Published in final edited form as:

Am J Primatol. 2015 March ; 77(3): 264–270. doi:10.1002/ajp.22342.

Long-Term Fidelity of Foraging Techniques in Common Marmosets (*Callithrix jacchus*)

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Abstract

The formation of behavioral traditions has been considered as one of the main building blocks of culture. Numerous studies on social learning in different animal species provide evidence for their capability of successful transmission of information. However, questions concerning the memory and maintenance of this information have received comparably little attention. After the innovation and initial spread of a novel behavior, the behavior should stabilize and be maintained over time. Otherwise, the behavioral pattern might collapse and no tradition formation would be possible. The aim of this study was to investigate long-term preferences in a two-action manipulation task in common marmosets (*Callithrix jacchus*). Three captive family groups (23 individuals in total) were trained on one of two possible techniques to open a wooden box and gain access to a food reward, by either pulling or pushing a flap door. The training phase took place in a family group setting, while the test phase was conducted individually. Although the subjects could experience the alternative technique during the test sessions, the majority preferentially used the technique learned in the group setting. Moreover, the subjects were re-tested six times over a period of more than four years, in order to examine the fidelity of their preferences. The longest break without exposure to the task lasted for 3.5 years. In all tests, the marmosets showed a similar preference as in the first test block shortly after the training. To our knowledge, this is the first lab study that experimentally demonstrates memory and fidelity of experimentally seeded information in a manipulation task over a time period of several years, supporting the assumption that socially learned foraging techniques can lead to relatively stable behavioral traditions.

Keywords

memory; fidelity; persistence; foraging techniques; traditions; habit formation

INTRODUCTION

The formation of traditions and culture has become a broad topic in behavioral and cognitive research. Aside of the exact social learning mechanisms, studies have focused on the conditions under which individuals use social information and how this information spreads in a group or population, respectively [Kendal et al., 2005; Laland, 2004]. It is then assumed that after the innovation and initial spread of a novel behavior in the group, the new variant would stabilize and be maintained over time, resulting in the potential formation of a tradition [Fragaszy & Perry, 2003; Huffman & Hirata 2003]. Interestingly, the question about the maintenance of the transmitted information has received limited empirical investigation [but see Gunhold et al., 2014; Schnoell et al., 2014; Whiten, 2005], even though it is possible that the expression of the learned behavioral variant might fade again and any steps towards forming a tradition are impaired.

To our knowledge, the majority of studies that investigated the memory capabilities of animals involved stimulus-response discrimination experiments [Fagot & Cook, 2006] or spatial [e. g. Bednekoff et al., 1997; Healy & Jones, 2002; Stevens et al., 2005], food avoidance [Laska & Metzker, 1998; Galef & Whiskin, 2003] or individual recognition tasks [Boeckle & Bugnyar, 2012; Matthews & Snowden, 2011]. A study by Moscovice and Snowden [2006] could show that cottontop tamarins (*Saguinus oedipus*), when given the possibility to interact with a trained mate, were able not only to learn from this knowledgeable demonstrator to locate and access hidden rewards in a novel foraging task, but also remembered the motor task over a delay of 17 months without exposure to the task. However, little is known about memory of learned alternative foraging techniques and their fidelity over time [Claidière & Sperber, 2010; Heyes, 1994].

So far, two mechanisms have been discussed as possible means to maintain socially learned behaviors on the group level and thus, the formation of traditions. Recent studies on captive chimpanzees [Hopper et al., 2011; Whiten et al., 2005] and free-ranging vervet monkeys [van de Waal et al., 2013] revealed that some individuals were likely to change their personal preferences and adopt the behavior shown by most other members of the group. Such a conformity bias towards the majority in the group [Van Leeuwen & Haun, 2013] may explain how newcomers adopt group-specific variants; simultaneously, they make it unlikely that alternative behaviors (that differ from the group norm) can spread. Another line of studies focused on the formation of individual habits, i.e. automated response dispositions triggered by cues of past performances [Bachevalier 1990; Dickinson, 1985; Mishkin et al., 1984; Neal et al., 2006], and found support for their persistence in daily social life despite the individuals' discovery of alternative techniques [Hopper et al., 2011; Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Pesendorfer et al., 2009]. However, the conditions under which animals memorize and maintain behavioral preferences are still poorly understood.

We here pursued the research on the second mechanism and, in particular, focused on the persistence of learned habits. Thus, the aim of the current study was to experimentally investigate long-term fidelity in a two-action manipulation task in common marmosets (*Callithrix jacchus*). This cooperative-breeding New World primate species is highly

sensitive to social information [Range & Huber, 2007], tolerant within the family [Burkart et al., 2007], and relatively cohesive while foraging and navigating through the home range [Digby & Barreto, 1993], making it an ideal candidate for studying social learning and traditions. In fact, several laboratory studies provided evidence for the marmosets' capability to successfully transmit information from one to another, including advanced mechanisms such as imitation [e.g. Bugnyar & Huber, 1997; Caldwell & Whiten, 2004; Voelkl & Huber, 2000, 2007]. In these studies, the behavioral transmission was investigated between selected pairs of animals, using some variants of the observer-demonstrator paradigm [Dawson & Foss, 1965; Drea, 2006; Warden et al., 1940]. Unlike in other primates [e.g. Frigaszy & Visalberghi, 1989], scrounging was found to facilitate social learning [Caldwell & Whiten, 2003], which may be explained by the marmosets' highly tolerant social system [Coussi-Korbel & Fragaszy, 1995]. A recent experimental field study not only confirmed these findings from the laboratory but also revealed an increased information transmission among those individuals, which were most often in close proximity to each other [Gunhold et al., 2014].

As the focus of this study was to understand the maintenance of traditions, we decided to use a more naturalistic approach during the initial learning phase and allow the monkeys to interact with the apparatus in a group setting. We thus 'trained' all members of a family group together on one of two possible opening techniques, i.e. pulling or pushing a flap door. Note that the resulting 'group tradition' in pulling or pushing the door could thus be based on both individual and social learning. After the training phase, the subjects had repeatedly access to the apparatus in individual test settings, in which they could potentially use both techniques. Notably, they were tested in several test blocks with different time spans in between ranging from four weeks to several years. To rule out that the animals re-learned the technique after each break (instead of remembering it), we compared their latencies until success with those of naïve control subjects that had no experience with the task beforehand. Previous studies have revealed conflicting results concerning the perseverance of foraging technique preferences in marmosets. While a group of captive subjects changed their preference from the more difficult pulling to the easier pushing technique over time [Bugnyar & Huber, 1997], wild marmosets did maintain their preferred method, irrespective of its difficulty and even when they had experienced an easier alternative [Gunhold et al., 2014; Pesendorfer et al., 2009]. We thus predicted that the subjects would remember the learned technique and would tend to maintain this preference over the entire study period. Furthermore, we hypothesized that primarily individuals using the more difficult pulling action would switch to the easier pushing technique rather than change vice versa.

METHODS

Subjects and Housing

We tested 23 common marmosets (*Callithrix jacchus*) from January 2007–July 2011. The monkeys were kept in three family groups (eight, six, and nine individuals; 11 males, 12 females; 1–10.5 years) at the Department of Cognitive Biology, University of Vienna, Austria (further details are provided in Table II). All animals were born in captivity and

lived in indoor/outdoor cages (each approx. $250 \times 250 \times 250$ cm) of welded mesh, equipped with ropes, branches, platforms and sleeping boxes. The monkeys were kept at a temperature of $24\text{--}28^{\circ}\text{C}$ during the day and the night and a humidity ranging from 50% to 65%. Daylight was the main source of lighting, but additional solar lamps were available. Moreover, five subjects (one male, four females) were used for control studies. These monkeys were kept at the Konrad Lorenz Institute for Evolution and Cognition Research in Altenberg, Lower Austria, under similar conditions. The research complied with protocols approved by the institutional animal care committee (approval number 2014-007) and adhered to the legal requirements of Austria. As the present study was strictly non-invasive, it was classified as non-animal experiments in accordance with the Austrian Animal Experiments Act (§ 2, Federal Law Gazette 2012). This research also adhered to the American Society of Primatologists principles for the ethical treatment of primates.

Apparatus

We used the artificial fruit-type apparatus of Bugnyar and Huber [1997]. It consisted of a wooden box (measuring $20 \times 10 \times 10$ cm) with an opaque plastic pendulum door on the front. The hinges allowed for an outward (pull) and an inward (push) motion. A plastic hook was attached on the left lower corner of the pendulum door to facilitate the pull manipulations. The door was kept in the closed position by its own weight and only a minimum effort was needed to open the box by pulling or pushing the pendulum door. On the top of the box there was an additional lockable door to refill the food pieces. To ensure that the subjects could reach the food pieces, an inclined plane was attached inside of the box, so that the rewards could not be pushed away and out of grasp.

Training Phase

The training phase took place in the home cage of each family group. Since the apparatus was presented to all members of a family group simultaneously, we had to ensure that as few animals as possible could manipulate the apparatus at the same time. Therefore, the apparatus was mounted onto a wooden base (30 cm height) with a little platform (10×10 cm) allowing only a maximum of three monkeys to sit in front of the box. A frame around the box was also attached, to restrain the animals from reaching the door in other ways (Fig. 1).

Overall, each family group received a total of 12 training sessions consisting of three trials each, with not more than one session per day. In all cases, one of the two actions was blocked during the training phase (group 1 and 2 were allowed to pull; group 3 to push). In each trial, the number of rewards, equivalent to the number of animals in the group, was positioned in the box. Consequently, each individual had the same chance to get one piece of reward per trial. However, the participation was not evenly distributed among group members because some of the individuals produced more actions and gained more rewards. Although this led to an unbalanced “experience level” it reflected a naturalistic setup. After each trial, the box was refilled with the respective number of rewards.

Two cameras (JVC hard disc camcorders) were used to record all training sessions. One camera was placed on a tripod outside of the cage (focusing on the whole apparatus and the

near surroundings) and the other one was placed inside the cage (focusing on the flap door). Verbal comments of the experimenter were recorded on the audio tracks of the cameras.

Test Phase

After the training phase, all subjects were tested individually in an experimental cage (146 cm length, 36 cm width, and 110 cm height) in a total of seven test blocks with both techniques available. Each test block consisted of three sessions (with a break of three days between each of them), whereby each test session consisted of three consecutive trials. The apparatus was filled with one piece of reward per trial. The first test block was administered immediately after the training phase. The second, third, and fourth test blocks were conducted with a break of 40 days between each block, while the fifth test block was carried out after a break of 3.5 years (without exposure to the task during the breaks). The sixth and seventh test blocks were performed after a further break of 23 days each (Table I). Over the course of the study, two monkeys died due to their old age and five individuals were transferred to another facility and thus did not participate in all test blocks. Specifically, one monkey (TH) was tested only in test block 1 and six individuals (MO, PI, CI, GI, MON, TO) were tested in blocks 1–4. The remaining sixteen subjects participated in all test blocks. Five control individuals were tested without any prior training in one test trial. The test procedure was identical, i.e. food was also present in the apparatus for the control animals so that odour cues were equal for all animals tested. All tests were recorded with a digital camera positioned on a tripod outside of the cage, focusing on the pendulum door.

Data Coding & Analysis

All videos were coded with Adobe Premiere Pro CS4. To obtain information about the experience in performing the technique which the monkeys gathered during the training, we recorded several parameters during each training trial: (i) the identity of the subjects manipulating the box; (ii) the number of manipulations; (iii) the number of successful openings (manipulations with reaching a reward); (iv) the number of scrounging events (defined as stealing food out of the box, the hands or the mouth of a conspecific, from the platform or from the ground without manipulating the pendulum door); and (v) the number of gained rewards. To investigate the motivation of the monkeys to perform the task and whether the subjects would continue with the method learned during the training, we recorded during each test trial: (i) the latency until the first contact with the apparatus; (ii) the number as well as; (iii) the technique of the manipulation actions (push or pull); and (iv) whether the manipulation was successful (opening the apparatus and reaching a reward) or not.

Due to deviation from normal distribution, non-parametric analyses were conducted, using IBM SPSS Statistics version 20. All analyses were two-tailed, P values ≤ 0.05 were considered as statistically significant, and P values > 0.05 and ≤ 0.1 as trends. We calculated a generalized linear mixed model (GLMM) with the proportion of push manipulations as dependent variable and several fixed predictor variables, such as condition, sex, age class, and 'training success' (i.e. number of successful manipulations during the training). To control for pseudoreplication, individual and group identity were included as random factors.

RESULTS

Training Phase

All except one individual (GI) were able to open the apparatus successfully during the training phase at least once. While some subjects manipulated quite often (range 1–52 times) and even tried to monopolize the apparatus, others gained the rewards mainly through scrounging (range 6–27 times). The total number of manipulations, successful openings, scrounging events, and retrieved rewards for each subject are shown in Table II.

Test Phase

To investigate which technique was preferentially used by the subjects, we compared the proportion of the learned and alternative technique for each individual. When both techniques were available, marmosets used the learned technique (mean $\pm$ s.e. = 0.926 ± 0.04) significantly more often than the alternative technique (mean $\pm$ s.e. = 0.075 ± 0.04) as the first action in every trial (Wilcoxon matched-pair test, $N = 23$, $T = 14.0$, $Z = -3.783$, $P = 0.001$). They generally performed the learned technique (mean $\pm$ s.e. = 0.845 ± 0.04) more frequently than the alternative technique (mean $\pm$ s.e. = 0.155 ± 0.04) (Wilcoxon matched-pair test, $N = 23$, $T = 4.0$, $Z = -3.978$, $P = 0.001$) and were more often successful with it (i.e. opening the apparatus and reaching a reward) (mean $\pm$ s.e. = 0.810 ± 0.07) than with the alternative technique (mean $\pm$ s.e. = 0.190 ± 0.07) (Wilcoxon matched-pair test, $N = 23$, $T = 38.5$, $Z = -3.031$, $P = 0.002$).

To investigate whether subjects maintained their preference for the learned technique over the test blocks and if their performance was affected by the difficulty of the technique, their age and/or experience during training, we calculated a GLMM with the proportion of push manipulations as the dependent variable and the following fixed factors: condition (push or pull), test block (1–7), sex (male, female), age class (adults: >1.5 years; juveniles <1.5 years), and ‘training success’ (number of successful openings during the training). As expected, condition had a significant effect on the technique used (GLMM, $N = 23$, $F = 48.179$, $df = 1$, $P = 0.001$), with subjects in the push condition pushing significantly more often than those in the pull condition (estimate $\pm$ s.e. = -0.691 ± 0.1 , $P = 0.001$) (Fig. 2). This effect of condition on the technique did not change across all seven-test sessions of the experimental period, as there was no significant interaction effect between condition and test block ($F = 0.796$, $df = 6$, $P = 0.575$). Moreover, test block alone did not show a significant main effect ($F = 0.671$, $df = 6$, $P = 0.673$), revealing that the individuals did not change their preferred technique over the course of the experiment although they had the possibility to experience the alternative technique during the test. Similarly, sex ($F = 2.211$, $df = 1$, $P = 0.140$) and age ($F = 0.498$, $df = 1$, $P = 0.482$) remained non-significant. Interestingly, ‘training success’ had a significant effect on the technique used ($F = 3.928$, $df = 1$, $P = 0.05$), revealing that subjects of the pull condition that were less successful in the training phase, switched more often to the pushing action during the tests.

Comparison With Control Group

As shown above, subjects maintained their preferred foraging technique over a course of seven test blocks, even with a long break of 3.5 years without exposure to the task. Still, it

could be that memory tended to fade and animals were re-learning the technique in the beginning of each test block. To examine this possibility, we measured the monkeys' latency to manipulate the door of the apparatus with a given technique in the first trial of the fifth test block (i.e. after the longest break of 3.5 years) and compared it with the corresponding latency in the first trial of the naïve control individuals that have not had the apparatus before. The mean latency of experienced individuals ($n = 16$) was much shorter (3.0 s) than that of the five naïve individuals (36.3 s; Mann Whitney U -test: $U = 0$, $Z = -3.309$, $P = 0.001$), suggesting that experienced subjects did not re-learn the technique but indeed remembered it.

DISCUSSION

Although common marmosets could discover and use an alternative foraging technique in individual test sessions, they preferentially used the technique learned in the group setting before. Notably, the subjects showed the same preferences across all seven-test blocks. Hence, (i) a learned preference established at the group level remained stable over time; and (ii) individuals that were confronted with two available methods in the tests showed a clear preference and thus, high long-term fidelity for the learned foraging technique even if the alternative method was easier. Even after almost four years without exposure to the task, experienced individuals were significantly quicker in solving the task than naïve control individuals. This result suggests that the subjects with experience were remembering how to use their preferred technique and did not simply use trial and error learning for accomplishing the task.

Bugnyar and Huber [1997] used the same apparatus to investigate whether marmosets were able to imitate a skillful model. Five subjects were allowed to watch a pull demonstrator. Although three out of five subjects showed initially pulling they changed their preference to frequently pushing within five individual sessions. Furthermore, all subjects from the control group succeeded in obtaining the reward by pushing only. The authors argued that the observers that initially copied the demonstrated pull behavior converged towards the simpler, alternative pushing, generally preferred by the non-observers. In contrast, we could not find such a convergence to the simpler method in the current study, except in those animals, which had less manipulation experience in the training phase. It thus seems likely that differences in maintenance patterns between the two studies are due to differences in the training phase, notably the opportunity to interact with and getting experience in manipulating the apparatus in a group setting versus just seeing a skilled family member opening the artificial fruit. Consequently, individuals with more experience could have formed a stronger habit than the others. Similarly, Price et al. [2009] found differences in performances between chimpanzees that learned a tool use task individually or socially from videos.

When a monkey opened the box in the training phase, others often tried to scrounge from the now available food. Scroungers usually inserted their head into the (opened) box, which is also part of the movements the monkeys showed during pushing. The movements shown for pulling, in contrast, are exactly the opposite (i.e. leaning aside and holding the door open with one hand, while grabbing for a banana piece with the other hand). These differences

could possibly explain why the monkeys with little training success in the pull condition were likely to switch to the push technique in the test but not vice versa.

The current results are perfectly in line with findings of a recent field study with common marmosets [Gunhold et al., 2014]. In this study, several family groups of different conditions were confronted with the same task. It was shown, that wild common marmosets were able to memorize, learn socially and maintain preferences of foraging techniques. Since the wild subjects were not tested individually but in a group setting, the present lab study nicely complements the field research by providing evidence for long-term preferences for learned foraging techniques on an individual basis and without the possibility of continuous social feedback due to observation of others' manipulations. Indeed, our test set-up controlled for any possible social effects and pressures like social norms [Boyd & Richerson, 2002]. Thus the marmosets' long-term fidelity in performing a particular foraging technique supports the assumption that they have formed a strong habit for a specific technique [Gunhold et al., 2014; Pesendorfer et al., 2009]. To our knowledge, this is the first study providing experimental evidence that long-term fidelity of experimentally seeded information in a manipulation task can be based on habit formation [Pearce, 2008; Wood & Neal, 2007]. Our findings may thus have important implications for further investigations of tradition formation in non-human animals.

ACKNOWLEDGEMENTS

We would like to thank Krisztina Kupán, Vedrana Šlipogor, and Ines Hofer for their help during the data collection. We also thank two anonymous reviewers for useful comments on the manuscript. The study complies with animal care regulations and the Austrian law.

Contract grant sponsor: European Commission; contract grant number: NEST 12929; contract grant sponsor: FWF (Austrian Science Fund); contract grant number: Y366-B17.

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Fig. 1.

Apparatus. The box mounted on a wooden base could be manipulated either by pulling or pushing the flap door in order to gain access to the rewards inside.

Fig. 2.

The mean proportion of push manipulations of the pull (white bars) and push (black bars) condition over the course of the whole experiment (consisting of seven test blocks).

TABLE I
Overview of Experimental Procedure

Training	12 sessions (3 trials each)
	3 sessions (3 trials each)
Test Block 1–4	3 days between each session
	40 days between each test block (1–4)
Break	3.5 years between test block 4 & 5
	3 sessions (3 trials each)
Test Block 5–7	3 days between each session
	23 days between each test block (5–7)

TABLE II
Individual Training Results

Condition	Name	Group	Age	Sex	Manipulation	Success	Scrounging	Reward
Pull	AU	1	7	F	7	5	19	23
Pull	PO	1	7	M	11	6	7	12
Pull	MO	1	4.5	M	23	18	19	36
Pull	FI	1	4	M	9	8	25	32
Pull	PA	1	3.5	F	14	13	14	27
Pull	YA	1	3.5	M	10	7	26	33
Pull	LO	1	3	M	31	30	15	44
Pull	ME	1	3	F	33	32	22	54
Pull	TH	2	10.5	M	39	35	8	43
Pull	CI	2	8	F	13	10	11	20
Pull	MON	2	6	M	19	14	18	32
Pull	GI	2	3	M	1	0	6	6
Pull	TO	2	3	F	52	46	16	61
Pull	WI	2	1	F	24	16	26	38
Push	KI	3	6	F	20	16	14	28
Push	ZA	3	4	M	32	32	8	40
Push	VE	3	2	F	13	12	26	36
Push	MI	3	1.5	M	17	14	10	25
Push	NE	3	1.5	F	19	16	20	36
Push	OL	3	1	F	24	21	16	37
Push	PI	3	1	F	12	11	20	31
Push	JA	3	0.5	M	15	14	24	38
Push	SP	3	0.5	F	17	14	27	41

Total numbers of manipulations, successful openings, scrounging events and rewards retrieved for each individual during the 12 training sessions. Age: in years. F, female; M, male.