



Attention in common marmosets: implications for social-learning experiments

FRIEDERIKE RANGE & LUDWIG HUBER

Department für Verhaltens-, Neuro- und Kognitions-Biologie, Universität Wien

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The question whether a certain species is or is not able to imitate has received much recent attention. However, the ability to copy a demonstrated action might depend not only on the imitative ability of the observer but also on its attention, a factor widely neglected in discussions and experiments. Since attention differs between species as well as between individuals, it is likely to influence the amount and type of information different species and/or observers may extract from a given demonstration. We studied attention in common marmosets, *Callithrix jacchus*. In a series of experimental sessions, individual marmosets watched different conspecific models that were searching, manipulating an object and feeding. The observers could see the demonstration through two observation holes, which allowed us to measure exactly how often and for how long they watched the model. Marmosets were more attentive towards conspecifics engaged in a problem-solving task than an exploring model. Individual variation in attention was large, ranging from less than 10% to over 49%. Attention also depended on the identity of the model with an increase in attention if it was of the opposite sex. Overall, attention of marmosets was short with a median duration of 6 s while the model manipulated an object. This study measured the real interest of the observer towards a model, which could be an important variable in social-learning experiments.

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Many recent studies have focused on social learning in animals, where an 'individual's learning is influenced by observation of, or interaction with, another animal or its products' (e.g. Heyes 1994, page 207). Whereas ethologists and ecologists have been interested in understanding the contribution of social learning to adaptive variation in behaviour within and between groups (reviewed in Laland et al. 1993), psychologists have been interested in experimentally identifying the psychological processes responsible for learning (reviewed in Heyes 1994) which can range from local and stimulus enhancement to imitation. At one end of the continuum, local and stimulus enhancement occurs when the observer's attention is drawn to where the model is, or to what the model is acting on, thus making the observer more likely to approach or touch the place or object than if no model were present (e.g. Spence 1937; Whiten & Ham 1992). Imitation, at the other end of

the continuum, is assumed to be more cognitively complex and refers to instances when an observer learns to do an act by seeing it done (Thorndike 1898; Thorpe 1956; Whiten & Ham 1992; Heyes 1993) or, according to Tomasello (1996, page 324), requires that the observer 'understands something about how the behaviour is designed to bring about the goal'. To test for the different underlying mechanisms of social learning, psychologists usually carry out experiments, where the observer watches one or more demonstrations by a model and is afterwards tested on whether and what it learned from the model. Two aspects have been neglected in most studies investigating social learning in these experimental set-ups, namely the attention the observer actually pays to the model and its actions and the influence of the identity of the model itself (Miklósi 1999).

Paying attention to a demonstration is crucial for learning something from a model. According to Cohen (1972), there are two attention processes in humans that might be important for the study of social learning in animals. The attention-getting process determines whether the subject will turn to look at the stimulus.

Correspondence: F. Range, Department für Verhaltens-, Neuro- und Kognitions-Biologie, Universität Wien, Althanstrasse 14, A-1091 Wien, Austria (email: friederike.range@univie.ac.at).

The attention-holding process, on the other hand, determines for how long the subject will continue to gaze at the stimulus once it has looked. With regard to social-learning tasks, it is likely that the frequency and the duration of the observer's looks towards a demonstration will influence the type of information that can be extracted about the task at hand. For example, if an observer looks briefly a few times during a demonstration, it might be able to extract enough information for stimulus enhancement to occur, but not enough to learn by imitation. Thus, especially in complex demonstrations such as action sequences or actions not previously part of the behavioural repertoire of the observer, the duration of looking towards the model might be more important than the frequency of looks. Furthermore, the duration of looking in itself must be sufficiently long for the observer to perceive the complete act to be copied; a relatively longer duration will be needed for more complicated and novel actions (Miklósi 1999). Attention patterns differ between species (Day et al. 2003) as well as between individuals (see Alberts 1994 and Caine & Marra 1988 for studies on individual and species-specific differences in vigilance) and probably according to the specific context (e.g. food versus object), and thus are likely to influence how much and what kind of information different species and/or observers may extract from a given demonstration.

Several factors (e.g. sex, age, relationship, repetitions of demonstrations) may influence how much attention animals pay to a certain demonstrator in a certain situation, which probably affects how much information they can learn socially. The influence of the demonstrator on social learning has been investigated to some extent but even in this case we have little knowledge about whether this effect is through the duration of attention paid to this individual.

Animals living in social groups often form close social relationships with certain partners and visual attention might be mainly directed towards those partners. Chance & Jolly (1970) showed that affiliative and status relationships affect how much individuals visually attend to others. Several other studies have also found an influence of familiarity and relatedness on the pattern of transmission of socially acquired behaviours (hens, *Gallus gallus domesticus*: Nicol & Pope 1994; chimpanzees, *Pan troglodytes*: Menzel 1973, 1974; Japanese macaques, *Macaca fuscata*: Nishida 1987). Dominance status, age and sex of the model are additional factors that influence how much and how quickly observers learn from the respective demonstrators (Nicol & Pope 1994; Valsecchi et al. 1996; Choleris et al. 1997; Choleris & Kavaliers 1999). Furthermore, Coussi-Korbel & Fragaszy (1995) suggested that in an egalitarian (tolerant) social system, socially acquired information spreads more equally across all group members than in more despotic (less tolerant) systems because of closer proximity and more tolerant relationships between all individuals. This would also suggest that the identity of the demonstrator might influence observational learning less in more egalitarian species than in despotic species.

We carried out an experimental study on attention in common marmosets, *Callithrix jacchus*. Marmosets live in small family groups in which all group members

participate extensively in caring for young (reviewed in Brown et al. 2005). Relationships between individuals are tolerant with regard to spatial proximity, dominance and food sharing (Day et al. 2003; Fragaszy & Visalberghi 2004; Brown et al. 2005). Several studies have investigated the underlying mechanisms of their social-learning abilities (Bugnyar & Huber 1997; Voelkl & Huber 2000; Caldwell & Whiten 2003, 2004; Day et al. 2003), but only three studies have reported general attention during the demonstration of a model (percentage of demonstrations observed: Bugnyar & Huber 1997; proximity to the demonstrator: Day et al. 2003; number of follows: Moscovice & Snowdon 2006). In the present study, we tested three groups of marmosets in an experimental setting comparable to studies investigating the mechanisms of social learning. We measured their direct attention to the model by providing restricted visual access through two round holes to the demonstration compartment, which allowed us to measure attention getting and attention holding. The rationale for using a two-hole procedure is that if animals are interested in the actions of the model, they will look through one of the two holes during the demonstration. Two holes are provided to allow some flexibility for the observer with regard to the angle of vision as well as its position within its own cage. We predicted that marmosets would be more attentive (look more frequently and for longer) when the model was engaged in activities that might provide useful information to the observer (e.g. manipulation of an object, eating specific food) compared to activities such as resting or investigating the cage. Furthermore, we predicted that individuals would vary in their attention, but that, according to Coussi-Korbel & Fragaszy (1995), the identity of the demonstrator would have only a small influence on attention processes in marmosets.

METHODS

Subjects

We studied 15 adult and four juvenile (5–8 months) common marmosets (Table 1). They are maintained in three family groups at the Department of Behaviour, Neurobiology and Cognition, University of Vienna, Austria. All animals were born in captivity and housed in indoor cages (250 × 250 × 250 cm), which contained ropes and branches. The marmosets were fed fruits, vegetables and protein supplements once a day; water was always available. The temperature was 28–34°C during the day and at night. The humidity ranged from 70 to 90%.

Experimental Set-up

The model/observer studies took place in an experimental cage (142 × 36 cm and 108 cm high) to which the monkeys had access through a passageway from the adjacent but visually isolated indoor cage. The experimental cage was divided in half to make an observation chamber and a demonstration chamber (Fig. 1). The two chambers were divided by an opaque wall with two round holes

Table 1. Group composition of the three test groups

Animals	Sex	Date of birth	Relatedness	Group
Augustina	F	1997	Mother	1
Pooh	M	1999	Father	1
Momo	M	2002	Offspring	1
Fimo	M	2002	Offspring	1
Yara	M	2003	Offspring	1
Pandu	F	2003	Offspring	1
Locri	M	2003	Offspring	1
Messina	F	2003	Offspring	1
Thomas	M	1996	Father	2
Cicoria	F	1998	Offspring	2
Monchichi	M	2000	Offspring	2
Gin	M	2003	Offspring	2
Tonic	F	2003	Offspring	2
Zaphod	M	2002	Father	3
Kiri	F	2000	Mother	3
Frodo	F	2004	Offspring	3
Veli	F	2004	Offspring	3
Mink	M	2005	Offspring	3
Nemo	F	2005	Offspring	3

In group 1 all animals served as observers and models seven times, in group 2 four times and in group 3 five times. F = female; M = male.

(4 cm in diameter) in the horizontal centre, 20 and 40 cm from the bottom, respectively. The observer compartment was empty and provided no distraction for the observer other than the visual access to the model compartment (e.g. there were opaque walls on two sides and a white curtain in the front). The model compartment was filled with a layer of wood chips 3 cm high. A passageway with one guillotine door per compartment connected both chambers.

Procedure

We conducted the experiments from June to August 2005. Before the experiment started the monkeys were familiarized with both the experimental set-up and the use of the passageways. Before testing started each animal was trained to open a film canister with the lid half closed and to retrieve a piece of food (Voelkl & Huber 2000). We used a shaping procedure to train the animals, where they first had to retrieve food from an open film canister, then from a film canister with the lid loosely attached and

finally with the lid half closed. Three successful openings of the half-closed lid were required for each animal to proceed to the test phase. During the test phase, all monkeys were fed their daily diet after the experiments, which were conducted between 0900 and 1200 hours.

Every individual served as a model and as an observer in every possible dyad within its own group. Individuals were tested once per experimental day and roles (model versus observer) were alternated between days. We conducted tests every 2–3 days. The type of food reward (a 1 × 1-cm piece of fruit from their daily diet) in the film canister was also varied between days to make it unpredictable.

At the beginning of a test session, the model was allowed to watch the experimenter put a piece of food into the film canister and bury that canister under the wood chips in the model chamber. After the canister was buried, the experimenter touched all other places within the model compartment with her hands to make it difficult for the model to locate the canister. To enable models to locate the film canister, the experimenter showed the model the food reward, placed it into the canister and buried the canister while the model watched the whole process. If the model looked away, the procedure was repeated. After the food was hidden, we let the observer into the observation chamber and gave him or her 3 min to explore and become familiar with the situation. Then the model was allowed to enter the model chamber (a metallic loud cling from the guillotine door at the same time attracted the observer to one of the holes) and search for the film canister. The session ended once the food was retrieved and eaten ($N = 96$) or after 10 min ($N = 10$). In 18 cases, where the model did not find the canister within 5 min ($N = 17$) or was unable to open it ($N = 1$), help was provided, for example the canister was retrieved and put on top of the wood chips or the lid was opened. In seven of the 17 cases, help to find the canister did not lead to manipulation (the animals ignored it) and the tests were terminated after 10 min. In the other three terminated sessions, the model refused to eat the food.

All sessions were videotaped with two digital cameras (Sony DCR-TRV 25E and DCR-PC5 NTSC): one focused on the behaviour of the model, the other on the two observation holes. In a frame-by-frame analysis, we analysed how long the model was searching, manipulating the canister, feeding or engaged in other behaviours. For the observer, we recorded the duration and number of looks while the model was searching, manipulating the canister, feeding or engaged in other behaviours. Searching was defined as moving slowly forward while visually scanning the floor, occasionally moving wood chips with the hands. Manipulating was defined as being in physical contact with the canister, and trying to open it with the hands or mouth (Voelkl & Huber 2000). Feeding was recorded when the model put the food item into its mouth and chewed. If the model was resting or investigating other parts of the model compartment (e.g. visually scanning the side partition, the top or the observation holes) it was said to be engaged in other behaviour.

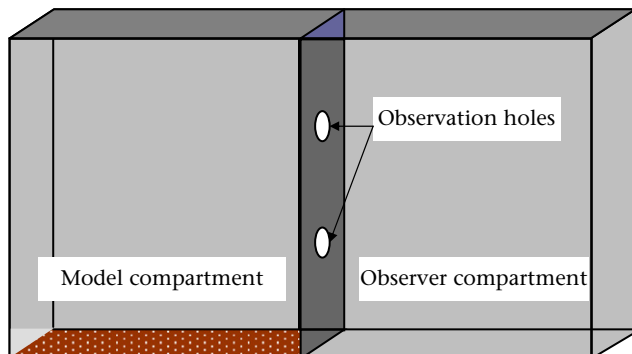


Figure 1. Diagram of the experimental cage.

Observational Data Collection

We collected data on members in the groups by focal animal sampling (Altmann 1974). Focal samples were 10 min long and conducted once per day for each animal. A total of 16 samples per animal were collected. All data were recorded by the same observer. The following affiliative behaviours were pooled into one category: allogrooming (the focal monkey cleaned another monkey's fur with the mouth and/or hands) and proximity (the focal monkey sat close (ca. 30 cm) or closer to another, but without physical contact).

Data Analysis

In the data analyses, we refer to the combination of searching, manipulating the canister and feeding as 'food-directed behaviour'. To be as precise as possible, we took the duration of time for which the observer was attentive (i.e. looking through either one of the observation holes) to a searching, manipulating or feeding conspecific as a percentage of its opportunity to attend to a searching, manipulating or feeding individual in the observation period (% observation time). We also calculated the number of looks through the two holes and the mean duration of looks of each individual. The mean duration is the sum of the durations of all looks during a specific activity of the model divided by the number of looks during that activity. Although not independent of each other, we report all three measurements since % observation time could be high because an animal is watching either frequently for short durations or seldom but for long durations, which might have different effects on the outcome of an experiment. It was impossible to record the exact eye gaze of the animals, so reported measurements are likely to overestimate the actual attention to the model and its activity (see Discussion).

Videotapes were analysed by E.R.; a subset of nine observer and nine model videos were also analysed by an independent researcher to confirm scoring consistency. In 92%, the difference between coders in the measured duration of observer's looks was within 30 frames and 75% were within 20 frames (Pearson correlation: $r_{50} = 0.962$, $P < 0.001$). The duration of searching, manipulating the canister and feeding by the model was scored within 90 frames in 78%, 93% and 77% of the cases, respectively (searching: $r_{16} = 0.987$, $P < 0.001$; manipulating: $r_{12} = 0.99$, $P < 0.001$; feeding: $r_{11} = 0.97$, $P < 0.001$).

To analyse whether observers paid more attention to individuals with which they frequently associate and groom, we created rectangular matrices for affiliative behaviour and the % observation time, number of looks and duration of looks. We tested the probability of a correlation between two matrices by using the Spearman rank correlation coefficient with the empirical distribution of this statistic estimated on the basis of random permutations (20 000) of the same matrices (de Vries 1995). We used a row-wise matrix correlation procedure to correct for individual differences in behaviour (Hemelrijk 1990a, b; de Vries et al. 1993).

Statistical Analyses

Before carrying out statistical analyses, we tested the parameters for normality by using a Kolmogorov–Smirnov test. Since only the parameter % observation time was normally distributed, we used nonparametric statistics to analyse all data. In the Results, we present the median (1st quartile; 3rd quartile) when referring to the % observation time, and the number and duration of looks. For all statistical analyses we used SPSS version 10.0.5 (SPSS Inc., Chicago, IL, U.S.A.) and MATMAN version 1.0 (Noldus Technologies, Wageningen, Netherlands). For the calculation of the multiple pairwise comparisons and in the case of small sample sizes, statistics were calculated according to Siegel & Castellan (1988). All tests were two tailed and alpha was set at 0.05; trends are reported for $0.1 > \alpha > 0.05$. When we analysed subsets of data, probabilities were corrected by a sequential Bonferroni procedure (Hochberg 1988); P values are reported before the Bonferroni correction. If results did not remain significant at the 5% level after the correction, they are indicated as P^* .

RESULTS

Activity of the Model

Overall, the models were engaged in other behaviours for the same duration as they were engaged in food-directed behaviour (Wilcoxon signed-ranks test: $Z = -0.241$, $N = 19$, $P = 0.801$; Table 2). Within the food-directed category, there was a significant difference between the durations for searching, manipulating the canister and feeding (Friedman test: $\chi_2^2 = 6.421$, $N = 19$, $P = 0.04$; Table 2), but multiple comparisons revealed only a nonsignificant trend towards a longer duration of manipulating than to feeding and no difference between the other conditions (searching–manipulating; searching–feeding).

Influence of the Model's Activity

Overall, observers paid attention to the demonstrator 22.89% (15.96; 31.73) of the time the model was present in the model compartment. They showed more interest in the model when it was engaged in searching, manipulating the canister or feeding (i.e. food-directed behaviour) than when it was engaged in other behaviours (Wilcoxon signed-ranks test: % observation time: $Z = -3.582$, $N = 19$, $P = 0.001$; number of looks: $Z = -3.822$, $N = 19$, $P = 0.001$; mean duration of looks: $Z = -2.495$, $N = 19$, $P = 0.013$; Table 2, Fig. 2). Furthermore, within the category of food-directed behaviour, marmosets also differed in % observation time according to whether the model was searching, manipulating the canister or feeding (Friedman test: $\chi_2^2 = 6.632$, $N = 19$, $P = 0.036$), but not in the number of looks ($\chi_2^2 = 2.548$, $N = 19$, $P = 0.28$), suggesting that individuals watched for a longer duration during certain activities of the model. When analysing the mean duration of looks, we found this expected overall

Table 2. Median (quartile 1; quartile 3) of observation parameters during different activities of the model

Model (s)	Observer		
	% Observation time	Number of looks	Duration of looks*
Other behaviour [147.41 (55.09; 241.82)]†	14.41 (9.06; 20.02)	2.57 (1.34; 4.45)	4.57 (4.24; 5.34)
Food-directed behaviour [108.14 (78.82; 134.66)]‡	29.20 (22.59; 37.53)	5.50 (5.00; 6.50)	5.57 (5.17; 8.13)
Searching [34.44 (24.14; 40.33)]	24.46 (19.32; 30.28)	1.67 (0.02; 2.50)	5.13 (3.54; 6.11)
Manipulating [41.31 (28.46; 53.45)]	31.15 (28.07; 40.33)	1.86 (1.67; 2.56)	6.06 (5.20; 9.55)
Feeding [31.47 (29.59; 41.47)]	22.65 (20.96; 35.89)	2.00 (1.10; 2.31)	6.08 (4.50; 7.29)

*For each individual, calculated as the sum of durations of all looks during a specific activity of the model divided by the number of looks during that activity.

†There was no significant difference in the amount of time the model was engaged in other behaviour and food-directed behaviour.

‡Food-directed behaviour of the model combines searching, manipulating a film canister and feeding.

difference ($\chi^2_2 = 11.111$, $N = 18$, $P = 0.004$). Multiple pairwise comparisons revealed that observers looked for longer and for a higher % observation time when the model was engaged in manipulating the canister rather than in searching (multiple comparisons, $P < 0.05$; Table 2). No significant differences were found between searching and feeding or manipulating the canister and feeding.

Group, Sex and Age Differences

There was no significant difference in the median (quartile 1–3) % observation time during food-directed behaviour between the groups (group 1: 33.16% (23.50; 38.85); group 2: 26.27% (15.08; 30.83); group 3: 31.50% (25.75; 36.91); Kruskal–Wallis test: $H_2 = 2.782$, $P = 0.249$). We found no difference between the groups in the number of looks while the model was engaged in food-directed behaviour ($H_2 = 2.18$, $P = 0.897$).

Although there was no difference in attention between groups, the variance in attention between individuals was

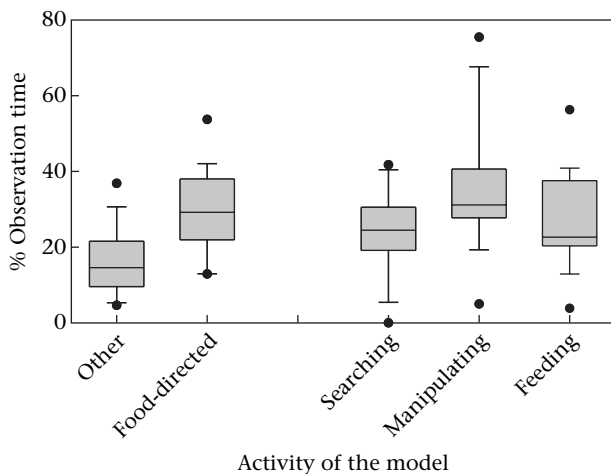


Figure 2. Box plots showing % observation time that the observers watched the model while it was engaged in other behaviours compared to food-directed behaviour and for the behaviours summarized in the category of food-directed behaviour (searching, manipulating a film canister and feeding). Shaded boxes represent the interquartile range, bars within shaded boxes are median values, whiskers indicate the 5th and 95th percentiles, and closed circles are outliers.

large with one individual watching on average \pm SD as little as $9.74 \pm 12.85\%$ of the demonstrator's handling time with a mean \pm SD looking duration of 3.29 ± 2.01 s, whereas another individual watched on average as much as $49.22 \pm 18.13\%$ with a mean looking duration of 11.05 ± 8.09 s. Neither sex nor age (adults versus juveniles) could explain the differences in attention (Mann–Whitney U test: sex: % observation time: $Z = -0.49$, $N_{\text{female}} = 9$, $N_{\text{male}} = 10$, $P = 0.624$; duration: $Z = -0.368$, $N_{\text{female}} = 9$, $N_{\text{male}} = 10$, $P = 0.72$; looks: $Z = -0.816$, $N_{\text{female}} = 9$, $N_{\text{male}} = 10$, $P = 0.447$; age: % observation time: $Z = -0.8$, $N_{\text{adult}} = 15$, $N_{\text{juvenile}} = 4$, $P = 0.469$; duration: $Z = -0.651$, $N_{\text{adult}} = 15$, $N_{\text{juvenile}} = 4$, $P = 0.53$; looks: $Z = -1.000$, $N_{\text{adult}} = 15$, $N_{\text{juvenile}} = 4$, $P = 0.357$).

Habituation Effects

Since each individual was tested with every other animal in the family group, individuals watched the same type of demonstration several times (7 times in group 1, 4 times in group 2 and 5 times in group 3) raising the possibility that animals lost interest in attending to the demonstrations over time. However, we found no habituation effects across experimental sessions in % observation time during activity of the model (Friedman test: group 1: $\chi^2_6 = 8.357$, $N = 8$, $P = 0.213$; group 2: $F_{1,3} = 2.46$, $N = 5$, $P = 0.5$; group 3: $\chi^2_4 = 4.480$, $N = 6$, $P = 0.345$; Fig. 3) or in the number of looks (group 1: $\chi^2_6 = 0.625$, $N = 8$, $P = 0.996$; group 2: $F_{1,3} = 1.26$, $N = 5$, $P = 0.5$; group 3: $\chi^2_4 = 6.973$, $N = 6$, $P = 0.137$) suggesting that individuals attended to the demonstration as much in the first as in the last sessions.

Effect of Demonstrator

Observers were more attentive towards demonstrators of the opposite sex than towards animals of the same sex in the % observation time and mean duration of looks during food-directed behaviour (Wilcoxon signed-ranks test: % observation time: $Z = -2.415$, $N = 19$, $P = 0.016$; mean duration of looks: $Z = -2.199$, $N = 19$, $P = 0.028$; $P^* < 0.1$), but not in the number of looks ($Z = -0.893$, $N = 19$, $P = 0.372$).

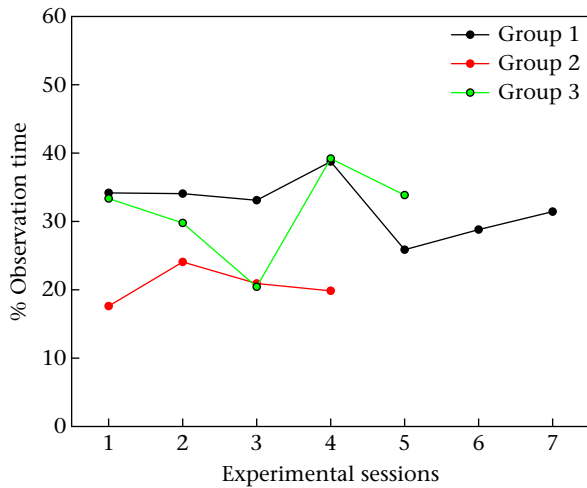


Figure 3. Mean % observation time that observers watched a model depending on the experimental session. Since the number of sessions differed between groups, all three groups are illustrated separately.

With regard to age, we could analyse the behaviour only of the four juveniles in group 3, since all other animals were older than 2 years and thus adults. Three of the juveniles spent a greater % observation time watching their siblings' food-directed behaviour (42.11% (33.22; 47.96)) than their parents' food-directed behaviour (24.40% (21.98; 28.22)), whereas the fourth juvenile paid more attention to his parents (35.33%) than to his siblings (25.35%).

For group 1 we analysed whether affiliation pattern influenced whether observers paid attention to a certain model (for groups 2 and 3 we had insufficient data). Row-wise matrix correlations revealed that observers looked more often at the model if they often groomed and associated with the model (row-wise matrix correlation – Rr test: $\rho_{\text{rw}} = 0.223$, $P = 0.047$). However, affiliation pattern did not affect the overall observation time or the mean duration of looks (row-wise matrix correlation – Rr test: % observation time: $\rho_{\text{rw}} = 0.01$, $P = 0.48$; mean duration of looks: $\rho_{\text{rw}} = 0.07$, $P = 0.31$).

DISCUSSION

Our results indicate that attention of marmosets in a situation similar to a social-learning test procedure depends on several factors. First, marmosets paid more attention to a model if the latter was engaged in a task (searching, manipulating a canister or feeding) than if it was merely resting or investigating the cage. Furthermore, the manipulation of an object attracted more attention than searching for it. Second, attention levels varied between individuals independently of sex and age. Finally, observers were more attentive to models of the opposite sex and at least in group 1, looked more frequently if the model was an affiliative partner. The repetition of the same demonstration did not decrease attention levels. These results have several implications for social-learning experiments.

Social learning, and thus attention to a model, is expected in circumstances where the observer can acquire some new knowledge, for example about predators (Mineka & Cook 1988), use of space (Warner 1988), tool use (Matsuzawa et al. 2002), how to solve an extractive task or what food is palatable (reviewed in Byrne & Russon 1998; Fragaszy & Visalberghi 2004), which will enhance the observer's fitness (Galef 1996). Our marmosets were most attentive during the manipulation of an object and least attentive when the model was merely investigating or resting, suggesting that marmosets selectively attended to the task that might be relevant for retrieving food (Fragaszy & Visalberghi 2004). The difference between attention during searching and manipulation by the model could not have been caused by observers being too slow to realize that the demonstrator had already entered the model compartment, since the frequency of looks and overall attention did not differ between the categories of searching and feeding. Another study carried out in our laboratory also suggests that a manipulating model is more attractive than a feeding model (M. C. Nussgruber, unpublished data). A confounding factor that might have affected these results is the unpredictability of the food reward, which could lead us to attribute the greater interest in the manipulation of the object to reward expectancy instead of to interest in the actions of the model. A reward expectancy model would also be consistent with the fact that the marmosets did not habituate to the experiments. However, all food rewards were items of their daily diet and neither special nor surprising for the animals, rendering this explanation unlikely to explain fully the observed differences.

Nevertheless, observers watched on average only 31% of the manipulation. In this experiment, observers knew the task beforehand and were able to solve the problem themselves, which could explain the low frequency and short duration of looks. However, there are several arguments that point against such an explanation. First, a certain novelty was also provided in our experiments, because the model (as well as the food reward) differed in each demonstration. Second, another study conducted in our laboratory compared the frequency of looks towards a model manipulating a new apparatus with those towards a model that was only feeding (M. C. Nussgruber, unpublished data). The study found an overall lower frequency of looks than we found in the present experiment even though the apparatus was new for the observers. Third, our measurements of attention getting as well as attention holding are likely to be overestimated, since, even if observers came to the holes and looked into the model compartment, attention might not have been focused on the model and its food-directed behaviour for the entire time. Finally, we found no habituation effects across sessions, suggesting that observers were no more interested in the first demonstration when the situation and the experiment were new than in the last demonstrations.

Attention levels also differed on the individual level with some animals watching as much as 40–50% of the demonstration, whereas others watched less than 15%. Although males and females differ in attention as well as

in motivational and perceptual mechanisms (reviewed in Choleris & Kavaliers 1999), we found no significant effect of sex in attention levels in the marmosets. These results are congruent with the absence of sex differences in a social-learning task in common marmosets (Bugnyar & Huber 1997) and vigilance patterns in tamarins, *Saguinus labiatus*, and squirrel monkeys, *Saimiri sciureus* (Caine & Marra 1988), although Lonsdorf (2005) found sex differences in termite fishing skills of chimpanzees. Age would also be expected to influence attention levels, because social learning facilitates access to and the processing of difficult foods in infants (Fragaszy & Visalberghi 2004; Schiel & Huber 2006). The fact that we did not find higher attention levels in the juveniles could be caused by the small sample size or their age (7–9 months). Schiel & Huber (2006) found in a field study that juveniles' visual attention to their parents and siblings was highest when they were 3–4 months old. However, juvenile *Saimiri oerstedii* paid little attention to older animals (Boinski & Fragaszy 1989) and Caine & Marra (1988) found no age difference in vigilance in tamarins and squirrel monkeys.

Although sex and age did not determine the amount of attention of observers, the sex of the model did have an influence with observers being more attentive if the model was of the opposite sex. This is surprising with regard to the social system of common marmosets, where all animals except the breeding pair are closely related (offspring and siblings, respectively) and do not breed with each other. Schiel & Huber (2006) found that infant and juvenile marmosets were more attentive to nonreproductive females than to males; however, the sex of the young animals was unknown. Three of four juveniles in our group were much more attentive to their siblings than to their parents, emphasizing the trend towards interacting with other group members besides the parents (Yamamoto 1993) and supporting Schiel & Huber's (2006) results. Apart from the influence of the demonstrator's sex, we also found that in group 1 animals looked more often if the model was an affiliative partner. However, this did not influence the duration of looks or the overall percentage of attention. These results are in line with Coussi-Korbel & Fragaszy's (1995) argument that in egalitarian social systems information should spread more or less evenly through the group.

Overall, the median duration of looks of 6 s while an object is being manipulated is little time for an observer to perceive an action to be copied especially if the model demonstrates a sequence composed of novel acts. In that case the observer has to learn not just new motor acts by observation alone, but also the sequential organization of the demonstrated actions (Miklósi 1999), an unlikely task even if animals pay attention to the demonstration for 31% of the time. In experiments that demonstrated imitation in marmosets (Bugnyar & Huber 1997; Voelkl & Huber 2000), the actual motor acts to be imitated were shorter (<5 s) than the attention-holding capacity of marmosets. Furthermore, the actions to be copied were demonstrated 10–20 times per observation session, thus increasing the probability that the observer saw the relevant acts. Another study that investigated whether marmosets were able to learn how to open an artificial

fruit by social learning reported that, compared to capuchin monkeys and apes (Whiten 1998; Custance et al. 1999; Stoinski & Whiten 2003), none of the marmoset subjects succeeded with the task although some clear demonstration effects were found (Caldwell & Whiten 2004). Unfortunately, Caldwell & Whiten (2004) did not report any attention measures of observers or how long the demonstration of the relevant actions took. One important difference between the marmoset study carried out by Caldwell & Whiten (2004) and the studies carried out on apes (Whiten 1998; Custance et al. 1999; Stoinski & Whiten 2003) is that Caldwell & Whiten (2004) used a conspecific model, whereas the ape studies used human demonstrators. The latter is important with regard to attention since a human demonstrator usually adjusts his/her demonstration of the relevant motor actions according to the attention of the observer. In this case, the failure of marmosets to copy the actions necessary to open the artificial fruit might have been a problem not of their imitative ability, but rather of their short attention span. However, further studies are needed to test whether inattentive marmosets are in fact less successful than attentive marmosets in solving a new task that is demonstrated by a model. Moscovice & Snowdon (2006) suggested that tontop tamarins, *Saguinus oedipus*, that follow a conspecific model more often are also faster in learning the task than individuals that do not follow as often. Furthermore, in ravens, *Corvus corax*, results of a social-learning study were also in line with the results of an attention study (C. Schwab & C. Scheid, unpublished data). Both studies indicate that attentiveness might influence success in learning tasks.

One criticism that could be raised with regard to our study concerns the procedure we used, because, although it provides substantial pragmatic advantages (with a relatively unambiguous measure of attention), it makes the situation very different from those typically used in social-learning experiments. When there is a mesh or Plexiglas wall between observer and demonstrator it is much more likely that the demonstrator's behaviour 'catches' the attention of the observer. However, we argue that if observers are really interested in the demonstration they will use the holes to look into the model compartment. Even if a movement of the demonstrator in an 'open' visual condition were to catch the eye of the observer, the observer might not pay attention to what the demonstrator is doing. Our procedure, on the other hand, measures the real interest of the observer towards the model, which is the important variable in social-learning experiments.

In conclusion, our study suggests that attention might be an important factor to consider when designing experiments that test learning after observing others or their environment (e.g. social-learning experiments, cooperative solving and spatial memory tasks). The duration of tasks should be within the attention span of the species to be tested and the number of demonstrations should be high enough to ensure that observers see the relevant act. However, repetition of demonstrations alone is not sufficient if the demonstrated action is a compound of several dependent elements that must be perceived in its entirety

to grasp the organizational structure. A better method would be to restrict the visual access to the demonstration, measure the actual attention of the observers and incorporate that variable into the analysis. Furthermore, the method we used to measure attention in marmosets allows for a direct comparison of attention getting and attention holding between species (Scheid et al., in press; F. Range, unpublished data), which might further explain differences in performance between species in many experimental settings.

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