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Learning about food quality in a social condition: Can common marmosets (*Callithrix jacchus*) use a conspecific's reaction towards food as a social cue to avoid unpalatable food?

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ABSTRACT

In the changing environment of food generalists the possible confrontation with unpalatable or even toxic foods might involve potential dangers to an animal's health or even survival. Individual trial and error learning is one way to cope with the changing palatability of foods, however, the use of a conspecific's knowledge or experience would be a more efficient and also safer way to avoid potential dangers.

In the present study it was investigated if common marmosets (*Callithrix jacchus*) are able to use a conspecific's disgust reaction towards a preferred food made unpalatable as social cue to (1) inhibit the impulse to ingest the same food in a go / no-go task and (2) avoid a food patch containing unpalatable food by choosing an alternative food patch containing palatable food in a two choice task. The animals were tested in dyads in an experimental design without physical separation that provided close interaction and the possibility to scrounge. The scrounging paradigm was adopted to increase attention towards the demonstrator and thereby enhance social learning by observation.

The results of this study indicated that common marmosets have major difficulties to inhibit the impulse to ingest presented food even after witnessing a conspecific's clear disgust reaction towards this food. The introduction of an alternative food patch and thereby the possibility to avoid the unpalatable food increased the overall success rate, however the majority of the animals still performed at chance level. Nevertheless, the performance of two subjects was significantly successful, indicating that common marmosets have the capability of using a conspecific's reaction towards food as social cue to avoid unpalatable food. The precise means by which these two subjects achieved success compared to the other tested animals however remain unclear and require further investigation.

Keywords: Common marmoset, social learning, unpalatable food, scrounging, observational learning

ZUSAMMENFASSUNG

In der sich ständig verändernden Umwelt eines Nahrungsgeneralisten besteht die potentielle Gefahr, durch ungenießbare oder giftige Nahrung gesundheitlichen oder sogar tödlichen Schaden zu erleiden. Individuelles Lernen durch Versuch und Irrtum ist eine Möglichkeit, mit der sich ändernden Genießbarkeit von Nahrung umzugehen, ein effizienterer und sichererer Weg aber wäre es, das Wissen und die Erfahrungen eines Artgenossen zu nutzen.

In der vorliegenden Arbeit wurde untersucht, ob Weißbüschelaffen (*Callithrix jacchus*) dazu fähig sind, die negative Reaktion eines Artgenossen auf ein bevorzugtes aber ungenießbar gemachtes Futter als sozialen Hinweis zu nutzen, um (1) den Impuls zu unterdrücken, das selbe Futter in einem Go / No-Go Versuch zu konsumieren und (2) einen Futterplatz, der ungenießbares Futter enthält durch die Auswahl eines alternativen Futterplatzes, der genießbares Futter enthält, zu vermeiden. Die Versuchstiere wurden in Zweiergruppen getestet, das experimentelle Design ohne physikalische Trennung ermöglichte nahe Interaktionen zwischen den Individuen und die Möglichkeit, Futter zu stehlen. Das Modell des Futterstehlens wurde angewendet um die Aufmerksamkeit auf den Demonstrator-Affen und dadurch soziales Lernen durch Beobachtung zu erhöhen.

Die Ergebnisse dieser Arbeit deuteten an, dass Weißbüschelaffen große Schwierigkeiten haben, den Impuls zu unterdrücken, präsentiertes Futter zu konsumieren, sogar nachdem sie eine deutlich negative Reaktion eines Artgenossen auf besagtes Futter beobachten konnten. Das Vorhandensein eines alternativen Futterplatzes und die dadurch gegebene Möglichkeit, das ungenießbare Futter zu umgehen, erhöhte die allgemeine Erfolgsrate. Dennoch blieb die Leistung der meisten Tiere auf Zufallsniveau. Zwei Versuchstiere waren allerdings signifikant erfolgreich, was darauf hindeutet, dass Weißbüschelaffen grundsätzlich die Fähigkeit besitzen, die Reaktion auf Futter eines Artgenossen als sozialen Hinweis auf die Genießbarkeit dieses Futters zu nutzen und dadurch die Konsumation dieses Futters zu vermeiden. Welche konkreten Mechanismen von diesen beiden Individuen letztlich genutzt wurden konnte im Rahmen dieser Arbeit nicht endgültig geklärt werden.

Schlüsselwörter: Weißbüschelaffen, soziales Lernen, ungenießbares Futter, Futterstehlen, Lernen durch Beobachtung

INTRODUCTION

Social living in animals can be seen as a balancing act between costs and benefits for all members living in a group. Although the costs as competition over resources (e.g. food or breeding partner), increased risk of parasites or increased attraction towards predators can be high and limiting for the individual, there are also considerable benefits of living in groups. Group living potentially bears easier mating opportunities or foraging help, increased vigilance in a group leads to earlier predator detection (many eyes hypothesis) and risk dilution (e.g. Lima, 1995).

Foraging behaviour in terms of locating, obtaining and handling food is one of the most important activities in an animal's life. One way to increase foraging success and to decrease searching time is to learn from others. Social learning occurs when an individual's learning is influenced by observation of, or interaction with, another animal or its products (e.g. Heyes, 1994). Group living increases the opportunities of information exchange between individuals (Lee, 1994) and can therefore reduce the costs of individual trial and error learning through observation of experienced conspecifics.

Extensive research on social foraging strategies or social influences on foraging respectively has shown that information gained from conspecifics provides individuals with knowledge of food acquisition, i.e. it provides them with useful information about the when, where, what and how to eat (Galef & Giraldeau, 2001). Addressing the questions of when and where to find food is especially important for species depending on food sources that are patchy distributed in time and space. Howler monkeys (*Alouatta palliata*), for instance, live in cohesive social groups and young individuals stay with their troop and learn what to eat and how to locate preferred foods efficiently. Spider monkeys (*Ateles geoffroyi*) seem to be "taught" by their mothers how to travel along foraging routes. Both species depend on seasonal foods (e.g. young leaves or ripe fruits), which are generally ephemeral in terms of optimal nutritional quality (Milton, 1981; 1988). Also juvenile walleye pollocks (*Theragra chalcogramma*) were found to exploit spatially variable ephemeral food patches more successful when foraging in groups, indicating that local enhancement and social facilitation can be taken into account (Baird et al., 1991, Ryer & Olla, 1992). A study on toque macaques (*Macaca sinica*) showed that subjects respond to food calls given by a conspecific referring to the presence, quantity and location of a feeding source, indicating semantic communication in this species (Dittus, 1984).

The question of how to eat addresses especially species that are dependent on food items that need to be manipulated in some way in order to ingest it. Well known examples include the puncturing of milk bottles by great tits, *Parus major* (Fisher & Hinde 1949, Sherry & Galef,

1990) or the study on black rats (*Rattus rattus*) showing that pups learn complex techniques of extracting pine seeds from cones via social transmission by observation of experienced adult rats (Terkel, 1996). A wide area of research has focused on tool use in primates and the ways of acquiring the essential techniques to use tools in order to extract or manipulate otherwise inaccessible foods. The most famous examples come from chimpanzees, *Pan troglodytes*: Young chimpanzees learn from their mothers, for instance, the skills of termite-fishing, a complex behaviour that involves inserting a self-made tool (e.g. twigs, blades of grass) into a termite mound and extracting the clinging termites from inside (e.g. Goodall, 1986; Lonsdorf, 2006) and nut-cracking behaviours, using a pair of stones as hammer and anvil to crack open thick shelled nuts (Boesch, 1991; Matsuzawa et al., 2001).

Last but not least, the question of what to eat respectively what not to eat should be important especially to species that forage on a wide variety of different foods, i.e. food generalists, since many plants and animals (e.g. insects) evolved chemical deterrence mechanisms against herbivory and predation (e.g. Bell & Charlwood, 1980). Triterpenoids (e.g. cardiac glycosides) for example are highly toxic to vertebrate herbivores (Freeman & Beattie, 2008).

Social learning is especially favourable in situations in which non-social cues acquired through trial and error learning are unreliable and when the consummation of a certain food can be fatal (e.g. Visalberghi & Addessi, 2003). The consumption of novel food, for instance, is either important when a specific food source a species depends on gets scarce or even extinct, or when animals move to a new habitat and encounter different ecological demands, forcing the animals to change their diet, or during infancy, when basically all food is novel. In all of these situations it would be more efficient and less risky to use social information of experienced conspecifics to cope with the new feeding demand. Thus, concerning the choice of an adequate diet, experienced conspecifics should be useful in learning to accept novel, edible foods but also to avoid toxic or unpalatable foods.

There are mechanisms by which infants socially learn about a certain diet via a passive transfer of information from mother to offspring. As it was shown in rats, food preferences can already be predetermined before birth (Hepper, 1988) or at weaning, influenced by the mother's diet (Galef & Sherry, 1973). Several other studies by Galef et al. on Norway rats (*Rattus norvegicus*) found empirical evidence for socially induced food preferences in a demonstrator-observer paradigm (for review see Galef, 1990). One of these studies demonstrated that changes of preferences for a certain diet were only established within a social context and not alone by mere exposure to the diet. These socially induced preferences lasted for at least 2 weeks. Also

the preference for a piquant, congenitally unpalatable diet (hot cayenne pepper) was induced by observing demonstrator rats ingesting this diet (Galef, 1989).

In common marmosets (*Callithrix jacchus*), Voelkl et al. (2006) investigated the role of social facilitation in a feeding paradigm with familiar food compared to novel food. The authors investigated whether the presence of experienced adults would influence the consumption of novel food items in infants, showing that infants either refused to ingest unknown items or ate only small amounts with longer latencies and more investigation when adult animals were absent. Also food transfers and the consumption of food that was acquired socially were higher for novel food than for familiar food items. However, food transfer attempts were mainly initiated by the infants, not actively by the adults, indicating the lack of any “teaching” attempts on side of adult subjects.

Focusing on situations in which animals were confronted with unpalatable or even toxic food, one would assume that an individual should even more rely on the experience and information of others rather than on individual learning. A broad field of scientific work has focused on the topic of food aversion learning, including a wide variety of different animal species (for an overview see Galef, Mainardi & Valsecchi, 1994). In many of the examined species, squirrel monkeys and common marmosets included (Laska & Metzker, 1998), foods that have been associated with gastrointestinal distress were afterwards avoided for a long time (Garcia & Koelling, 1966).

Regarding socially induced food aversion learning, especially studies on various bird species have shown positive results: in a study on house finches (*Carpodacus mexicanus*), an altricial birds species, the offspring of birds that avoided oats during the late nestling and fledgling stages showed a lower preference for these seeds in comparison to offspring raised by adults without any aversion towards oats (Avery, 1996). Sherwin et al. (2002) could show in an experimental study that domestic hens are sensitive to food preferences of a conspecific but on the other hand are not able to learn socially to avoid noxious or toxic novel foods, although the demonstrator hens displayed obvious disgust reactions. The authors suggest that social food avoidance learning might be age-dependant, since these results are inconsistent with a previous study by Johnston et al. (1998) on day-old domestic hen chicks that learned by observing the responses from a same aged conspecific about an aversive, bitter-tasting stimulus. Mirza and Provenza (1994) could show socially induced food avoidance in lambs, however, not as a result of direct maternal influence, but through indirect maternal influence, i.e. not the avoidance of a certain shrub itself was adopted but rather the preference for another shrub.

Surprisingly, studies on socially triggered food avoidance in nonhuman primates, especially monkeys, are relatively rare. Examining active prevention of the ingestion of unpalatable food, i.e. knowledgeable individuals informing naïve individuals about the palatability of a certain food, Fletemeyer (1978) reported in a study on free-ranging chacma baboons (*Papio ursinus*) that juveniles were threatened away by the high ranking male when approaching fruit drugged with cynalin. In contrast, studies on pig-tailed macaques (*Macaca nemestrina*), free-ranging red spider monkeys, *Ateles geoffroyi* (Fairbanks, 1975), chacma baboons and vervet monkeys, *Cercopithecus aethiops* (Cambefort, 1981) failed to show affirmative results. In these experiments, not even the knowledgeable individual's avoidance of the unpalatable food was sufficient to elicit a similar avoidance in the observing individuals, indicating that individuals must go through a direct learning process. Including more recent studies, Visalberghi and Adessi (2000) tested capuchin monkeys in their ability to adapt to changes in the palatability of familiar food. Primarily palatable food was made unpalatable by adding white pepper and in a third phase again palatable. The three phases were tested similarly under social and individual conditions. The monkeys easily adapted to the changing palatability of food, however the condition (social or individual) had no influence on the results. Another study using common marmosets investigated the question of begging and food transfer in and towards infants (Brown et al., 2005). It was hypothesized that adults may facilitate infant learning by differing in their willingness to transfer food depending upon the food's novelty or palatability. The results of this study showed that neither the novelty nor the palatability influenced the rates of refusal and transfer: adults transferred palatable and unpalatable novel foods with similar frequencies. The authors suggested that a potential flaw of this study could have been the insufficient inedibility of the chosen food items (unpalatable foods were "items that were tasted by the animals but then rejected without being eaten much", e.g. kiwi fruits or cherry tomatoes), i.e. the food was not unpalatable enough to elicit a proper aversive reaction in adult marmosets. This assumption could be valid, since Snowdon & Boe (2003) were able to show that cotton-top tamarins, *Saguinus oedipus*, socially learned to avoid a preferred food when it was made unpalatable with white pepper but showed no aversion towards the same food not made unpalatable. Aversive responses that could potentially have served as social cues included facial reactions of disgust, alarm-call vocalization and a reduction in food-associated call. The authors suggested that the behavioural coordination in cooperative infant care, communication about food, and well-established social relationships may explain this social avoidance of unpalatable foods in tamarins and the absence of social avoidances in less cooperative species. According to this findings, common marmosets (*Callithrix jacchus*), should have the same potential to learn about the palatability of foods by

observation of conspecifics, since they have a comparable social system: Both species live in a highly cooperative breeding system, in fact the most distinctive system of cooperative breeding in monkeys and apes (Snowdon, 2007), which forces the monkeys to communicate with conspecifics and to coordinate their actions in a social way.

Common marmosets have previously been shown to be able to cooperate in an instrumental task (Werdenich & Huber, 2002) and also to imitate a demonstrator's specific opening technique of food containing film canisters (Voelkl & Huber, 2000). However, in some situations, inhibition of actions obviously should be favored over merely copying everything a conspecific does, e.g. grabbing for an unpalatable or noxious piece of food. Regarding inhibition capacities, Stevens et al (2005) found in an experimental study on "patience" and "self-control" that common marmosets, compared to cotton-top tamarins, wait significantly longer for a delayed large reward than for an immediate small reward. However, in two studies dealing with the subject of intentional control in a demonstrator-observer paradigm in common marmosets when confronted with unpalatable food, the animals failed to use the demonstrator as a cue to locate preferred or unpalatable food respectively (Brüning, 2006; Schlöderitzko, 2007). The authors suggested that the failure were mainly due to side preferences of the observers (Brüning, 2006), to the disability to solve a previous problem concerning local and stimulus enhancement and to missing attention towards the demonstrator (Schlöderitzko, 2007). In both experimental setups, the demonstrator and the observer operated in separated, oppositely arranged experimental compartments. Brüning considered a perspective problem as an additional reason for monkeys' failure to use conspecific cues, conceding the possibility that the animals did not understand the 180° transfer from the observation compartment to the model compartment. However, the failure could also have been due to the separation of the demonstrator and the observer, potentially preventing enhanced learning facilitated by close social contact and the possibility to scrounge. Scrounging, per definition, means exploiting the food others have made available (e.g. Barnard & Sibly, 1981). Although the common experimental design of the last century required a physical separation between demonstrator and observer, because scrounging was commonly thought to have an inhibiting effect on learning (e.g. Frigaszy & Visalberghi, 1989), Caldwell & Whiten (2003) showed in an experimental set-up that scrounging facilitates social learning in common marmosets. As mentioned earlier, common marmosets provide convenient qualification for social studies and particularly for studies involving close social contact required for a scrounging paradigm. A model of the relationship between scrounging and learning suggests social and ecological conditions to determine the amount and quality of social learning in dyadic interactions (Fritz & Kotrschal, 2002). Considering social factors, tolerance is probably one of the most important factors

for the influence of scrounging on the amount and content of learning by observation. Common marmosets are cooperative breeders and not only known for passive food sharing but also for the extremely rare behaviour of tolerated mouth-to-mouth food transfer between adults (Kasper et al., 2008).

In a preliminary study that tested the same captive common marmosets that were tested in the studies by Brüning (2006) and Schlöderitzko (2007), the members of one family group successfully solved a local enhancement task by the use of social information in a demonstrator-observer paradigm with close physical contact and the possibility to scrounge (Nobis et al., under review). In this set-up, also the potential perspective problem was eliminated, since both animals, the demonstrator (producer) and the observer (scrounger), were positioned in the same compartment at the same time. This set-up might also serve to solve or at least minimize potential attention problems. Attention differs not only between species but also between individuals (common marmosets have an attention-holding capacity of approx. 6 s) and could therefore influence the amount of information gained by the observer from the demonstrator (Range & Huber, 2007).

The question remains whether common marmosets are able to intentionally control their scrounging behaviour in a task introducing unpalatable food. Hence, the aim of this study was to investigate whether subjects that were tested in dyadic groups of adult captive common marmosets are able to learn to use a demonstrator's reaction towards a distasteful reward as social cue and thus to (1) inhibit the impulse to scrounge or follow and ingest the same unpalatable reward in a go / no-go task (experiment 1) and (2) avoid a food patch containing unpalatable food by choosing an alternative food patch containing palatable food in a two choice task (experiment 2).

Additional exploration applied to the impact of the social status of the individuals in a given dyad, to the impact of experience over the testing period and to the question of increased learning in experiment 2 compared to experiment 1 due to the introduction of an alternative food patch.

Addressing the question of the role of the social status of the individuals in a dyad, I expected the dominant individuals to act as demonstrators in the beginning of the testing period in both experimental setups and a change towards subordinate demonstrators over time, after the animals had learned about the possibility to encounter unpalatable food in experiment 1 and the possibility to choose the alternative food patch in experiment 2. Furthermore, I expected dominant observers to be more successful compared to subordinate observers due to their potentiality to aggressively displace the subordinate demonstrator from the food source containing palatable food and therefore encounter more chances to consume palatable food in experiment 1 and to consume potentially always palatable food in experiment 2. This expectation was based on the

finding in a study on cooperation in common marmosets, that only those dyads cooperated successfully in which the subordinate individual took the role of the producer and the dominant individual the role of the scrounger (Werdenich & Huber, 2002).

Concerning social relationships, I expected increased social learning in affiliative or tolerant dyads compared to less tolerant or aggressive dyads. Affiliative relationships affect the probability of an individual attending visually to another individual in the group (Chance & Jolly, 1970) and it is assumed that visual attention is required for behavioural coordination, social learning and what is socially learned (Coussi-Korbel & Fragasz, 1995).

Finally, I expected an increased success rate in experiment 2 (two choice task) compared to experiment 1 (go / no-go task) due to the difficulty of complete inhibition of the impulse to consume any food. Although, as mentioned above, the study by Stevens et al (2005) showed that common marmosets waited significantly longer for food than tamarins in a self-control procedure (marmosets: $14.4 \pm 1.5s$, tamarins: $7.9 \pm 0.6s$), the experimental setup allowed animals to see and compare the different amounts of rewards before their choice. Altogether, monkeys seem to have difficulties in delay of gratification tasks, i.e. to wait longer for a delayed, bigger reward instead of immediately consume a small reward (e.g. Anderson et al, 2010). Moreover, the present study did not provide a bigger reward worth waiting for when inhibiting the impulse of ingesting the unpalatable food (experiment 1). In condition 2, however, there was always the possibility to find palatable food in one of the two food patches.

In contrast to studies exploring the demonstrator's awareness of being the source of information, e.g. parents trying to actively inform their offspring about potentially harmful food, this study concentrated on the observer's use of social cues given by the demonstrator, because social foraging depends mostly not on specialized signals but rather on information-bearing cues or signs (e.g. Markl, 1985; Hauser, 1996). Therefore it was not necessary to provide the demonstrators with knowledge about when (experiment 1) or where (experiment 2) unpalatable food was presented, i.e. each individual was supposed to act as demonstrator and observer in a ratio of 50:50 in a given dyad. As the underlying mechanism observational conditioning was presumed, defined as a variation of classical conditioning, however implicating that the observer acquires an emotional response to a given stimulus from the demonstrator (Mineka & Cook, 1993).

In experiment 1 the observer had 3 different possibilities to react correctly, i.e. according to the demonstrator's reaction: In case of a motivation trial where the food was always palatable, he should either wait until the demonstrator left the food patch (in case of a subordinate observer), force the demonstrator to leave the food patch (in case of a dominant observer) or he should join the demonstrator at the food patch and scrounge (in case of an affiliative relationship

within the dyad). During a test trial (always unpalatable food), the observer should watch the demonstrator's disgust reaction and use this information to intentionally control any scrounging behaviour respectively stay away from the food patch after the demonstrator had left it, i.e. the observer had to inhibit the impulse to approach the food patch and ingest the unpalatable food.

In experiment 2 there was the possibility to avoid the unpalatable food by changing to the alternative food patch. In case the demonstrator chose the patch containing unpalatable food and showed some kind of disgust reaction, the observer should choose the alternative food patch. If the demonstrator changed to the alternative food patch before the observer could reach it or if the demonstrator chose the correct patch on the first attempt, the observer should either wait until the demonstrator left the food patch or otherwise join and scrounge.

MATERIAL AND METHODS

Subjects

I tested 15 adult common marmosets, *Callithrix jacchus*, (7 males, 8 females) from two family groups that were housed at the Department of Cognitive Biology at the University of Vienna (Table 1). Group 1 (KIRI) consisted of eight (3 males, 5 females), group 2 (POOH) of seven individuals (4 males, 3 females). Both families lived in indoor cages (250 x 250 x 250cm), connected to outdoor facilities by tunnels. The cages were equipped with branches, ropes and platforms as well as baskets and blankets to rest and the floor was covered with wood chips. Fruits and vegetables were provided at a daily basis. Additional diet supplies (e.g. insects, marmoset jelly, protein and vitamins) were provided according to a weekly schedule. Water was available ad libitum. Both family groups were housed in the same room in visual isolation from each other, but in range of audibility.

Due to social incompatibilities within group 2, one female individual (PA) had to be excluded from experiment 2. All individuals previously participated in a scrounging experiment (2008) and were shown to possess enhanced learning about the location of food. For the present study, individuals of group 1 participated in experiment 1 and individuals of group 2 in experiment 2. All subjects were tested in dyads, one individual acting as the demonstrator, the other as observer.

Table 1: List of subjects regarding sex, kinship, year of birth and groups

Individual	Sex	Kinship	Year of birth	Group
Kiri (KI)	F	Mother	2000	1
Zaphod (ZA)	M	Father	2002	1
Veli (VE)	F	Offspring	Nov. 2004	1
Mink (MI)	M	Offspring	May 2005*	1
Nemo (NE)	F	Offspring	May 2005*	1
Oli (OL)	F	Offspring	Oct. 2005	1
Jack (JA)	M	Offspring	March 2006*	1
Sparrow (SP)	F	Offspring	March 2006*	1
Augustina (AU)	F	Mother	1997	2
Pooh (PO)	M	Father	1999	2
Fimo (FI)	M	Offspring	August 2002	2
Pandu (PA)	F	Offspring	March 2003**	2
Yara (YA)	M	Offspring	March 2003*	2
Locri (LO)	M	Offspring	August 2003*	2
Messina (ME)	F	Offspring	August 2003*	2

* twins; ** excluded

Apparatus

All experiments were conducted in a separate cage, the experimental cage (146 x 40 x 110 cm). All individuals voluntarily participated in all experiments and entered the experimental cage by passageways that connected the home cages of both family groups with the experimental cage. These passageways were occluded by curtains to prevent visual contact to non-tested group members or members of the other family group. Several guillotine doors in the passageways enabled the experimenter to separate particular animals from the rest of the group.

Set-up Experiment 1

The experimental cage was divided into two compartments (Fig. 1): the experimental chamber (70 x 40 x 110cm) and the video compartment (74 x 40 x 110cm). The experimental chamber (70 x 40 x 110 cm) had one entry (for both of the participating individuals, the demonstrator and the observer), accessible via a guillotine door. Food was provided inside the experimental chamber by a small food container (20 cm above the ground) with a wooden platform fixed 5 cm beneath it, which enabled the animals to sit right in front of the container. The food patch was mounted on the wire mesh separating the two compartments. The food container could be baited from the video compartment and a sliding door in front of the food container controlled access to the baited container during individual trials. Two video cameras were positioned at two different locations, i.e. one camera was mounted on a tripod inside the video compartment and one was mounted on the ceiling inside the experimental chamber.

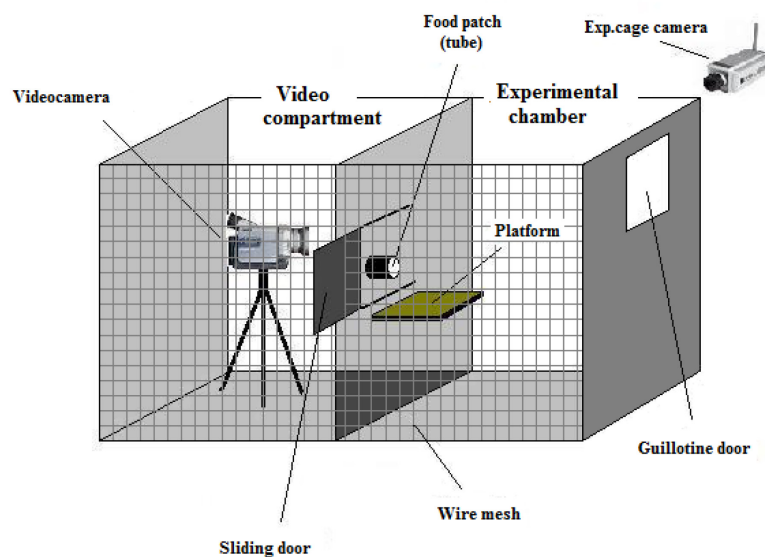


Figure 1: Experimental cage 1 was divided into two compartments: the experimental chamber and the video compartment.

Set-up Experiment 2

Other than in experiment 1 the experimental cage was not divided into two compartments and there were two distinguishable food patches (cut-out areas in the wire mesh) at the front of the experimental cage (Fig. 2). Instead of food containers, the food was presented in syringes. A wooden platform (45 x 10cm) was located inside the cage below the food patches. The distance of 30cm between the two food patches was chosen to make sure that the animals had to change their entire body position to switch between both sides. Due to the different arrangement of the food patches (food presentation occurred from the front instead of a sidewise presentation as in experiment 1), all trials were recorded from the front (outside the experimental cage).

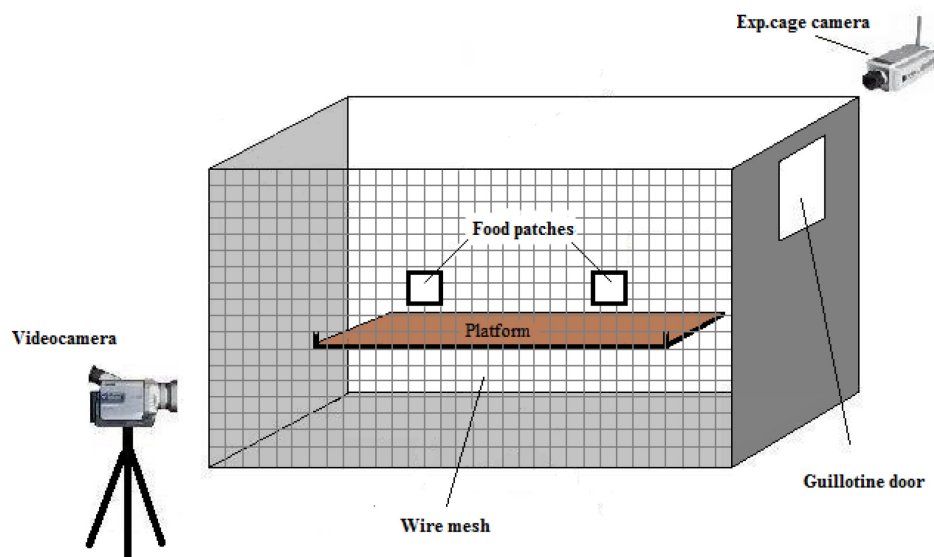


Figure 2: Experimental cage 2 had one unseparated compartment. Two cut-out holes in the front wire mesh served as distinguishable food patches.

Procedure

Prior to the actual experiments, additional information was collected from subjects inside the home cages about the social structure within groups and the type of food that would reliably elicit proper behavioural responses in demonstrators, which then served as social stimuli for the observer. Furthermore, all subjects were habituated to the experimental set-up before testing started.

Assessment of social status and hierarchy inside family groups

Focal samples. In order to clarify the impact of the social rank of both subjects in a dyad on the behaviour of observer, focal samples (Altmann, 1974) were conducted for each group prior to the experiments. During these, each individual was observed twice for 10 minutes in three different situations, i.e. before, during and after feeding. Consequently, each individual was observed for 60 minutes. The recorded behaviour was categorized into three different classes: avoidance (e.g. leave, flee, lean/jump aside), affiliative (e.g. grooming, sitting/resting contact, food sharing) and agonistic (e.g. chasing, fighting). Agonistic and avoidance behavioural variables were then combined to assess a dominance hierarchy in both family groups. Affiliative behavioural variables were used to assess affiliative social relationships. Non-social actions were excluded from analysis.

Monopolization tests. This test served to control for any shifts in rank among family members over the testing period. In both groups, two sessions were conducted after the experiments, one session was defined as 1 to 5 consecutive trials in one day. Hence, also less dominant individuals had the chance to monopolize the food patch (over the least dominant individuals), after highest-ranked individuals lost interest in the provided food and left the food source. As a food, yoghurt was chosen to prevent subjects from taking food pieces and leaving the food patch. It was provided in a bowl (7.5 cm diameter) from which only one subject per time could feed upon. As a measure of dominance, the duration of eating times per individual was recorded. A trial was terminated as soon as the food patch was completely depleted and the animals lost interest in it, the amount of trials during a session was dependant on the interest of the least dominant individual. Each session was video recorded.

Individual habituation training

All individuals were habituated to the experimental chamber. Each subject was given access to the experimental chamber individually until no stress behaviour like excessive scent marking, agitated locomotion or vigilance was observed anymore and the subject instead showed comfort behaviour like autogrooming or contact calling. Additionally, the individuals were trained to pick up food pieces or lick out liquid food out of the food container respectively. Each individual had to accomplish ten training trials to ensure a proper routine using the food container. During these training trials, the reward was always palatable. The sliding door was closed after each training trial to ensure that the animals would understand the closed door as the termi-

nation of a trial in the following test trials. For experiment 2, two syringes were introduced instead of food containers. The animals were then trained to lick drops of yoghurt from the tips of the syringes. Each individual was trained until it showed a proper routine using the syringes, i.e. taking only a few seconds after entering the experimental chamber to lick from both syringes.

Pretesting of reaction towards unpalatable food

Although no particular demonstrator training was necessary, I had to identify food items that would reliably elicit behavioural responses of disgust (e.g. facial expressions like tongue flicking, head shaking, spitting, or other reactions like vocalizations or withdrawal from the food source) in the subjects prior to the experiments. Furthermore, these food items should not be distinguishable by olfactory or visual cues but by taste only to prevent observers from acquiring information about food quality from any other cue than the behaviour of the demonstrator. The unpleasant taste sensation had to be strong enough to trigger behavioural reaction of disgust but it should not lead to a complete avoidance of this certain type of food. This requirement had to be met because initially introduced food remained the same throughout the entire experiment to ensure comparability of behavioural responses across subjects and within subjects across time.

To determine the appropriate type of food, the individuals were initially confronted with pieces of untreated banana or bun and pieces that were treated with bitter, non-toxic additives (“Beiß-ex” or extract of gentian). These additives had been reported to make food unpalatable without changing odour or visual appearance of treated food (Brüning, 2006; Schlöderitzko, 2007). In this pre-testing only one individual at a time was confronted with one palatable and one unpalatable piece of food, presented 8cm apart from each other on the wooden platform inside the experimental cage. The side of palatable and unpalatable food was counterbalanced across trials. The choices were supposed to occur by chance, since the individuals should not be able to tell a difference by odour or appearance.

Due to a high variability in disgust responses across individuals (ranging from no reaction at all to reactions elicited only by smell), several other substances were tested (lemon juice, white pepper and salt) to find one manipulated food type that would elicit similar responses in all subjects. This led to the selection of fruit yoghurt (which was familiar to all participating animals) that was made unpalatable with white pepper in experiment 1. For group 2, yoghurt confounded with salt was sufficient to elicit a clearly visible disgust reaction in all individuals. Both adulterating additives (white pepper and salt) are known to not add any visual or olfactory cues to original food items (Snowdon & Boe, 2003; Prescott et al. 2005).

Experimental procedure

Each subject participated in all possible dyads within its family group (e.g. 8 individuals in group 1 resulted in 28 possible dyads for each individual). Each individual participated at least in one session per day (depending on motivational states), three days a week. Each individual was supposed to act as demonstrator as well as observer in a ratio of 50:50 in a given dyad. Both individuals of a dyad entered the experimental chamber simultaneously and the first subject reaching the food patch and starting to consume the reward (respectively the reward made unpalatable) acted as the demonstrator for this trial. The individuals were able to move freely around in the experimental chamber, thus allowing for close physical contact and the possibility to scrounge. Only trials in which the observer clearly watched the demonstrator eating or reacting to the reward, i.e. when the observer turned its body or head towards the demonstrator and thus potentially perceived social information entered further analysis relating to socially acquired information. A trial was finished as soon as the observing individual either approached and consumed food or inhibited approaching the food patch (experiment 1) or chose one of the two food patches (experiment 2). In experiment 1, inhibition was defined as staying away from the food patch for 40 seconds. The intensity of the demonstrator's reaction was rated, ranging from -3 (very strong disgust reaction, e.g. spitting, shaking) to +3 (very positive reaction, e.g. food calls, in case of palatable rewards), assigning 0 to the absence of any reaction. The latency of observers' reactions was recorded. Trials that lasted longer than 90 seconds without food consumption due to lack of interest of either animal or trials in which strong agonistic interactions occurred between the individuals were terminated.

Experiment 1: Inhibition of foraging due to socially transmitted information about food quality (Go – no go task)

In this experiment, only one food patch was available, randomly baited with palatable or unpalatable food. The food container was either baited with two drops of pure yoghurt (palatable food, provided in motivation trials) or with yoghurt treated with white pepper (unpalatable food, provided in test trials) from the video compartment behind a visual barrier to prevent knowledge about the food's quality in each trial. Each session comprised 6 trials. To maintain motivation and to ensure that demonstrators could not predict food quality by any pattern in the order of food provision, one test trial (defined by the provision of unpalatable food) was inserted randomly between trial 2 and 5, i.e. the test trials were embedded in motivation trials at a ratio of 5:1. In

cases in which the demonstrator consumed all of the reward, the container was refilled, after the demonstrator had left the food patch. A test trial was defined as successful when the observer clearly watched the demonstrator's reaction and subsequently inhibited the consumption of the unpalatable reward until the end of the trial. Inhibition was defined as focusing on the food patch without consuming the unpalatable food, after the demonstrator had left the food patch, for at least 40 seconds. Altogether, each individual had to accomplish 10-15 test trials as an observer, defined according to that it was not the first at the food patch.

Experiment 2: Avoidance of unpalatable food according to socially acquired information about food quality (Two choice task)

In contrast to experiment 1, two food patches were available to enable the observer to choose an alternative food patch instead of inhibiting the impulse of approaching the unpalatable food after the demonstrator's disgust reaction (as in experiment 1). The two food patches were equipped with syringes containing palatable respectively unpalatable yoghurt. Again, the baiting occurred visually concealed from the animals and the side at which palatable and unpalatable food was provided randomly changed across trials, leaving both individuals naïve about the position of the palatable food. Every trial counted as a test trial, since in every trial there was the possibility to avoid the unpalatable reward by using the demonstrator as a cue.

After every trial the syringes were refilled to avoid visual cuing by different amounts of yoghurt inside. To ensure that none of the two participating individuals sat right in front of the syringes at the beginning of a trial, the animals were enticed to the top of the experimental cage by small pieces of bread, grapes or banana between the trials. The experimenter's eyes were covered by sunglasses, so the animals could not follow the experimenter's unintended gaze to a certain side.

One session consisted of 5 trials on average. However, the different motivational states of the individuals and dyads caused a broader variety of trials per session (1-7). Altogether, the observers accomplished between 25 and 35 trials within one particular dyad. The focal samplings, the monopolization test, the pre-testing of unpalatable food and both experiments were conducted from February 2009 to September 2010, between 10:00 a.m. to 1:30 p.m., before all subjects were fed to ensure motivation during the trials.

Data analysis

Both experiments as well as the monopolisation test were filmed with a digital camera (Sony DCR-TRV 25E and DCR-PC5) and a fixed live laboratory camera inside the experimental cage. Previous to each trial the quality and the position of unpalatable food (left or right syringe in experiment 2) were recorded. Other recorded parameters were the social hierarchy in a given dyad, the social interactions between the acting individuals (aggressive or affiliative behaviours) and vocalisations of either individual. The videos were coded regarding the demonstrator's latency to approach the food patch and start consuming the food, the demonstrator's side choice in experiment 2, the observer's position and state of attention towards the demonstrator, the demonstrator's reaction to the consumed food (ranging from -3 to +3), the observer's final choice, including its reaction to the provided food, and the duration of the trial.

To assess the social ranks inside the family groups, the data collected during focal samples were analysed via sociometric matrices used for the analysis of the dominance hierarchy, using the program MatMan (De Vries et al., 1993). From these winner-loser matrices, the sociometric parameters h (Landau's linearity index), h' (linearity index corrected for unknown relationships), K (Kendall's coefficient of linearity) were calculated, using the option "linear hierarchy" of the MatMan software. These sociometric parameters evaluate the degree of linearity of the social ranks in a group. In a hypothetical group with perfect linearity, the α -individual is dominant over all other individuals of this group; the β -individual dominates all other individuals except the α -individual and so forth. At the lower end of the hierarchy, the least dominant individual is found, which is dominated by all other individuals of this group (rule of transitivity). Kendall's coefficient of linearity refers to the number of circular triads in a group, i.e. α dominates over β , β dominates over γ and γ dominates over α . Each of the above-mentioned indices varies from 0 (absence of linearity) to 1 (perfect linearity). Values of h or $h' \geq 0,9$ are generally indicating a strong linear hierarchy (Lehner, 2007).

Additionally, the percentages of unknown, one-way, two-way and tied relationships were calculated. The directional consistency index (DCI) describes the frequency of a behavioural type (e.g. dominance behaviour) for a given dyad in its main (more frequent) direction relative to the total number of times it occurred (Van Hoof & Wensing, 1987). This index also varies from 0 (equal occurrence of behaviour) to 1 (asymmetric occurrence of behaviour).

In the monopolisation test, only the first minute of each trial was included in the final statistical analysis, in order to ensure comparable data. At that point, the food source was depleted

in most cases. In cases where two or more trials were conducted in one day, percentage rates of eating times per individual were weighted accordingly to include the fact that the dominant individuals, who were fed up eventually after the first two or three trials, had no more interest in monopolizing the food source.

The observers' latencies in motivation and test trials (experiment 1) were tested for normal distribution by use of a Kolmogorov-Smirnov test. To compare the latencies of motivation and test trials a paired T-test was conducted. The overall success rate in both experiments, the individual success rates, the extend of use of social information, demonstrators' side preferences, the quality of the demonstrators' first choices and the dependency of observers' success rates on demonstrators' first choices were analysed using a binomial test. To compare the success rates between the two setups (experiment 1 and 2) a Pearson's Chi-squared test was conducted. The overall group analysis of learning over time (experient 2) was analysed using a Wilcoxon matched paris test. Corellations between social ranks and success rates and between the observer's strategies and success rates were analysed using Spearman's rank correlation coefficient.

All statistical analysis was performed with SPSS 19 for Windows and MatMan (Noldus Information Technology). All diagrams were created using SPSS with the exception of the sociograms, which were created with the software "Sociogram (v. 1.0)".

RESULTS

Habituation and pretesting

Individual habituation training

All individuals fulfilled the requirement of establishing a proper routine in licking the food out of the food container (experiment 1) and from the tips of the two syringes (experiment 2) in the predetermined ten trials. In experiment 2, none of the subjects showed a side preference for one of the syringes during habituation training (Binomial test: all $p > 0.38$).

Pretesting of reaction towards unpalatable food

The choices between palatable fruit yoghurt and fruit yoghurt adulterated with white pepper (experiment 1) or salt (experiment 2) occurred by chance in all individuals (Binomial test: all $p > 0.05$), which indicates that the subjects were not able to distinguish palatable from unpalatable yoghurt merely by odour or appearance.

Social status and relationships

Analysis of dominance

A total of 900 minutes were recorded during focal samples, i.e. 60 minutes samples of each individual in three different conditions: before, during and after feeding. Altogether, a total of 736 interactions were analysed (group 1: 406; group 2: 330), including dominant respectively submissive behaviours (20,3 %), affiliative behaviours, e.g. grooming, close physical contact (50,8 %) and tolerance behaviour at the food source (28,9 %).

Table 2 shows interactions showing behaviours reflecting dominance, i.e. agonistic and avoiding behaviours were used to assess the linearity of the hierarchy in the family groups.

Table 2: Sociometric indices of group 1 (n=8) and group 2 (n=7) in three different conditions.

Group 1	Before feeding	At feeding	After feeding	Total
Number of dyads	28	28	28	28
Agonistic interactions (AI)*	35	83	12	130
Landau's linearity index (h)	0,143	0,786	0,143	0,786
Landau's index, corrected (h')	0,345 (n.s.)	0,821 (p < 0,005)	0,405 (n.s.)	0,810 (p=0,0066)
Kendall's index (K)	0,1	0,775	0,1	0,775
DCI	0,886	0,880	1	0,754
Unknown relationships (%)	60,71	10,71	78,57	7,14
One-way relationships (%)	32,14	75,0	21,43	67,86
Two-way relationships (%)	7,14	14,29	0,0	25
Tied relationships (%)	3,57	3,57	0,0	7,14
Group 2	Before feeding	At feeding	After feeding	Total
Number of dyads	21	21	21	21
Agonistic interactions (AI)*	22	49	12	83
Landau's linearity index (h)	0,321	0,464	0,214	0,732
Landau's index, corrected (h')	0,482 (n.s.)	0,536 (n.s.)	0,446 (n.s.)	0,786 (p < 0,05)
Kendall's index (K)	0,321	0,464	0,214	0,732
DCI	0,818	0,714	0,833	0,663
Unknown relationships (%)	42,86	19,05	61,90	14,29
One-way relationships (%)	47,62	57,14	33,33	47,62
Two-way relationships (%)	9,52	23,81	4,76	38,10
Tied relationships (%)	9,52	19,05	0,00	9,52

*Dominance related interactions

This test revealed in both groups a linear hierarchy with a clear structure of dominances (group 1: $h' = 0,81$; $p = 0,007$; group 2: $h' = 0,786$; $p < 0,05$), when all conditions were included, however showing that in the conditions before and after feeding no significant dominance hierarchy was established. The high directional consistency index (group 1: $DCI = 0,754$; group 2: $DCI = 0,663$) indicates an asymmetric occurrence of dominance behaviours, i.e. low ranking individuals rarely showing agonistic behaviours towards higher ranking individuals. For further analysis, the preliminary matrices were reordered to fit the linear hierarchy, using the option "Reorder matrix". In this step, the total strength and the number of inconsistencies was minimized (De Vries, 1998). The result was a rank order that best fit the linear model. The final rank order was calculated from the total dataset, including all three feeding conditions (Table 3).

Table 3: Final rank order based on animal focal samples for (a) group 1 and (b) group 2. The higher the number on the x-axis (“wins” of dominance related interactions), the higher the social rank.

(a)	JA	SP	OL	VE	MI	NE	KI	ZA	Total
JA	*	1	1	<u>1</u>	0	2	7	4	16
SP	0	*	0	2	2	17	5	3	29
OL	0	0	*	3	2	6	4	3	18
VE	<u>2</u>	0	0	*	2	2	4	5	15
MI	0	0	2	1	*	10	5	3	21
NE	0	0	0	1	1	*	8	2	12
KI	0	0	0	0	0	0	*	9	9
ZA	1	0	0	0	0	0	9	*	10
Total	3	1	3	8	7	37	42	29	130

(b)	PO	YA	PA	AU	FI	LO	ME	Total
PO	*	0	4	3	2	2	2	13
YA	0	*	4	0	2	5	2	13
PA	1	1	*	5	3	6	2	18
AU	3	0	0	*	0	12	3	18
FI	0	0	0	0	*	5	3	8
LO	1	0	0	0	0	*	4	5
ME	0	1	0	2	3	2	*	8
Total	5	2	8	10	10	32	16	83

According to the focal samples, the rank order of group 1 showed a clear dominance hierarchy with only two individuals (OL and JA) holding equal ranks. In group 2, only FI and AU held equal ranks. This rank order reflected the social hierarchy before the experiments.

To assess if there was a shift of dominance over the testing period, a monopolization test was conducted after the experiments for both groups. In group 1, MI changed from intermediate rank to the most dominant individual, KI and ZA (the breeding pair of the family) were ranked after but stayed in the highest ranking section. NE, who was ranked as second highest individual dropped to the far end of the hierarchy, equalling with JA and SP, who did not change their lowest ranking positions. VE changed from intermediate rank to low rank and OL from low rank (ranked equal to JA before the testing period) to intermediate rank. In group 2, LO, who held the highest rank before the testing period, made a shift to intermediate rank, as well as AU, who equalled the position with FI. ME and FI stayed at the top ranks, PA and YA at the lowest ranks, whereas PO made a shift from the second lowest rank to the third highest rank in the whole group (Table 4).

Table 4: Rank order before (a) and after (b) the experimental period of group 1 and group 2.

Group 1	(a)	Rank	1	2	3	4	5	6,5	6,5	8
		Individual	KI	NE	ZA	VE	MI	OL	JA	SP
	(b)	Rank	1	2,5	2,5	4	5	7	7	7
		Individual	MI	KI	ZA	OL	VE	NE	JA	SP
Group 2	(a)	Rank	1	2	3,5	3,5	5	6	7	
		Individual	LO	ME	FI	AU	PA	PO	YA	
	(b)	Rank	1	2	3	4	5	6	7	
		Individual	ME	FI	PO	LO	AU	PA	YA	

Analysis of affiliative relationships

For the analysis of affiliative relationships between the members of the two family groups, affiliative interactions (grooming, close physical contact, active or passive food sharing and support in aggressive encounters) were evaluated for group 1 and group 2 (Table 5).

Table 5: Matrices showing affiliative interactions of animals of group 1 (left) and group 2 (right).

Actor Receiver	KI	ZA	VE	MI	NE	OL	JA	SP	Total
KI	*	25	2	2	13	2	0	3	47
ZA	16	*	3	2	12	5	0	3	41
VE	2	0	*	6	3	5	5	2	23
MI	1	3	2	*	4	1	4	4	19
NE	8	4	15	4	*	13	0	0	44
OL	1	0	8	4	3	*	3	6	25
JA	1	0	4	2	0	0	*	5	12
SP	4	3	1	3	0	2	2	*	15
Total	33	35	35	23	35	28	14	23	226

Actor Receiver	PO	AU	FI	PA	YA	LO	ME	Total
PO	*	8	1	0	4	2	1	16
AU	8	*	7	5	10	9	10	49
FI	2	0	*	5	4	9	7	27
PA	0	0	4	*	3	2	6	15
YA	3	3	5	3	*	12	1	27
LO	0	3	2	1	0	*	0	6
ME	0	1	0	0	4	3	*	8
Total	13	15	19	14	25	37	25	148

In group 1, a total of 226 affiliative behaviours were observed. The strongest affiliative relationship was found between the breeding pair (KI towards ZA: 16, ZA towards KI: 25 socio-positive actions). Overall, KI received most affiliative behavioural actions (20,8 % of all events), followed by NE (19,5 %) and ZA (18,1%). No affiliative interactions were observed between NE and SP as well as NE and JA. In group 2, a total of 148 affiliative behaviours were observed. The strongest reciprocal affiliative relationship was again found between the breeding pair (AU and PO: 8 socio-positive actions in both directions), however not as pronounced as in group 1. The breeding female received most affiliative behaviours (AU: 33,1 %), the breeding male, however, was at intermediate range (PO: 10,8 %). The highest ranking individuals received the few-

est affiliative behaviours (LO: 4,1 %, ME: 5,4 %). No affiliative interactions were observed between PO and ME as well as between PO and PA (Figure 3).

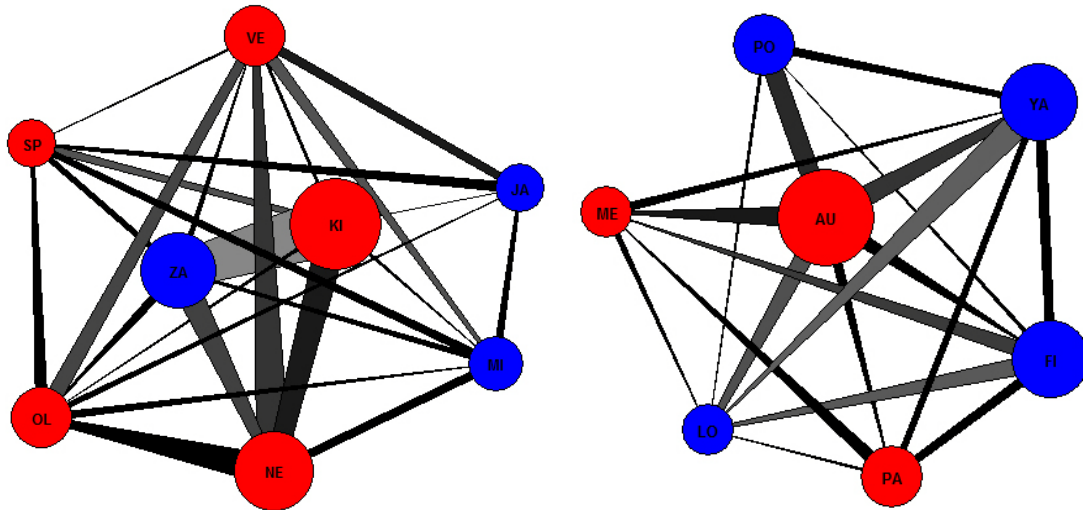


Figure 3: Sociogram of group 1 (left) and group 2 (right), visualising affiliative relationships between all group members. The strength of the lines represents the frequency and direction of affiliative interactions. The size of the circles surrounding the names of the individuals represents the total number of affiliative behaviours towards this individual.

Experiment 1

Due to the exceedingly frequent occurrence of aggressive behaviours between certain dyads and the lack of motivation in some of the individuals, I had to terminate experiment 1 before the scheduled number of test trials (10-15 per dyad) was achieved. In 33,8 % of all sessions I had to interrupt prior to the test trial, equally due to serious fights (16,2 %) and lack of motivation (17,7 %). Highly aggressive behaviour was observed from MI towards OL and from OL towards KI (66,7 % respectively 37,5 % of all trials had to be terminated). The dyads NE+SP and NE+JA could not be conducted due to serious fights in the beginning and subsequent fear behaviour in both low ranking individuals (JA and SP).

Explicitly tolerant dyads were rather scarce, however, dyads involving KI (dominant female) were significantly tolerant with the only exception of the combination with OL (Binomial test: $p < 0,0003$). Other tolerant dyads were MI+JA, VE+NE and VE+SP (all, > 80 % overall tolerant trials). However, scrounging only occurred in 21,2 % of all sessions and again mainly concerning dyads involving KI (66,7 % of all scrounging events, n.s.).

Overall, none of the 8 animals of group 1 (acting as observers) significantly inhibited foraging during test trials after watching the demonstrator's disgust reaction (Binomial test: all, $p >$

0,64). Pooling the results of all subjects, only in 18,5 % of the test trials the observer was able to avoid the unpalatable food, i.e. to inhibit food ingestion after the demonstrator had left the food patch for at least 40 seconds (this threshold was chosen according to the mean latency of 27,9 seconds during motivation trials). Positive test trials were evenly distributed over the testing period, excluding the occurrence of a learning effect over time.

Closer examination of the observers' latencies to consume food after the demonstrator had consumed and reacted towards palatable or unpalatable food during test trials compared to motivation trials revealed that there was no significant difference between latencies: paired T-test: $t(75) = 0,368$, $p = 0,714$). For the calculation, only the motivation trials right before the accordant test trials in the same session were used. Pooling latencies from all subjects of group 1, mean values were almost identical in motivation and test trials ($N = 76$; motivation trials: $MV = 27,97$; test trials: $MV = 27,04$). Figure 4 shows the latencies of motivation and test trials for each subject of group 1.

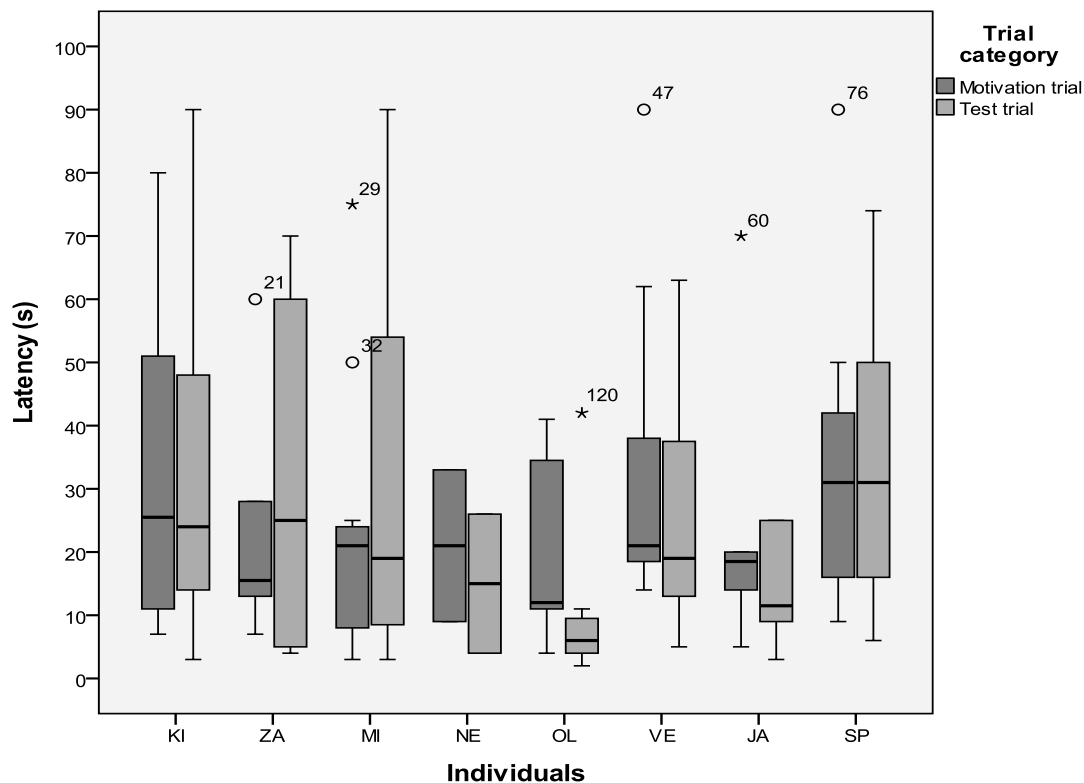


Figure 4: Observer latencies of group 1 to consume food after the demonstrator's reaction to palatable (motivation trials) or unpalatable (test trials) food.

To analyze what might have impaired the animal's learning abilities (apart from the above mentioned lack of tolerance between subjects) in experiment 1, I investigated first, whether the observers generally met the prerequisite of being attentive towards the demonstra-

tors, i.e. how often observers watched the demonstrator's reaction towards palatable or unpalatable food in order that social information could potentially be extracted. In 77,5 % of all trials (motivation trials and test trials taken together) the observer focused its attention towards the demonstrator tasting the food (Binomial test: $N = 547$, $p < 0,0001$). Furthermore, I analysed if the observer adapted its reaction according to the demonstrator's reaction towards the presented food. Examining motivation trials (trials in which the observer did not watch the demonstrator were excluded as well as trials with highly aggressive behaviour), the observers coordinated their behaviour with the demonstrator's behaviour, i.e. if the demonstrator ingested palatable food, the observer subsequently also consumed the reward in 79,4 % of all motivation trials (Binomial test: $N = 373$, $p < 0,001$). However, in test trials (again only trials with the precondition of watching the demonstrator were included), only in 16,7 % of all trials the observer behaved accordingly to the demonstrator's disgust reaction, i.e. inhibited the consummation of the unpalatable food (Binomial test: $N = 77$, $p > 0,05$).

Due to the low success rate on individual basis (best performance by ZA: $n = 8$, $p = 0,637$, all others: $p > 0,8$), the intended correlation between successful trials and social status could not be calculated, concerning both, dominance and affiliative relationships. However, in 41,2 % of all successful trials, KI, who was the dominant female before and after the experimental period and had the highest proportion of affiliative interactions in group 1 (17,7 % of all observed affiliative interactions), was involved.

Food calls after the consummation of palatable food were elicited only in 6 cases ($N = 451$, $p > 0,05$), mainly by the dominant female (KI: 66,7% of all calls). No alarm calls after the consummation of unpalatable food were observed.

Experiment 2

Due to insuperable social incompatibilities, one individual (PA) had to be excluded from experiment 2. Moreover, two of the 15 planned dyads were not accomplishable (ME with PO and ME with YA) due to highly aggressive behaviour in these dyads as soon as food was presented in the experimental cage. In the remaining 13 dyads, the observers accomplished between 25 and 35 test trials, with the exception of AU, who stopped acting as observer after 12 trials with LO and 20 trials with YA (Table 6).

Table 6: Number of test trials used for the final analysis in experiment 2. Bolt numbers indicate a minor number of trials in this dyad.

Observer ↓	PO	AU	ME	LO	FI	YA
PO	*	25	<i>no data</i>	26	28	27
AU	35	*	26	12	25	20
ME	<i>no data</i>	30	*	25	28	<i>no data</i>
LO	35	27	27	*	26	25
FI	35	29	27	35	*	35
YA	35	28	<i>no data</i>	27	25	*

This quite broad range of test trials was chosen because of the precondition that observers clearly watched the demonstrator's choice and reaction towards palatable or unpalatable food. Further exclusion was applied to trials in which both individuals approached the food patches simultaneously and trials in which subjects acted as observer when they already met the maximum of 35 trials. The precondition of the use of social information, i.e. that the observer was attentive towards the demonstrator and watched the reaction towards palatable or unpalatable food, was met in 88% of all cases (Binomial test: $N = 890$, $p < 0,001$, $SD = 4,86$).

Although the success rate of the animals of group 2 was significantly better in experiment 2 compared to the success rate of animals of group 1 in experiment 1 (Pearson Chi-squared test: $\chi^2 = (1, N = 816) = 38,23$, $p < 0,001$), overall success was still at chance level (Binomial test: $N = 720$, $p = 0,263$). Figure 5 shows the comparison between the two groups respectively the two experimental set-ups.

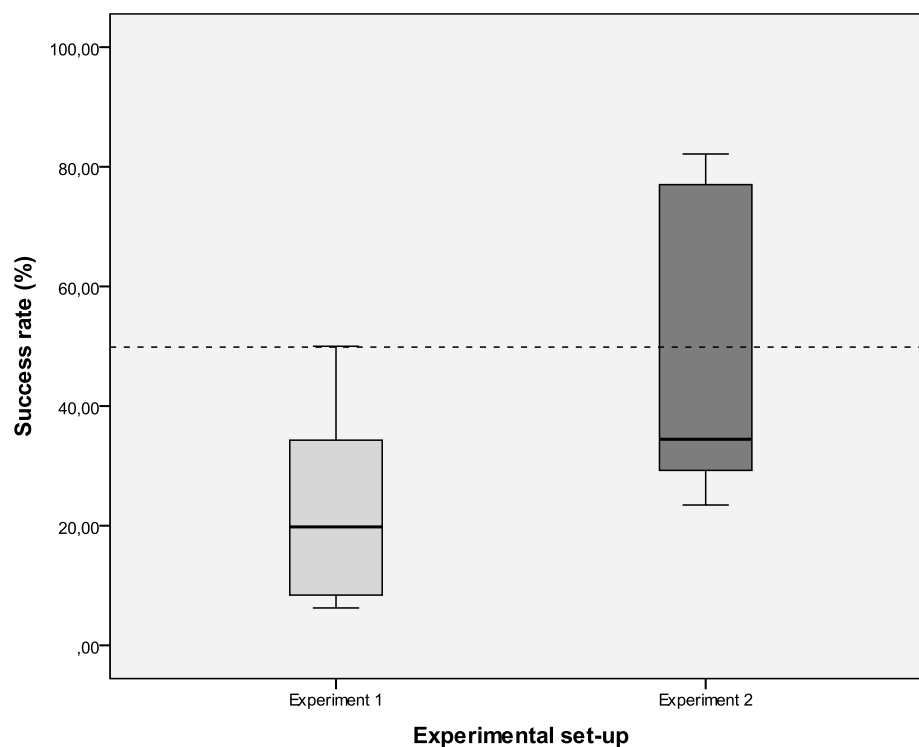


Figure 5: Comparison of overall success rate between group 1 (experiment 1) and group 2 (experiment 2).

However, two of six subjects were significantly successful when acting as observers in all possible dyads (Binomial test, LO: $N = 140$, $p < 0,001$; FI: $N = 161$, $p < 0,001$; Figure 6).

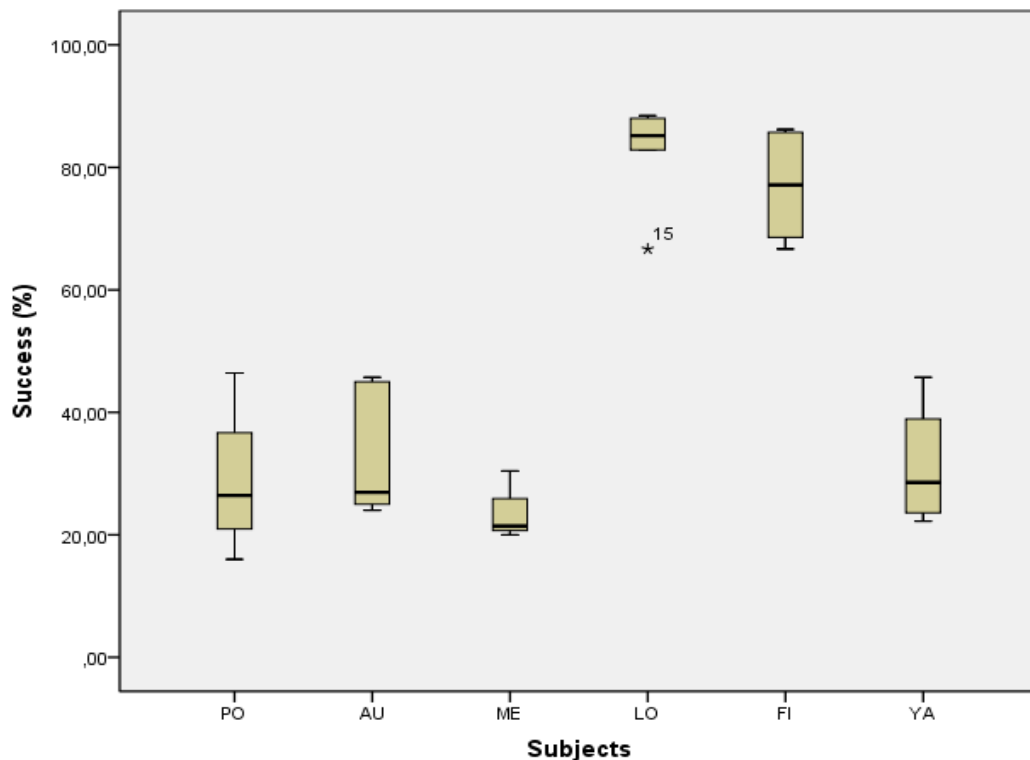


Figure 6: Box plots of all subjects of group 2, showing individual success rates as observers in diverse dyads. Two subjects were significantly successful (LO and FI, indicated by **) in their overall performance.

In both subjects, the only dyad in which the success rate remained at chance level was the dyad involving ME as demonstrator (LO+ME: $N = 27$, $p = 0,06$; FI+ME: $N = 27$, $p = 0,06$). Figure 7 shows the success rates of LO and FI in all conducted dyads.

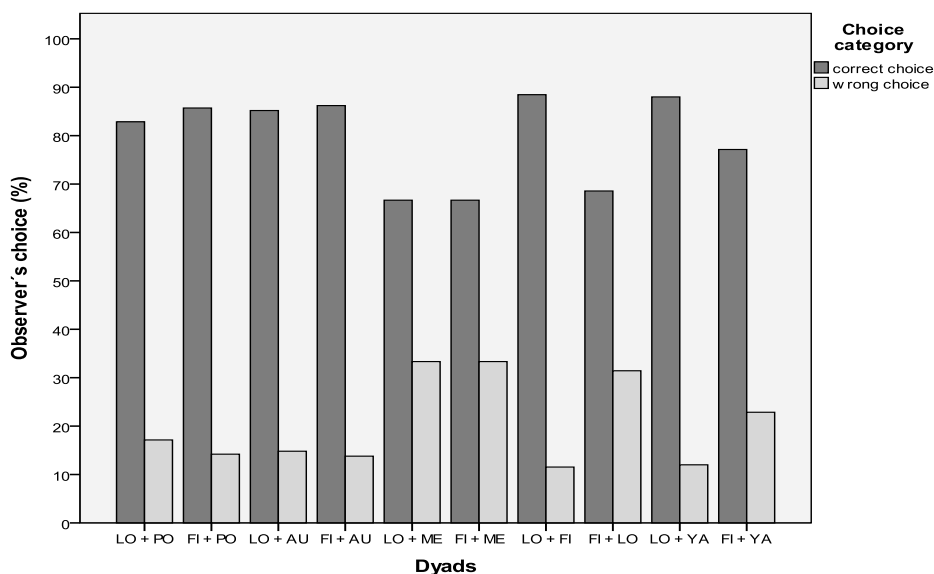


Figure 7: Observer's choices of LO and FI in all available dyads.

In order to unravel what might have impaired the overall success of the entire group or otherwise enhanced learning in the two significantly successful subjects, additional analyses were conducted, concerning the demonstrator's influence on the observer's choice due to

- i. side preference and demonstrator's first choice of correct or wrong syringe
- ii. the impact of the rank order and socio-positive relationships on success rates
- iii. differences in learning over time between successful and non-successful subjects
- iv. the observer's different strategies of choice after the demonstrator's reaction:
 - join and scrounge or wait until the demonstrator has left the food patch in case the demonstrator initially chooses the correct syringe (palatable food)
 - wait until the demonstrator has found the correct syringe and subsequently join and scrounge or choose the alternative syringe right away in case the demonstrator initially chooses the wrong syringe (unpalatable food)

i. Demonstrator behaviour

Table 7: Demonstrator's side preference: R = right syringe, L = left syringe; p-value < 0,05 indicates a significant preference for one side.

	PO	AU	ME	LO	FI	YA
R	110	80	45	73	75	63
L	107	72	44	78	71	61
Σ Trials (N)	217	152	89	151	146	124
p-value	0,446	0,285	0,5	0,372	0,402	0,464

Table 7 shows that none of the subjects acting as demonstrators showed a significant side preference during the experimental period (Binomial test: all, $p > 0,285$). For this analysis also trials in which the observers did not fulfil the precondition of watching the demonstrator's reaction were included. There was no significant difference in the demonstrators' first choice, i.e. if the demonstrator in a given trial chose the correct (containing palatable food) or the wrong (containing unpalatable food) syringe at the first attempt (Binomial test: $N = 786$, $p > 0,05$). The order of which syringe was visited first (palatable or unpalatable food) by the demonstrator did not influence the success rate in the observers: 51 % of the trials in which the demonstrator chose the syringe containing palatable food at first resulted in the observer's correct choice (Binomial test: $N = 416$, $p = 0,365$).

ii. Dependency of success rates on social status

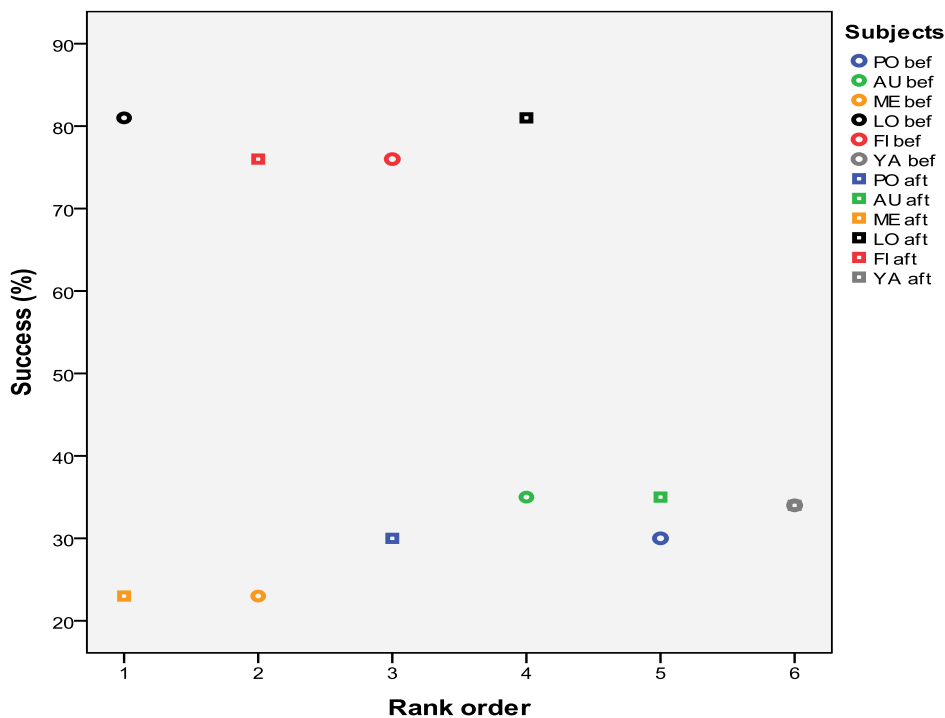


Figure 8: Scatter plot of the correlation between the rank order (1-6) and the success rates (%) of subjects in experiment 2. Circles indicate the rank positions before, squares indicate rank positions after the experimental period. One subject did not change its position over the experimental period (YA).

Figure 8 shows the scatter plot of the correlation between the rank order and the subjects' individual success rates in experiment 2. There was no significant correlation found, neither with the rank order before (Spearman-Rho, 2-tailed: $N = 6$, $r_s = .314$, $p = .554$) nor with the rank order after the experimental period (Spearman-Rho, 2-tailed: $N = 6$, $r_s = -.371$, $p = .468$).

The impact of socio-positive relationships on success rates was not analysed, because both successful subjects occupied intermediate affiliative ranks (LO: 43; FI: 46 socio-positive events in both directions), whereas AU and YA, whose success rates were below chance level, were involved in most affiliative interactions (AU: 64; YA 52 socio-positive events) and PO and ME, also ranging below chance level, had the lowest number of socio-positive events (PO: 29; ME: 33). Also the strong socio-positive relationship between AU and PO (breeding pair of group 2) did not result in success rates above chance level.

iii. Success rates over time

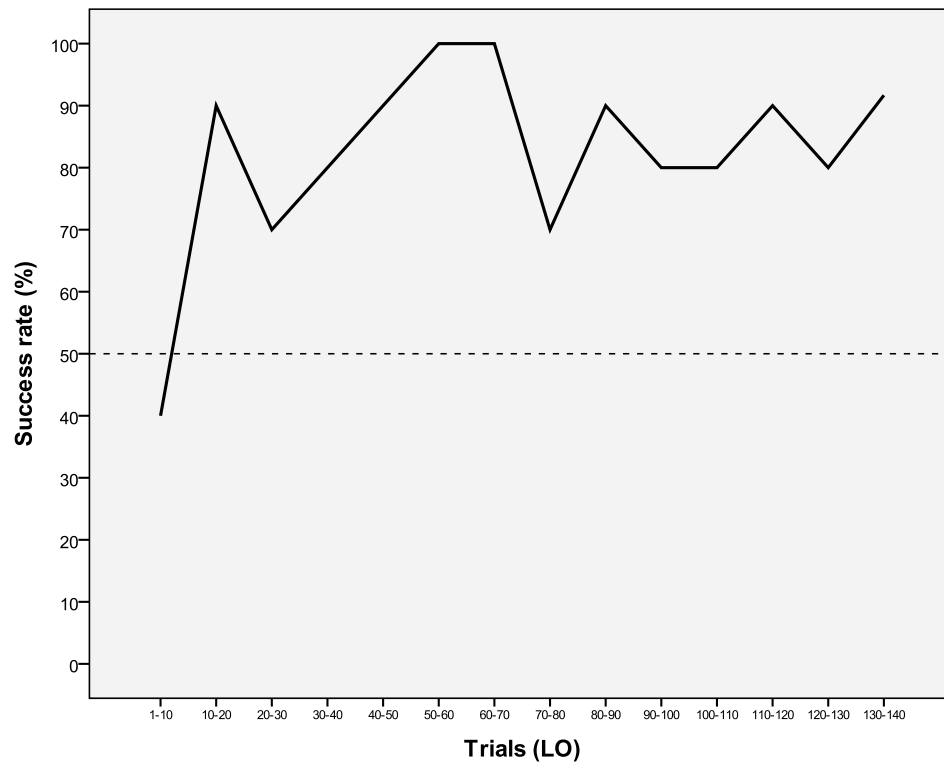
In order to assess if there was a learning effect over time, the individual success rate of the first ten trials was compared with the overall success rate and the success rate of the last ten trials for each individual (Table 8).

Table 8: The observer's success rate for all individuals of group 2. The first 10 trials are compared with the last 10 trials and with the overall success rate of each individual.

Individual	Total number of trials (N)	First 10 trials (%)	All trials (%)	Last 10 trials (%)
PO	106	40	29,2	16,7
AU	118	50	34,7	55,6
ME	81	30	23,5	27,3
LO	140	40	82,1	91,7
FI	161	50	77,0	90,0
YA	114	30	32,5	40,0

The overall analysis of the group showed no significant learning effect over time when comparing the first 10 trials with the last 10 trials (Wilcoxon matched pairs test: $N = 6$, $Z = -1,153$, $p = 0,249$). However, when analysing the learning effect of the two successful subjects (LO and FI) separately, there was a significant difference between the first 10 trials and the last 10 trials (Pearson Chi-squared test: $\chi^2 = (1, N = 40) = 9,231$, $p = 0,006$). All other individuals showed no learning effect over time and remained below or at maximum at chance level. In two individuals the success rate in the last 10 trials was even lower compared to the first 10 trials (PO: 40 % in first, 16,7 % in last 10 trials; ME: 30 % in first, 27,3 % in last 10 trials). The learning curves (success rates over trials) of two individuals are exemplarily shown in Figure 9.

(a)



(b)

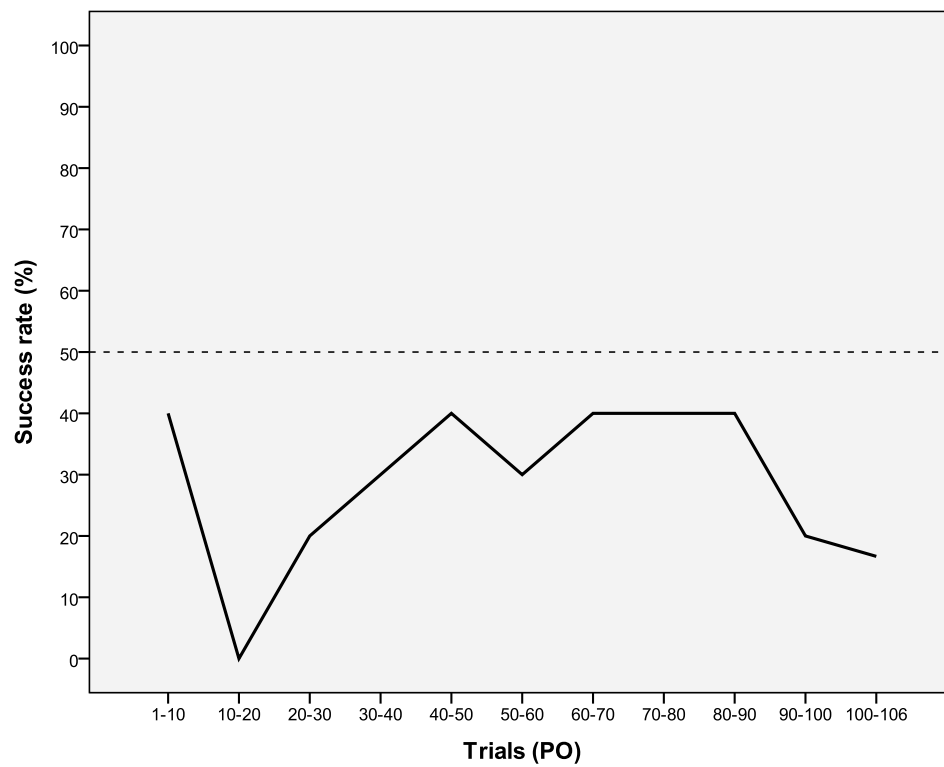


Figure 9: Learning curves of two individuals (a) LO and (b) PO, indicating success rates (%) over increasing trials. Success rates are plotted at intervals of every ten trials. The horizontal broken line indicates success at chance level.

The learning curve of LO (one of the significantly successful subjects) shows an acceleration of the success rate over time whereas the learning curve of PO shows no learning effect and stays below chance level for the entire experiment.

iv. Observer strategies

In experiment 2 the observer had different possibilities to react according to the demonstrator's behaviour: if the demonstrator chose the syringe containing unpalatable food and displayed disgust, the observer could either choose the alternative food patch right away or otherwise wait for the demonstrator to change to the syringe containing palatable food and then join and scrounge. In case the demonstrator chose the correct syringe at the first attempt, the observer could either immediately join and scrounge or wait until the syringe was empty and the demonstrator left the food patch. In this case the empty syringe was refilled with palatable food. Table 9 illustrates an overview of the individual strategies of subjects.

Table 9: Observers' strategies after watching the demonstrators' reactions, class-divided into successful and unsuccessful behaviours of each subject. Bolt numbers indicate significantly successful subjects (LO and FI).

	Successful trial			Unsuccessful trial			
Observer	Scrounge	Alternative correct	Wait + same correct	Alternative wrong	Wait + same wrong	Total number of trials	Success rate (%)
PO	4	24	3	72	3	106	29,25
AU	17	19	7	60	15	118	36,44
ME	1	16	2	52	10	81	23,46
LO	97	18	2	13	10	140	82,14
FI	108	14	2	29	8	161	77,02
YA	23	7	7	71	7	115	32,46
Total	250	98	23	297	53	721	

Overall, scrounging behaviour accounted for most successful trials (67,4 %). Unsuccessful trials were mainly based on the observer's choice of the alternative syringe when the demonstrator occupied the syringe containing palatable food (84,9 %). However, regarding successful trials, only the two significantly successful subjects (LO and FI) used the scrounging strategy above significance level (Binomial test: LO: $N = 241$, $p < 0,0001$; FI: $N = 124$, $p < 0,0001$). A correlation between success rate and scrounging rate proved significant (Spearman-Rho, 2-tailed:

$N = 6$, $r_s = 0,886$, $p = 0,019$), as well as a negative correlation between success rate and the observer's choice of the alternative (unpalatable) food patch (Spearman-Rho, 2-tailed: $N = 6$, $r_s = -0,829$, $p = 0,042$).

Food calls after the consummation of palatable food were elicited in 25 trials (PO: 52 %, YA: 24 %, AU: 16%, LO and ME: 4%) of which 19 trials resulted in successful observer choices. No alarm calls after the consummation of unpalatable food were observed.

DISCUSSION

The present study investigated if common marmosets adapt their behaviour in a social foraging task according to that of a conspecific and therefore are able to (a) inhibit ingestion of a preferred food (fruit yoghurt) after observing a demonstrator's disgust reaction towards this food made unpalatable in a randomly inserted test trial (experiment 1) and (b) use the demonstrator's reaction as a cue to avoid this unpalatable food when there is an alternative food patch available (experiment 2).

I expected that the experimental setup in this study, i.e. the close social contact between demonstrator and observer and the resulting possibility to scrounge, would enhance the observer's attention towards the demonstrator and therefore increase behavioural coordination and social learning (Coussi-Korbel & Fragaszy, 1995). Moreover, the quality of the relationships between the tested dyads was expected to influence the observers' success rates, i.e. that dominant observers would be more successful compared to subordinate observers due to their potential capacity to aggressively scrounge or aggressively displace the subordinate demonstrator from the palatable food source. Concerning pro-social behaviours, I expected that scrounging would occur more often in affiliative dyads, leading to increased success rates in these dyads. Finally, an improvement of the overall success rate was expected in experiment 2 compared to experiment 1 due to the simplification by introducing an alternative food patch and thereby increasing the animals' chance of being successful in each trial and superseding the need of total inhibition of the impulse to approach and ingest presented food in the test trials of experiment 1.

The basic assumption of this study, i.e. that in common marmosets, a species commonly regarded as highly tolerant, food sharing and scrounging occurs on a regular basis, proved incorrect in most of the tested dyads. Hence, the question of the animals' ability to intentionally control their scrounging behaviour when unpalatable food is introduced could not be answered in experiment 1, since in group 1 scrounging hardly occurred at all. One reason for the absence of scrounging could have been the high aggression rates between subjects of group 1. In order to investigate if there were changes in the social structure over the testing period that could have accounted for higher aggression during the experiments, monopolization tests were conducted after the experimental period in both family groups. However, even though in group 1 such a change in the social hierarchy was found, this alone could not have accounted for the higher aggression rates in experiment 1 compared to experiment 2, because in group 2 the changes in the social hierarchy were even more pronounced. Altogether, experiment 1 had to be terminated be-

fore the scheduled number of trials was achieved due to increasing incidents of serious fights between various subjects and an overall decline of motivation.

In experiment 2 scrounging occurred only slightly more frequently (34,7 %). However, scrounging was never observed in cases where the demonstrator ingested unpalatable food at the first try. In these cases, after watching the demonstrator's disgust reaction, the observer either waited until the demonstrator left the food patch and subsequently chose the same food patch containing unpalatable food (unsuccessful trial) or he chose the alternative food patch right away or waited until the demonstrator changed towards the food patch containing palatable food and then scrounged (both strategies counting as successful trials). Interestingly, in situations of successful trials scrounging occurred more often and therefore accounted for the most successful strategy used by observers.

Confirming the expectations, the results of the overall comparison between experiment 1 and experiment 2 revealed a significant higher success rate when introducing an alternative food patch. However, when examining the success rates of subjects in experiment 2 separately and on individual basis, only two of six animals performed significantly above chance level. The performance of the other four subjects remained below or at maximum at chance level. As mentioned above, the best strategy leading to success was found in scrounging – and scrounging was the successful concept applied by both of the overall successful subjects, independent of which food patch was chosen by the demonstrator beforehand. The examination of all employed strategies revealed that in most cases the observers chose the alternative food patch, however mostly in trials in which the demonstrator chose the food patch containing palatable food at first attempt. This leads to the assumption that the primarily adopted strategy was to avoid the occupied food patch. However, in trials in which the demonstrator chose the food patch containing unpalatable food at first attempt, the observers (except the two successful subjects) did not choose the alternative food patch equally often (which would lead to a successful trial) but rather waited until the demonstrator had left the food patch (after showing a disgust reaction) and chose the same incorrect food patch. Here it is important to mention that the demonstrator's first choices were balanced according to which food patch was visited first. An explanation could be that observers only then avoided the occupied food patch when the demonstrator stayed there for a prolonged time. This was usually the case when the demonstrator chose the correct (palatable) food patch at first, because he then continued eating until the syringe was empty. After a short latency of few seconds the observer could possibly not inhibit the impulse to approach the unoccupied food patch. In case of an incorrect first choice, the demonstrator left the food patch right away. According to this explanation the adopted mechanism of social learning was most likely local

enhancement, only omitted by the two overall successful subjects maintaining the scrounging strategy.

Following this up, the question arises which preconditions have to be met to allow scrounging or otherwise who scrounges from whom. Werdenich & Huber (2002) found in their experimental study on cooperation in common marmosets that only those dyads cooperated successfully in which the dominant individual took the role of the scrounger whereas the subordinate individual took the role of the producer. This result of a specific role distribution supports similar findings in capuchins (Visalberghi, 1990) and keas (Tebbich et al., 1996), in the latter species however established by the dominant individual monopolizing the food and aggressively forcing the subordinate into the producer role. In common marmosets this monopolization of food was not found, the reward was rather shared with the subordinate individual. Furthermore, the authors discovered that all adult male-male dyads cooperated successfully and additionally observed tensions between same-sexed twins.

When comparing these findings with the results of the present study, only partially comparable analogies can be found: firstly, the social rank did not correlate with the success rate, i.e. dominant individuals neither scrounged more often than subordinate individuals nor did they aggressively displace subordinates from the food patch containing palatable food when acting in the role of observers (scroungers). Although both successful subjects (LO and FI) occupied ranks in the upper half of the social hierarchy (taking together the results established before and after the experimental period), the overall most dominant subject (ME) was neither successful in any dyad nor found scrounging during the experiments (only 1 incident observed). Interestingly, there was also no overall correlation between affiliative relationships and scrounging found. Only KI, the dominant female and mother of group 1, was involved in most pro-social and affiliative interactions as well as in most scrounging incidents during the experimental phase. However, with her prominent role as being the mother of group 1, the impact of this coherence is rather low, given that in all other subjects of both groups no corresponding trend was observed.

When analysing differences in performance due to variation of sex combinations in dyads (male-male, female-female or male-female) no significant results were found supporting the findings by Werdenich & Huber. Although both successful subjects of group 2 (FI and LO) were significantly successful when acting as observers in all male-male dyads, the sex distribution of all participating subjects in experiment 2 did not provide an adequate proportion of females to express any statistical validity: one female (PA) had to be excluded from the experiment, both subjects (FI and LO) were equally successful with AU (the mother of group 2) and equally unsuccessful with ME (the dominant female of group 2), which rather indicates that the main prob-

lem causing negative performance in these two subjects was the absence of any cooperation by ME. This is also supported by the fact that the dyads ME + PO and ME + YA could not be tested due to aggressive behaviour by ME. The data were too limited to test if this absence of cooperation could be explained by different sexes. Concerning tensions between same-sexed twins no supporting evidence was found due to the absence of any same-sexed twins in the two participating family groups. Similarly, in group 1 no evidence was found for higher tolerance between male-male dyads. In contrast, most tolerant trials were observed in the breeding pair (KI + ZA) respectively in dyads between the mother and her offspring.

Examining the question of active influence of demonstrators on the observers' choice, the occurrence of food calls was recorded. In both experiments food associated calls after the consummation of palatable food were remarkably scarce. In group 1, most food calls were elicited by the KI (mother of the family), in group 2 by PO (father of the family). After the consummation of unpalatable food no alarm calls were observed in both experiments. This leads to the question if food calls are mainly relevant between parent and offspring or even most relevant between parents and juveniles or rather infants. In both tested groups juveniles or infants were absent during the experimental period. However, Brown et al. (2005) examined in their experimental study on common marmosets the quantity and quality of food transfer between parents to offspring (infants), focusing besides novel food items on unpalatable food items. Food transfer usually occurs combined with food calls, the refusal to transfer food is often combined with threatening vocalizations. The authors found that no differences in transfers were made by adult animals. Supporting results come from another study examining transfer of novel food items from adult to infant common marmosets (Voelkl et al, 2006), again showing no modified behaviour (including food calls) in adults in terms of enhancing the infant's learning about novel food. The authors suggested that the results of their study could have been due to the absence of any "teaching" behaviour in common marmosets, which contrasts to results in other callitrichids (e.g. cotton-top tamarins and golden lion tamarins) where changes in the adult's behaviour, including food associated calls and alarm calls, were found (Roush & Snowdon, 2001; Rapaport, 1999). Roush & Snowdon also revealed in their study on tamarins that in adults with offspring rates of food calls while eating were higher than in adults without offspring.

One explanation for this divergence could be the lack of first order intentionality in common marmosets. A hierarchy of intentional systems, i.e. levels of intentionality, was proposed by Dennett (1987): Zero-order intentional systems have no beliefs or desires at all but merely react to a given stimulus. First-order intentional systems have beliefs and desires but no beliefs about beliefs of others. Second and higher-order intentional systems have beliefs and de-

sires about beliefs and desires of other, i.e. they have beliefs about own and other's state of mind. Applying this concept on existing studies on common marmosets, this study included, the demonstrator's response towards food (either positive or negative) was a mere reaction towards a stimulus and potentially elicited calls were not meant to change the observer's behaviour, i.e. to invite to or warn from palatable or unpalatable food.

However, the fact of excluding the demonstrator's role as intentional signaller alone cannot account for the failure of the majority of subjects participating in the present study, since unintentionally cuing or leaving signs of use for conspecifics is widely spread in diverse animal species. In agoutis for example, the rasping sound made when eating nuts attracts conspecifics to feeding sites and Norway rats unintentionally create trails leading to food or water that are used by following conspecifics (for an overview see Galef & Giraldeau, 2001). Even though none of the marmosets emitted alarm calls after the ingestion of unpalatable food, other clearly visible disgust reactions were shown by all demonstrators. The precondition for a trial to be included into analysis was that the demonstrator after consuming unpalatable food at least left the food patch right away (-1) or otherwise displayed clear reactions as shaking the head (-2) and spitting or shaking the entire body (-3), whereas in most cases reactions between -2 and -3 were displayed. Interestingly, the intensity of the reaction was not reflected in the observer's choice, especially in experiment 1 there were repeated occasions where the observer sat right next to the demonstrator and closely watched a disgust reaction (-3) and still consumed the same unpalatable food as soon as the demonstrator left the food patch, without showing any delay.

To date, the only study showing evident results of social learning and communication about unpalatable foods in monkeys is presented on cotton-top tamarins (Snowdon & Boe, 2003). The authors suggested that the cooperative breeding system and high levels of tolerance between family members in tamarins accounted for the positive results. Common marmosets live in comparable family structures and should therefore be a promising species to achieve similar results. The fact that in the present study common marmosets overall failed to show equivalent abilities requests for closer comparison between the two applied study designs: First of all tamarins were tested in family groups with subadults and infants present, accounting for more than half of all participating animals. Secondly, the presented unpalatable and palatable foods were of two different kinds, i.e. canned tuna (adulterated with pepper) and canned peaches (unadulterated). Animals were presented once a week with each food type, for three consecutive weeks. Subsequently the animals were presented unadulterated tuna for additional three weeks. Only 14

of 44 subjects ever tasted the adulterated tuna and 13 subjects continued to avoid unadulterated tuna even after 15 weeks after the experimental period.

The question rises whether the listed differences in the experimental design could account for the contradicting results. As mentioned above, the presence of subadult and infant individuals could account for an increased occurrence of food associated calls and alarm calls in tamarins of which both were rare respectively absent in the present study. Furthermore, testing in family groups might also reduce diverse factors causing impairment which only emerge when testing in dyads (e.g. effects of dominance or affiliation between subjects). The most striking difference however was that the unpalatable food presented to tamarins remained unpalatable whereas the palatable food remained palatable and unpalatable and palatable foods were never presented simultaneously or even the same day. In the present study the animals had to adapt to a permanent change of palatability of the same food by relying on the demonstrator's reaction in each trial.

As a potential learning mechanism for the given experimental setup observational conditioning was presumed, implicating that the observer acquires an emotional response to a given stimulus (unpalatable or palatable food) from the demonstrator. Studies examining observational fear learning are well documented in various species as birds (Curio, 1988), cats (John et al., 1968) and primates (e.g. Mineka et al. 1984). In all of these studies, animals readily learned fears by observing a conspecific expressing fear behaviours towards a certain stimulus. In rhesus monkeys (*Macaca mulatta*), emotional reactions as facial expressions and vocalizations towards a snake were found reliable to elicit responses in the observer monkeys (Mineka & Cook, 1993). Even when accepting that fear responses towards a dangerous stimulus (e.g. a snake) and disgust reactions towards unpalatable (but not toxic) food are not quite the same threatening level to elicit comparable emotional expressions, it is worth enlightening what could have caused the marmosets impairment to use the demonstrator's disgust reactions and learn by observation in the present study, not least because facial expressions (besides vocalisations) were also described as cues probably used by tamarins.

The applied experimental setup without physical separation between demonstrator and observer provided the advantage to watch the demonstrator's reaction from the same perspective as well as the possibility to scrounge and additionally enhanced attention towards the demonstrator. The missing attention was one of the main problems in the experimental study by Schlödertzko (2007) and was largely eliminated in the present experimental setup. As mentioned above, a striking difference between the experimental designs of the present study compared to the study conducted by Snowdon & Boe (2003) was the presented palatable and unpalatable food as well as the sequence of food presentation. The present design required fast and continuing read-

justment towards an initially preferred food. This contrasts with most social studies involving unpalatable food and the avoidance of the same as well as studies examining social fear learning via conditioning. Even though it is possible to extinct conditioned responses, this generally takes prolonged learning, which was not given in the present setup where unpalatable food was presented in either one of six trials (experiment 1) or even in each trial (experiment 2). For that reason, observational conditioning might not be the adequate term to describe the underlying learning mechanism sought-after in this study but rather some other, more flexible mechanism of observational learning. Altogether, the two study designs seem too divergent in order to compare the learning abilities between cotton-top tamarins and common marmosets and a closer matching experimental design would be preferable.

Although it seemed that the fast adaptation to the changing palatability by mere observation of the reaction towards ingested food was too challenging for the monkeys to learn, it would be interesting for future research to disentangle through experimental designs with different levels of complexity where the learning capacities of common marmosets lie. At this point it is worth asking the question how important it is in the natural environment to be able to respond to such quick changes of the palatability of familiar and preferred foods, given that the unpalatability does not cause serious damage. In species depending on foods with changing palatability (e.g. seasonal fruits) discrimination could also be achieved by visual or olfactory cues. The total absence of any such cues might be rather uncommon and if so, the consequence of ingestion would possibly have to be more serious than facial disgust reactions.

However, although the present study could not show overall significant results on socially acquired information about unpalatable food, the significant success of two individuals in experiment 2 shows that common marmosets are in principle capable to use a conspecific's disgust reaction as a cue to avoid unpalatable food, even in this demanding experimental design. The means by which these two subjects achieved success compared to unsuccessful subjects, i.e. why they in contrast to all other subjects adopted the successful scrounging strategy, remain however unclear and request for further research.

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