded anymore. In the social sessions, in case another monkey opened the box beforehand, the first touch was still coded, but only once.
Open demonstrated^{L} /Open non-demonstrated^{L}	The time needed to open the positive/demonstrated or negative/non-demonstrated box.
Eat out of demonstrated^{L} /eat out of non-demonstrated^{L}	The time needed to start eating from the positive/demonstrated or negative/non-demonstrated box for the first time.
Eat out of demonstrated^{D} /Eat out of non-demonstrated^{D}	Time spent eating out of the demonstrated/non-demonstrated box. The coding started the moment the head or hand of the focal was in the box and stopped as soon they stopped chewing.
First touch demo^{P}	The proportion of times the focal touched the demonstrated box first to the total number of touching.
First open demo^{P}	The proportion of times the focal opened the demonstrated box first to the total number of openings of either box.
First eat demo^{P}	The proportion of times the focal ate from the demonstrated box first to the total times eating from both boxes.
Eat demo^{DP}	The proportion of time the focal ate out of the demonstrated box to the total time spent eating.
Exclusively in the group sessions	
End test^{L}	299,99 seconds after the first monkey of the group entered C1.
Outside^{DF}	Focal is outside the experimental compartment C1, in the observation compartment C2. "Outside^{D}" starts at the time the first monkey of the group enters the experimental compartment and ends the moment the focal enters. If the Focal exits C1 during the experimental phase it also is coded as "Outside^{D}".
Initiate affiliative behaviour^{LDF}	Focal is initiating huddling, playing, or grooming a groupmate.
Receive affiliative behaviour^{LDF}	Focal is receiving huddling, playing, or being groomed by a groupmate.
Initiate aggressive behaviour^{LDF}	Focal is initiating a physical fight, is geckering at a groupmate or is in any other way chasing a groupmate away from their location.
Receive aggressive behaviour^{LDF}	Focal is being fought, geckered at or chased away by a groupmate.

Results

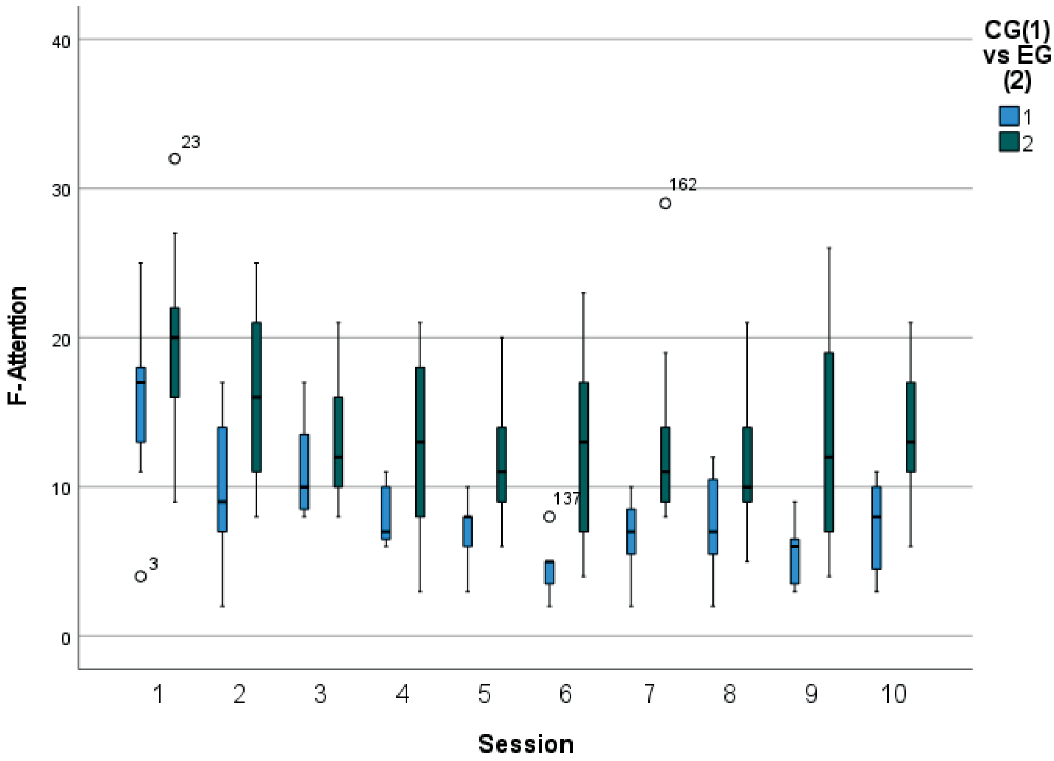


Figure A3. Mean frequency ±SD of the observer monkey paying attention to the demonstration ("F-Attention") throughout the dyadic sessions (1-10). Boxplots in blue (1) represent the control group (CG), i.e., marmosets that had a non-social demonstration, and boxplots in green (2) represent the experimental group (EG), i.e., marmosets that received a social demonstration during a demonstration phase.

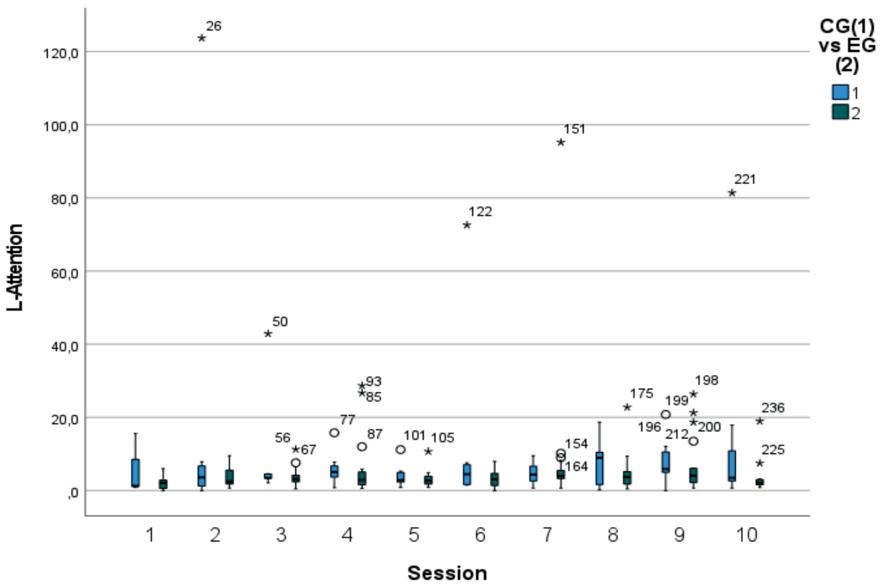


Figure A4. Mean latency ±SD of the observer monkey paying attention to the demonstration ("L-Attention") throughout the sessions (1-10). Boxplots in blue (1) represent the control group (CG), i.e., marmosets that received a non-social demonstration during the observation phase, and boxplots in green (2) represent the experimental group (EG), i.e., marmosets that received the social demonstration.

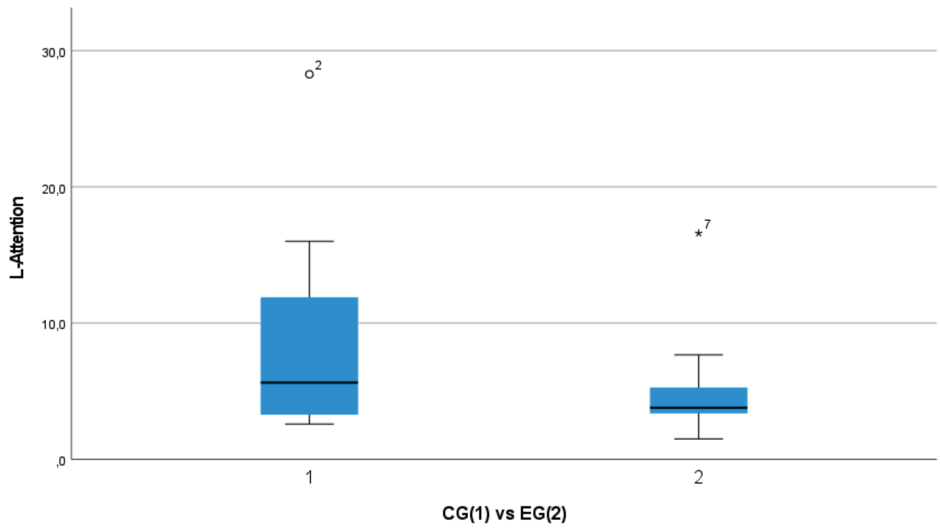


Figure A5. Mean latency ±SD of the observer monkey paying attention to the demonstration; (1) the control group (CG), i.e., marmosets that received a non-social demonstration, and (2) the experimental group (EG), i.e., marmosets that received the social demonstration.

Dyadic sessions

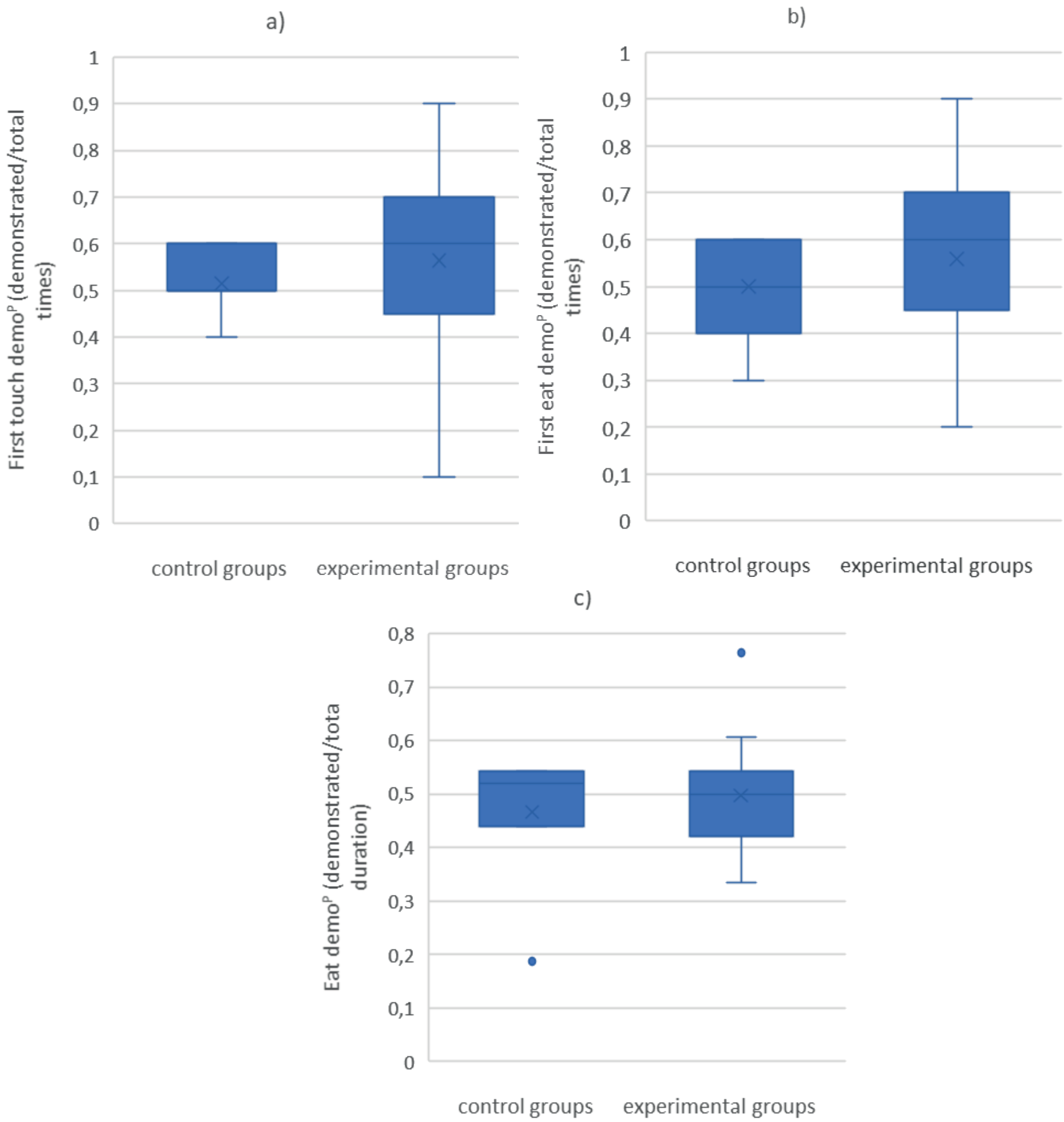


Figure A6. Comparison of the mean proportions ±SD of times marmosets were a) opening, b) eating out of the demonstrated box first than the non-demonstrated one, and c) time that the marmosets were eating out of the demonstrated than the non-demonstrated box during the dyadic sessions; the control group (CG), i.e., marmosets that received a non-social demonstration, and the experimental group (EG), i.e., marmosets that received the social demonstration.

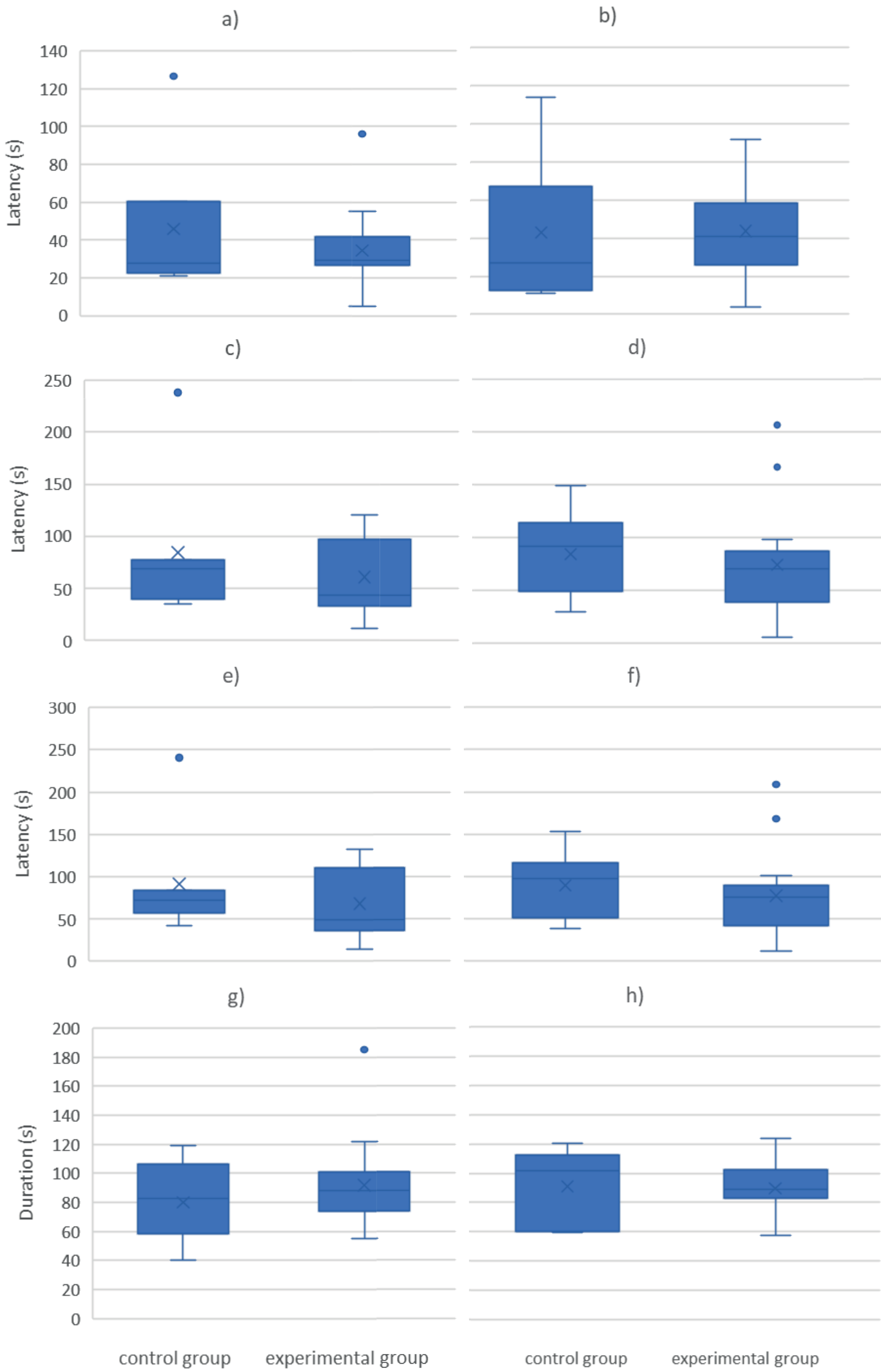

a)
b)
140
120
100
80
60
40
20
0
Latency (s)
c)
d)
250
200
150
100
50
0
Latency (s)
e)
f)
300
250
200
150
100
50
0
Latency (s)
g)
h)
200
180
160
140
120
100
80
60
40
20
0
Duration (s)
control group
experimental group
control group
experimental group

Figure A7. Comparison of the mean latency ±SD to a) touch the demonstrated box for the first time, b) touch the non-demonstrated box for the first time, c) open the demonstrated box for the first time, d) open the non-demonstrated box for the first time, e) eat out of the demonstrated box for the first time, f) eat out of the non-demonstrated box for the first time, g) duration of eating out of the demonstrated box, h) duration of eating out of the non-demonstrated box during the dyadic sessions; (CG) the control group, i.e. marmosets that received a non-social demonstration, and (EG) the experimental group, i.e. marmosets that received the social demonstration.

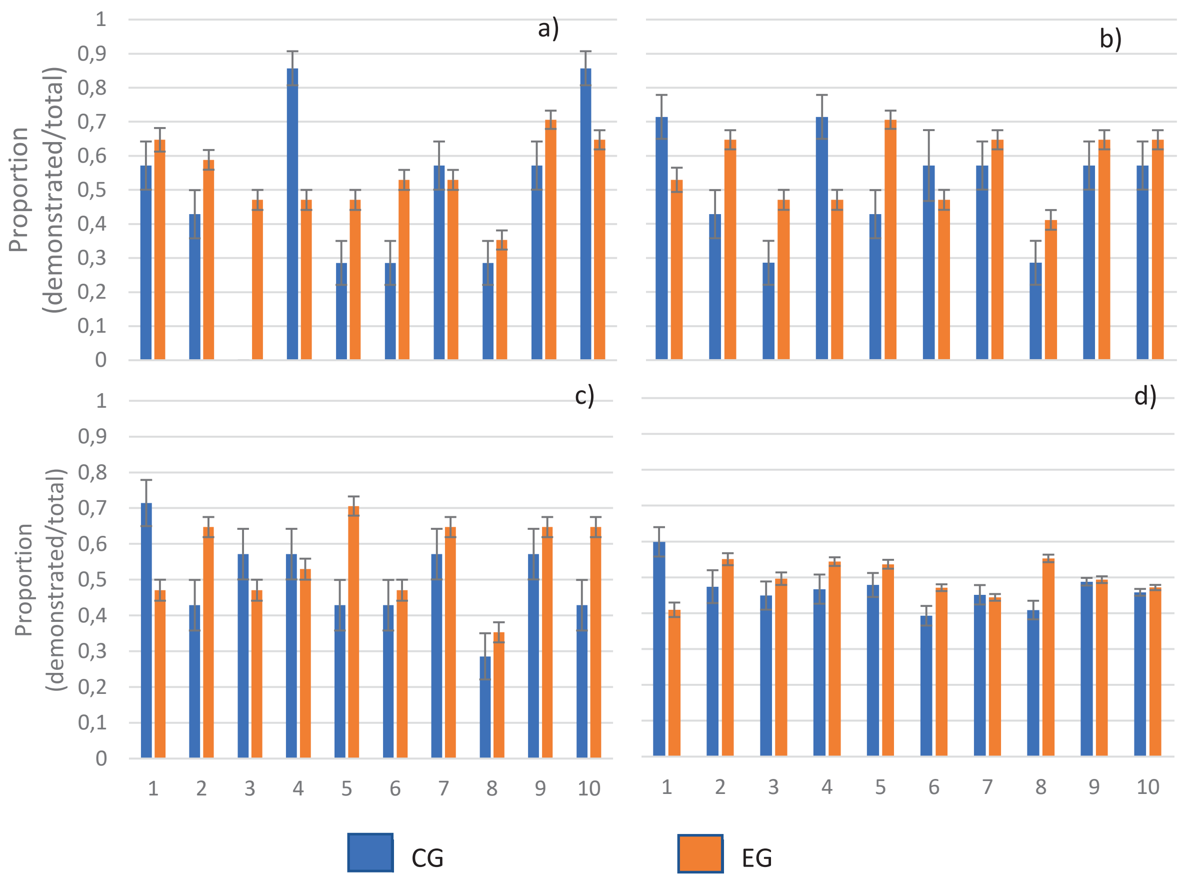
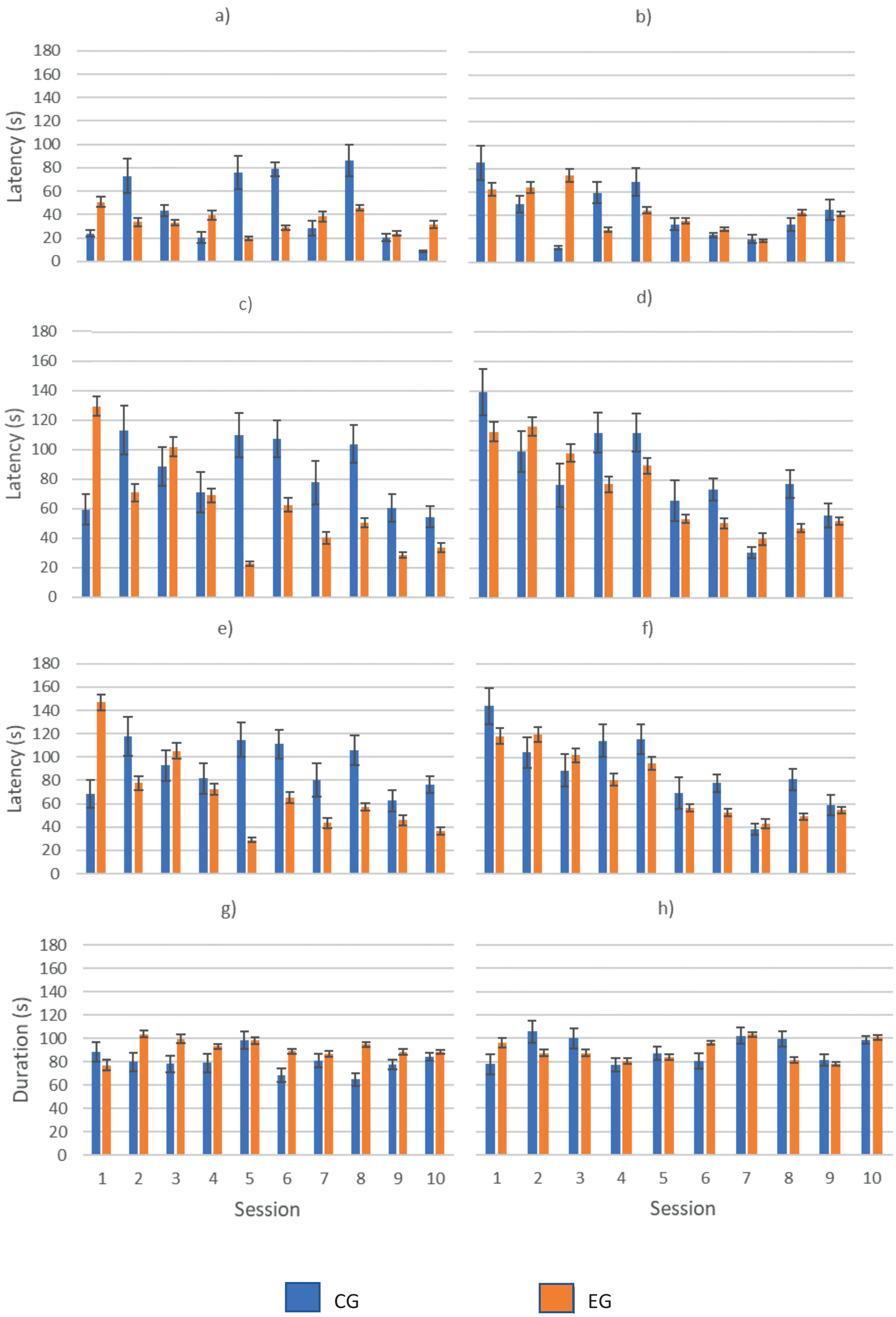


Figure A8. Comparison of the mean proportion ±SEM to a) touch, b) open, c) the eat out of the demonstrated box first, and d) the duration of time spent eating out of the demonstrated box vs. the non-demonstrated box. Blue bars represent the control group (CG), i.e., marmosets that received a non-social demonstration, and orange bars the experimental group (EG), i.e., marmosets that received the social demonstration.



a)
b)
c)
d)
e)
f)
g)
h)
Latency (s)
Duration (s)
0
20
40
60
80
100
120
140
160
180
1
2
3
4
5
6
7
8
9
10
Session
CG
EG

Figure A9. Comparison of the mean latency ±SEM to a) touch the demonstrated box b) touch the non-demonstrated box for the first time, c) open the demonstrated box, d) open the non-demonstrated box for the first time, e) eat out of the demonstrated box, f) eat out of the non-demonstrated box for the first time, g) duration of eating out of the demonstrated box and h) duration of eating out of the non-demonstrated box in the dyadic sessions. Blue bars represent the control group (CG), i.e., marmosets that received a non-social demonstration, and orange bars represent the experimental group (EG), i.e., marmosets that received the social demonstration.

Group sessions

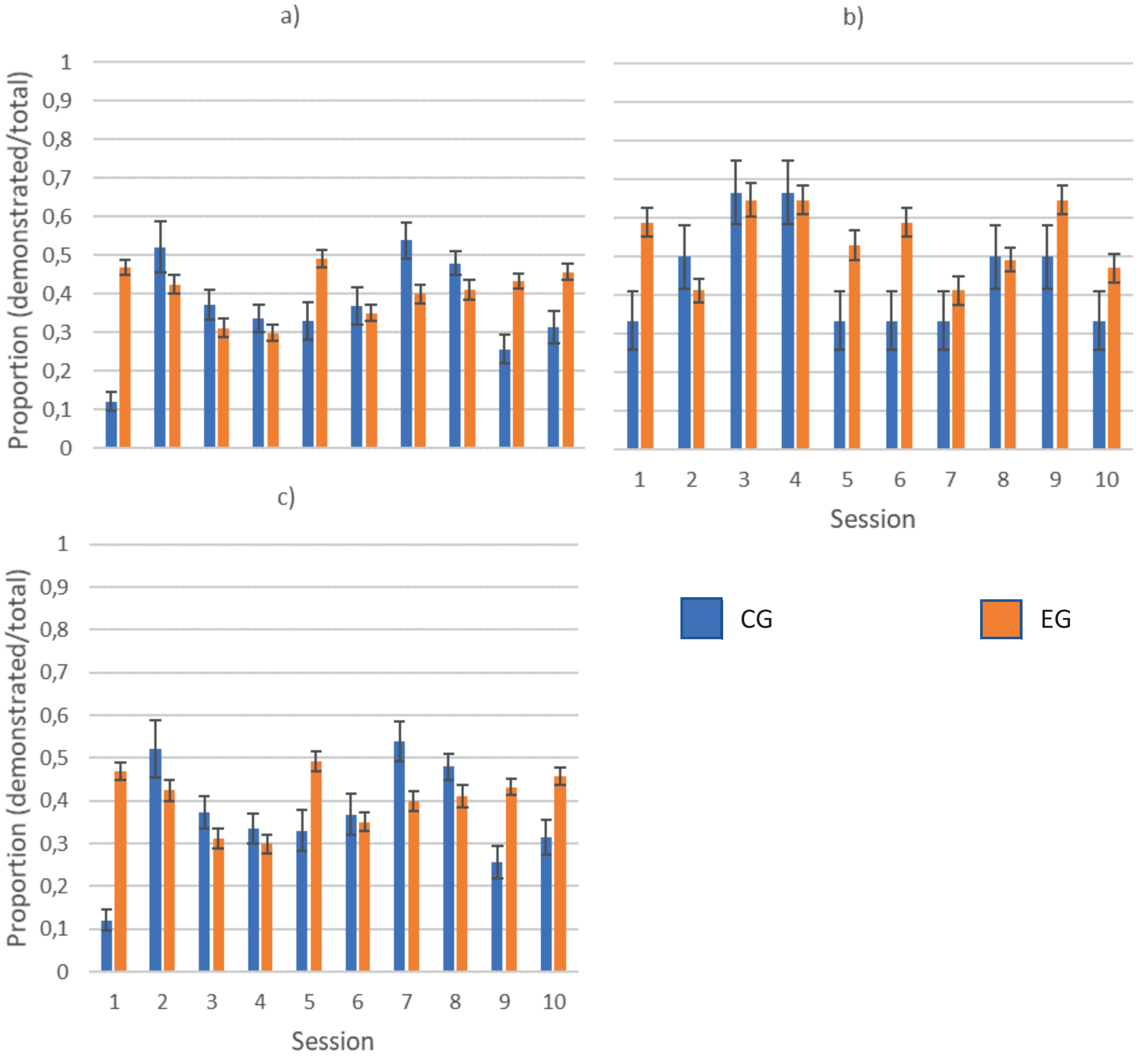


Figure *A*10. Comparison of the mean proportion ±SEM to a*)* touch*,* b*)* eat out of the demonstrated box first*,* to the total amount of a monkey interacting in those ways with either box, and c*)* the time that the marmosets were eating out of the demonstrated box during the group sessions in proportion to their total time eating out of either box; blue bars indicate the control group (CG), i.e., marmosets that received a non-social demonstration, and orange bars indicate the experimental group (EG), i.e., marmosets that received the social demonstration.

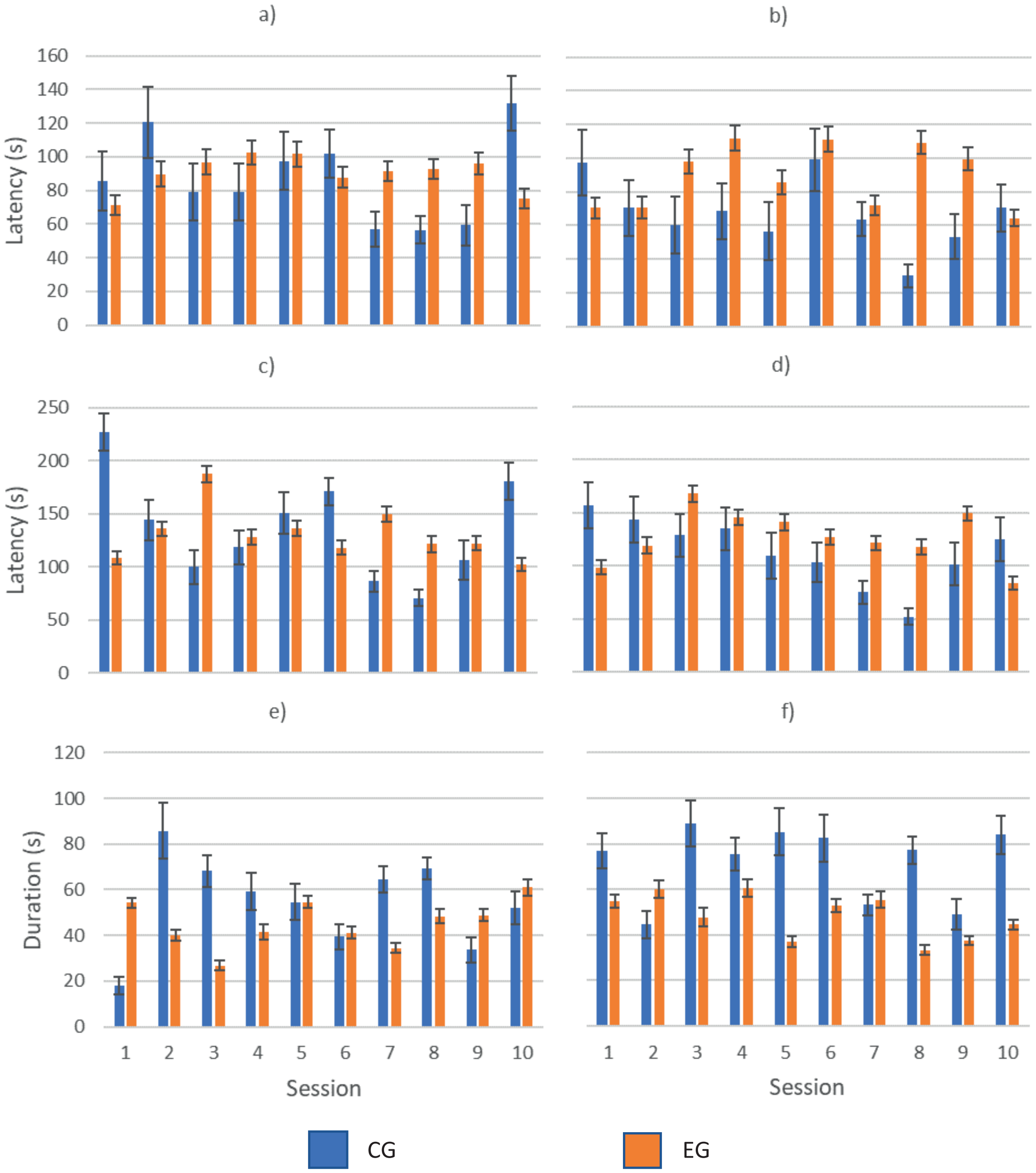


Figure A11. Comparison of the mean latency ±SEM to a) touch the demonstrated box, b) touch the non-demonstrated box for the first time, c) eat out of the demonstrated box, d) eat out of the non-demonstrated box for the first time, and mean duration ±SEM of e) eating out of the demonstrated box and f) of eating out of the non-demonstrated box. Blue bars indicate the control group (CG), i.e., marmosets that received a non-social demonstration, and orange bars indicate the experimental group (EG), i.e., marmosets that received the social demonstration.

Comparison of behaviour in dyadic sessions and group sessions

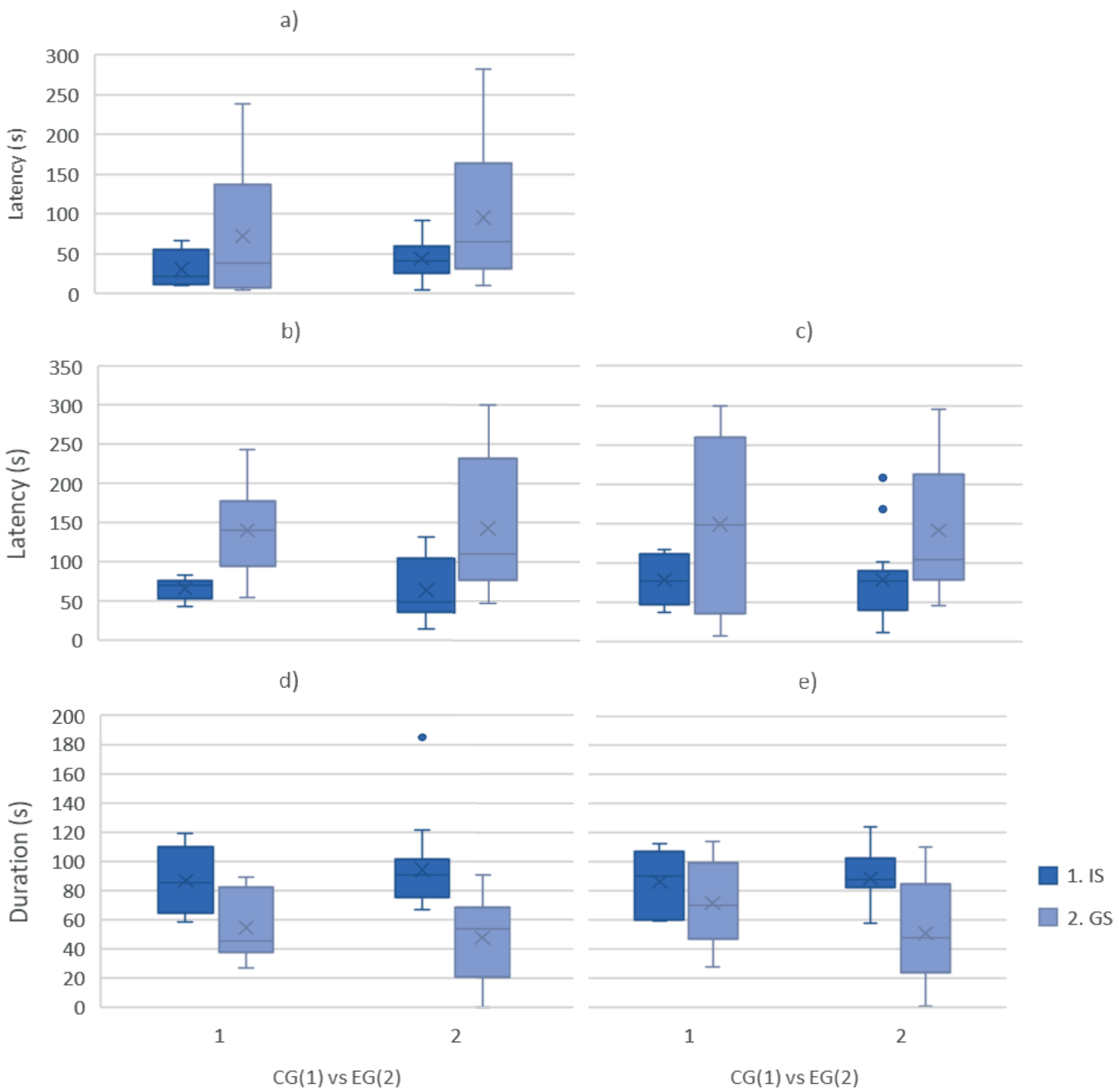


Figure A12. Comparison of the mean latency ±SD a marmoset needed to a) touch the non-demonstrated box, b. eat out of the non-demonstrated box for the first time, and c) eat out of the non-demonstrated box for the first time, d) the duration ±SD of marmosets eating out of the demonstrated box for the first time, and e) the duration ±SD of marmosets eating out of the non-demonstrated box for the first time; (1) the control group (CG), i.e., marmosets that received a non-social demonstration, and (2) the experimental group (EG), i.e., marmosets that received the social demonstration, dark blue colour indicates the dyadic sessions, light blue indicates the group sessions.