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MASTERARBEIT

SOCIAL LEARNING IN THE RED-FOOTED TORTOISE (*Geochelone carbonaria*)

Non-social reptiles can learn from observation

Verfasserin

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Abstract

The ability to learn socially is adaptive as it can potentially save on the costs of learning via trial and error. Learning by observing a conspecific has long been thought to be an ability restricted to group-living species like mammals, birds and fish. However no study has investigated social learning in reptiles, where most of the species are solitary.

In this study, I asked whether a non-social reptile species, the red-footed tortoise *(Geochelone carbonaria)*, is capable of learning from observing the actions of a conspecific. The tortoises were presented with a detour task. The non-observer group (N=4) had to try to solve the task via individual learning. All animals failed to reach the goal in twelve trials. The observer group (N=4) was allowed to watch a demonstrator navigate the detour, and feed from the goal, before their trial commenced. All observer tortoises were successful in completing the task. Two of the four observer tortoises were successful after a single demonstration. Observer tortoises tended to make the detour in the same direction as the model (rightward). However, they also completed the task by going leftwards.

In a second experiment, the former non-observer tortoises received twelve demonstration trials. They were still unable to reach the goal. The former observer group now received twelve non-demonstration trials in the second experiment. All four tortoises were successful in navigating the detour. In a third and last experiment, these tortoises again were allowed to observe a demonstrator making the detour, and they again received twelve trials each. A comparison of the success rate over all three experiments did not reveal a significant difference.

The results show that a non-social species can use social cues to solve a task they cannot solve through individual learning. To our knowledge, this is the first evidence of social learning in reptiles. It has been claimed that the capability to learn socially is an adaptive specialization for group-living animals. However this study rather suggests that it might be part of a more general learning system and may be therefore more wide-spread than previously thought.

Keywords: social learning, tortoise, detour task, *Geochelone carbonaria*, reptile

Zusammenfassung (Deutsch)

Im Gegensatz zu vielen in Gruppen lebenden Säugern oder Vögeln sind die meisten Reptilien, und somit auch die Schildkröten, eine taxonomische Gruppe, die sich hauptsächlich durch solitäre Vertreter auszeichnet. Die Köhlerschildkröte (*Geochelone carbonaria*) ist ein solches Beispiel und lebt in tropischen bis trockenen Wäldern Südamerikas. Über das Verhalten dieser Spezies in der Natur ist nicht viel bekannt, es wird ihnen jedoch eine gewisse Intelligenz und Gedächtnisleistung zugesprochen. In meiner Masterarbeit ging ich der Frage nach, ob diese Schildkrötenart dazu fähig ist, durch Beobachtung eines Artgenossen ein Problem zu lösen. Das zu lösende Problem bestand aus einem V-förmigen Zaun, der umgangen werden musste, wollte das Tier zu dem mit Melonen bestückten Futternapf. Alle vier Schildkröten, die im ersten Experiment keine Demonstration erhielten, waren nicht dazu im Stande, diesen Umweg zu gehen. Sie blieben entweder an der falschen Zaunseite stehen oder marschierten in eine der beiden dem Zaun nahe gelegenen Ecken der Arena. Das Training der Demonstrator-Schildkröte dauerte 6 Wochen. Danach erhielten die restlichen vier Schildkröten zwölf Versuche, den Futternapf nach aufmerksam beobachteter Demonstration zu erreichen. Alle vier Beobachtertiere waren fähig etwas zu lernen und den richtigen Weg zum Futter zu finden. Zwei der vier Beobachter-Schildkröten konnten dies bereits nach dem ersten Versuch.

Im zweiten Experiment wurden die Konditionen der beiden Gruppen umgedreht. Jetzt bekamen auch die früheren Nichtbeobachter die Möglichkeit von einer Demonstration zu lernen. Interessanterweise waren diese Schildkröten auch nach Beobachtung der Demonstrator-Schildkröte nicht dazu fähig das Umweg-Problem zu lösen. Die Erfolgsrate der anderen Gruppe sank ein wenig ab, jedoch statistisch betrachtet nicht signifikant.

Im dritten und letzten Experiment erhielten die Beobachter-Tiere des ersten Experiments erneut zwölf weitere Demonstrationen. Ein Vergleich der Erfolgsrate dieser Schildkröten in allen drei Experimenten ergab keinen signifikanten Unterschied.

Die Resultate dieser Studie zeigen, dass auch nicht soziale Tiere wie die hier untersuchte tropische Schildkrötenart dazu fähig sind sich von Artgenossen etwas abzuschauen. Es lässt daher vermuten, dass Leben in einer Gruppe keine Voraussetzung für die Fähigkeit sozialen Lernens ist. Die Fähigkeit von Artgenossen zu lernen sollte eher als Teil eines allgemein bestehenden assoziativen Lernsystems angesehen werden.

INTRODUCTION

What is social learning?

Social learning can be considered to be "*any process through which one individual (the demonstrator) influences the behaviour of another individual (the observer) in a manner that increases the probability that the observer learns* (p. 108, Hoppitt and Laland 2008)". This definition is very broad, and of course, there are a number of ways that an animal can learn something from a conspecific. With one short example, the case of social learning can be illustrated quite clearly. Instead of foraging on my own, marching through the forest to find something edible, I decide to look what and where others are eating and join in. In this specific case I have the opportunity to learn *where* to search for food and therefore save important time, and also *which* plants or animals to forage upon. In this case, the models (other conspecifics) attracted my attention towards a specific place and/or stimulus (food). This is a very low-level case of socially influenced learning. However, imagine a case in which there are nutrient-rich food sources that are difficult to access. Through trial and error learning gaining access to the food can take time and success levels may also be low. However if another animal has already learned to access the food, then watching that animal closely and trying to replicate its body movements, is very likely to result in a greater success. Copying others' body movements, also termed as imitation, is thought to be cognitively sophisticated, because it is believed to be mediated by highly cognitive processes like "perspective taking" or "mind reading" (Heyes, 1996). It has so far been found in only a few species (see, for instance, Voelkl and Huber, 2000, 2007; Huber et al., 2009).
Still, simpler types of social learning are relatively common in the animal kingdom. However, almost all research that has been conducted has concentrated on the functions and mechanisms of social learning in group-living animals. It has even been hypothesised that social learning evolved as a result of the pressures of group living (Klopfer, 1969). But, is the capability to learn socially really dependent on the sociality of a species? To examine this question, one must run social learning experiments with non-social animals. Reptiles are ideal for this as many species are not only solitary in their adult life but they also exhibit no parental care (Spiess, 1997). Therefore my master's study took the first step into this direction of social learning research.

Ultimate explanation: The function of social learning

Broadly speaking, there are two main ways in which the study of behaviour can be approached – on a **functional (ultimate) and a mechanistic (proximate) level**.

When behaviour is observed, biologists ask questions about the adaptive value of it. How does it benefit the animal, i.e. why has evolution shaped this behaviour in a species? In the specific case of social learning researchers investigate the conditions animals use socially influenced learning and when they do not.

The function of social learning has been demonstrated in many different species, including fish (Brown and Laland, 2006), birds (Hunt and Gray, 2002, Curio 1988) and mammals (Steiniger, 1950; Terkel, 1996; Cook and Mineka, 1989). Evidence for social learning in these taxa are presented in terms of foraging behaviour (what/how/where/when to eat?), anti-predator behaviour (which animal to avoid?) and mate-choice (with whom to copulate?, Galef and Laland, 2005).

It has been demonstrated that learning from others can be advantageous as it allows avoidance of unnecessary negative consequences. For example, learning from social companions *what* to eat, thus avoiding potentially toxic food is highly advantageous to some species, e.g. a rat (Steiniger, 1950). This may allow rats to invade new areas where essential nutrients are hard to find. In this case the function is clear; social learning prevents the rats of becoming ill and can potentially broaden their diet. Some food sources require a specific technique to gain access, like pinecones, which are consumed by rats from Israel. The animals cannot learn this alone and either need a model to observe *how* the scales are efficiently stripped from the pinecone, or to encounter a half-stripped pinecone, to learn this technique (Terkel, 1996).

Social learning also appears to be important when animals have to learn what to fear. Here the advantage of this behaviour is again very obvious. It is much safer to learn from knowledgeable conspecifics which animals are dangerous than to discover it through trial and error. Social transmission of predator recognition has been shown in studies with European blackbirds *Turdus merula* (Curio et al., 1978), rhesus monkeys *Macaca mulatta* (Cook and Mineka, 1990) and danio fish *Brachydanio rerio* (Suboski et al., 1990). The adoption of behaviours from an experienced other, such as a parent, allows naïve individuals "*to shortcut many iterations of trial and error necessary for most individual learning, and to move directly to solutions previously tested by others" (*Galef and Laland, 2005, pp.495*).*

However, it is not adaptive to use social learning indiscriminately. Environments can change rapidly, and therefore individuals should not solely rely on public information but also obtain new information about environmental states via individual learning. Several theoreticians, e.g.

Boyd and Richerson (1985) have pointed out that indiscriminative copying of the behaviour of others is unlikely an adaptive strategy. They point to game-theory models of producer (asocial learner) – scrounger (social learner) interactions, which reveal that indiscriminative copying will not increase the individuals' mean fitness in a population. Social learning thus only becomes beneficial, or adaptive, if individuals sometimes also engage in asocial sampling of the environment (Laland, 2004). Thus, the context in which animals copy others is considered a selective process, and the investigation of the question when and/or whom to copy is currently being intensively investigated.

Proximate explanations: Social learning mechanisms

It is clear that social learning plays an important function in the everyday lives of many animals. However, it is also essential to understand the cognitive underpinnings of this behaviour. How is the acquisition of behaviour by one animal influenced by social interaction with others of its species? What cognitive capacities does an individual need to obtain information from a conspecific, to store it, and to elicit it in a similar, not to say identical manner? To answer these questions, researchers from such diverse areas as cognitive biology, comparative psychology, anthropology, and computer science are investigating social learning in a vast range of species.

This research has resulted in a number of social learning mechanisms of varying complexities. The cognitive capacities required to perform these behaviours also vary, with imitation being considered as the most complex one (Heyes, 1994).

So far, it has been shown that many species of such diverse taxa as insects, fish, birds and mammals are capable of learning socially (e.g. bumble bees, *Bombus terrestris***,** Leadbeater&Chittka 2009:, guppies, *Poecilia reticulata*, Reader et al. 2003; budgerigars, *Melopsittacus undulatus*, Dawson and Foss 1965; pigeons, *Columbia livia,* Palameta& Lefebvre 1985; Japanese quail, *Coturnix japonica*, Akins and Zentall1998; ravens, *Corvus corax,* Fritz and Kotrschal 1998; Bugnyar and Kotrschal 2002; rats, *Rattus rattus*, Heyes and Dawson 1990; domestic dogs, *Canis lupus familiaris*, Pongrácz et al. 2001; Range and Huber, 2007; marmosets, *Callithrix jacchus*, Voelkl and Huber 2000, 2007, capuchin monkeys, *Cebus apella*, Dindo et al. 2008). There have been numerous attempts to define and categorise the different mechanisms involved in their social learning behaviour (e.g. Galef 1988, Whiten and Ham 1992, Heyes 1994, Zentall 2006). These are based on theoretical frameworks upon which different forms of social learning can be discussed. Whiten and Ham (1992) suggested three different processes through which two individuals could show identical behaviour.

1) There could be no interaction between individual A and B at all, in which case another mechanism, like convergence, common descent, or individual learning may account for their similar behaviour.

2) It could be the result of socially influenced learning, where individual A is influenced by the presence of individual B, however no social learning takes place, because nothing new is learned. Animals only exhibit natural behaviours that are triggered by others performing them, e.g. contagion, social facilitation and matched dependent learning.

3) They suggested that identical behaviour could be produced if an individual A actually learns some part(s) from individual B's behaviour, then it can be considered as social learning. For details of the latter two see table 1.

Table 1: Socially influenced learning and social learning mechanism (after Whiten and Ham, 1992)

SOCIAL INFLUENCE	Definition
Social facilitation	*The mere presence of a conspecific may affect the motivational level of an observer and lead to a better performance. (Zajonc, 1965)*
Contagion	*No new behaviour is learned. The probability that the observer will perform the action seen is increased. These are considered as reflex-like actions. (Hoppitt et al. 2007)*

SOCIAL LEARNING	Definition	Evidence
Local/Stimulus Enhancement	*The behaviour (or simply the presence) of an individual attracts the attention of another individual to a particular location or stimulus, about which the naïve individual subsequently learns something. (Brown and Laland, 2003)*	Reader et al. (2003), *Poecilia reticulata* guppies; Fisher and Hinde (1949), *Parus caeruleus* blue tits; Gajdon et al. (2004), *Nestor notabilis* keas
Observational conditioning	*The observer individual learns to associate the action or behaviour of another individual with a certain outcome. (type of Pavlovian conditioning)*	Leadbeater and Chittka, 2009), *Bombus terrestris* bumble bees; Subosky et al. (1990), *Danio rerio* zebra fish; Curio (1988), *Parus*

		caeruleus blue tits; Heyes (1994), *Rattus rattus* rats; Mineka&Cook (1988), *Macaca mulatta* rhesus monkeys
Emulation	*Copying the results of the model's action instead of copying the action itself. Learning about operating characteristics of objects or the environment.*	Whiten and Horner (2005), Nagell et al. (1993), *Pan troglodytes,* chimpanzees; Huber et al. (2001) *Nestor notabilis,* keas
Imitation	*Copying of a novel or otherwise improbable act or utterance, or some act for which there is clearly no instinctive tendency (p. 135; Thorpe, 1963)*	Akins and Zentall (1996), *Coturnix japonica,* quails, Hayes and Hayes (1992), human raised apes, Taylor and Saayman (1973), *Tursiops aduncus,* dolphins; Voelkl and Huber (2000, 2007), *Callithrix jacchus,* marmosets, Huber et al. (2009), *Canis lupus familiaris,* dogs

Almost all of the evidence for social learning in animals comes from studies conducted with group-living animals (mostly mammals and birds) that experience social contact on a daily basis. So far, no research has been conducted on this topic with reptiles.

Social learning tasks

The majority of social learning studies have examined the presence or absence of imitation in animals. Therefore, instead of testing for the more simple mechanism of social learning, the two-action or bidirectional control procedures (Heyes and Dawson, 1990) are designed to control for them. The experimental animals in these tasks are generally skilled in manipulating objects with their hands or beak (like monkeys, mammals and birds). However other species, like tortoises, simply do not have the capacity to do so.

In a recent set of studies, Pongrácz et al. (2001, 2003) used a classic detour task to see whether observing a human demonstrator complete the detour affects the performance of dogs in this task.

In this procedure, the dogs had to watch a demonstrator make a detour around a V-shaped fence. Depending on the motivation of the dog, the reward at the other side of the fence was either its favourite toy or a piece of food. The researchers found an effect of a human demonstration on the performance of the dogs. Even after six trials control group dogs did not circumvent the fence faster, however, if a human demonstrator was present, completion time dropped significantly within two to three trials. They easily adopted the detour behaviour of the human, but did not choose to use the same path as the demonstrator did, but either stuck to the direction of their first successful trial when they did not receive demonstration.

Why study reptiles?

Reptile cognition

Birds, mammals and reptiles developed independently from a common amniotic ancestor which lived around 280 million years ago (MacPhail, 1982). Consequently, the observations of similar cognitive skills in the first two taxa indicate that either the mechanisms that control this behaviour evolved very early or the convergent evolution of similar abilities in the two classes. Considering this fact, it is necessary to find out the degree to which reptiles share these cognitive skills.

In comparison to other vertebrates, cognitive research on reptiles has been somewhat neglected, with only a few scientists dedicating their work to these cold-blooded animals. One of the main reasons why the study of reptile cognition has not been as popular as with birds and mammals, may be the fact that they operate on a different, namely lower, time scale than warm-blooded animals, and thus they seem not particularly expressive to us. However, cognitive abilities did not evolve de novo in endotherms, so reptiles should be studied for the phylogenetic precursors of complex behaviour and their underlying mechanisms (Burghardt, 1991). Most of the research on reptile cognition so far has been conducted by Burghardt and his colleagues (e.g.1988, 2002). There are a lot of anecdotes underpinning the opinion that many reptile species are more “intelligent” than previously thought, however it still lacks of experimental evidence for this impression. Findings on play behavior in dragons (Burghardt et al. 2002), alligators (Lazell & Spitzer 1977) and turtles (Kramer & Burghardt, 1998; Burghardt, 1998) imply that non-avian reptiles are very well capable of higher cognition. One study (Manrod et al., 2008) that investigated problem solving capacity of black-throated iguanas revealed some interesting results. Eight juvenile black-throated iguanas were tested

with a novel task apparatus, receiving three consecutive trials. They were confronted with a transparent food-tube containing prey. Food access could be obtained by using hinged doors at either ends. All of them learned to open the tub and capture the prey within the first trial. During trials 2 and 3 the mean latencies for prey capture decreased significantly, as did the use of ineffective responses such as tube-shaking.

As with the other topics of animal cognition, there is also a lack of research on social cognition in reptiles. Though there are reptile species that are far from being regarded as non-social animals (e.g. green iguanas *Iguana iguana*, Burghardt 1977), most of them do not engage in parental care or other kinds of social behaviour, except during mating season. Gaze sensitivity, which is the ability to recognise the gaze of e.g. a predator and react to it in some way, has been shown in two reptile species, the black iguanas (*Ctenosaura similis*, Burger et al. 1992) and the hognose snake (Burghardt and Greene, 1988). Another very interesting study on gaze-following was conducted at our lab (Wilkinson et. al. 2010). Though solitary, red-footed tortoises were able to follow another's gaze, i.e. the animals oriented its gaze direction to that of another tortoise in a lookup task. This suggests that these tortoises too are sensitive towards another's gaze and might have learned to use a gaze as a cue via associative learning. Given this fact, it might be possible that the red-footed tortoise is also capable to extract some information from observing a demonstrator in a social learning task.

The red-footed tortoise

The red-footed tortoise (*Geochelone carbonaria*) is, like many other reptiles, a solitary species. However, if they are kept together in captivity, they tolerate each other. Not much is known about their behaviour, neither in the wild nor in captivity, but a series of experiments conducted by Wilkinson and colleagues (2007, 2009, 2010) shows that these tortoises are able to use landmarks to navigate successfully a radial-arm maze and are sensitive towards the gazes of another tortoise.

The red-footed tortoise is a tropical species living in many Central and South-American countries, where it occupies a number of habitats like all types of forests (rain-, temperate- and dry forest), but also occurs in savannas. Since they are living in this area they do not hibernate and are therefore available for cognitive research all year around. Furthermore, they are very lively and also their great attraction towards food makes them good subjects for food-rewarded experiments.

Social learning in non-social animals

To understand the evolutionary origin of social learning it is important to investigate its distribution not only in mammals and birds, but also in other taxa like reptiles. Mammals and birds that are solitary in adult life still receive parental care whereas the red-footed tortoise is a truly solitary species, which lacks of parental care and meet for reproductive reasons or, potentially, under fruit trees. But is sociality really the driving power behind social learning ability of a species?

There is only one study that has looked at observational learning ability in a solitary species. This study used an invertebrate, namely the common octopus, *Octopus vulgaris* (Fiorito and Scotto, 1992). The findings revealed that those individuals that observed a demonstrator exhibited faster and better learning of a discrimination task compared to those that learned through trial and error. However, the observer octopuses watched a demonstrator shoot and attack a specific stimulus with no subsequent reward or punishment given to the demonstrator. Fiorito and Scotto stated that the function of this ability remains unknown, but it is apparently part of the general learning system of the octopus.

Biederman and Davey (1993) criticized this study and pointed out that, if associative learning controlled the observers' behaviour, one might expect that they then would not engage in an attack towards the stimulus, since it would only be a waste of energy. Instead of attacking a non-reinforced stimulus, the observers should have been inhibited due to latent inhibition of stimulus pre-exposure. This means that they should have learned to associate the stimulus with a neutral outcome, and therefore the attack as a response would have become unnecessary.

The role of the reward

Since the tortoises in this study are going to observe a demonstrator that will feed from a bowl after successfully navigating a detour, it raises the question about the role of this reward for the copying behaviour of the observers. Is copying a demonstrator's action a goal-directed behaviour? Does the outcome of an action influence the observers' behaviour or not?

In most of the studies on social learning scientists used a food reward as a reinforcer. Actually, how important is the role of the reward? Palameta and Lefebvre (1985) found that observer pigeons that saw a conspecific demonstrator piercing a paper but not eating did not show a tendency to copy the action. Further, observer pigeons which saw a trained model piercing and eating were able to solve the problem much faster than those who just observed a feeding demonstrator. Another study (Japanese quail, Akins & Zentall, 1996) also revealed

the importance of a demonstrator being rewarded for its action. Copying by the observers only occurred when the demonstrator found food in the box.
These results suggest that pigeons and quails engage in imitative behaviour when the actions of the demonstrator are followed by a specific outcome (e.g. food reward). Interestingly, another study with pigeons (McGregor et al., 2006) revealed something contrary, namely the occurrence of blind imitation in these birds. Even when not rewarded, observer pigeons showed a greater proportion of the observed action. Furthermore, there was no difference in the imitative behaviour of the observer pigeons if the demonstrator was rewarded for each response or only at variable intervals.

The evolution of social learning: Three Hypotheses

The ability to learn from others appears to be widespread in the animal kingdom. This is unsurprising, given its important function. However, the evolution of social learning has received surprisingly little attention.
There are currently three hypotheses that attempt to explain the origins of social learning, the "phylogenetic view", the "animal model perspective" and the "adaptive specialization hypothesis".
The phylogenetic view suggests that humans, as copying "perfectionists" are the most sophisticated social learners and that learning from others plays an important part in human culture. This hypothesis supports the idea of continuity of descent, and it assumes that similar social learning abilities are likely to be shared by closely related species. Therefore, it suggests that more sophisticated forms of social learning should be present in animals that are closely related to humans, and that this ability should decrease with increasing phylogenetic distance from them. Experiments therefore focus on identifying imitation in primates, particularly chimpanzees (e.g. Tomasello and Call, 1997; Whiten et al., 2004). According to this hypothesis we should not expect tortoises to be able to learn from observing a conspecific.
In contrast to this, the ***animal model perspective*** strives to identify similarities across different species. This hypothesis suggests that any case of social learning can be described by an equivalent asocial learning mechanism (Heyes, 1994). Researchers supporting this perspective suggest that observational learning is a general phenomenon based on relatively general learning processes and therefore has the potential to be shared by many different species. This hypothesis would predict that tortoises could learn from observing a conspecific.

The third hypothesis is the ***special adaptation hypothesis*.** It does not expect a primate bias like the phylogenetic hypothesis, and does not predict social learning to be a general phenomenon; instead it suggests that social learning is an adaptation to social living. The classic test for the adaptive specialization hypothesis compares the social learning abilities of closely related species that differ in terms of behavioural ecology. Lefebvre (1995) used doves (solitary) and pigeons (gregarious) to investigate the difference in the use of learning through observation between these species. The study revealed that pigeons performed significantly better in the social learning condition. However, the performance of the birds in control tasks, where they were tested for individual learning capacity, also differed. Therefore Lefebvre (1995) concluded that because *"interspecific learning differences apply to both social and non-social tasks, the results do not provide support for the view that social learning is an adaptive specialization to group-living* (p.168)."

Further research has revealed that the evidence for a relationship between sociality and the evolution of social learning is weak (see Reader and Lefebvre, 2001). However, contrasting results were found by Templeton et al. (1999). They compared social pinyon jays with less social Clark's nutcrackers; both species performed equally in an individual learning task. However, a comparison of the performance in the social learning condition, revealed a significant difference between pinyon jays and nutcrackers, with the pinyon jays performing significantly better. It should be noted that beyond this study, no other evidence for a correlation between social learning and social living has been found. "*However it is plausible that social group size may be a poor or inexact measure of social complexity, and that a better measure of social complexity would reveal an association with social learning"* (Reader and Lefebvre, 2001, pp.355).

According to the adaptive specialization hypothesis one might expect that the performance of observer and non-observer tortoises would not differ significantly.

"Clearly all three perspectives are firmly grounded ***in evolutionary theory****, although they emphasise to differing extents the forces of continuity of descent versus specialisation of adaptation"* (Caldwell and Whiten, 2002, p. 195).

Aim of the study

The main aim of my master's thesis was to investigate the evolutionary origins of social learning. To do so I examined social learning in a solitary species of reptiles, the red-footed tortoise. So far no social learning research has been conducted with a reptile species and little

is known about social learning in non-social species. The only evidence from the study on observational learning in the common octopus (Fiorito and Scotto, 1992) is equivocal at best. I therefore presented eight red-footed tortoises with a detour task reminiscent of that run by Pongrácz et al. (2001). In such a detour task, an individual had to walk along a fence, turn and then walk back along the other side towards the goal. The observer group was allowed to watch a demonstrator walk a rightward detour and the performance of this group was compared with a second group of tortoises that were not given the opportunity to observe a demonstrator.

EXPERIMENT 1

Introduction

To investigate whether tortoises can or cannot learn from observing a conspecific, a detour task was conducted. Four of eight red-footed tortoises were randomly assigned to an observer and non-observer group. The groups were size-matched.
Due to the small number of tortoises, only one tortoise was trained to be a demonstrator. I looked at the side-preferences of the control group tortoises, and decided afterwards in which direction we would train the demonstrator tortoise.

Methods

Subjects and Housing

The subjects were eight red-footed tortoises (*Geochelone carbonaria)* of different ages and sizes, these ranged from 9 to 17 cm. None of tortoises had reached sexual maturity when the study started. All animals were bred in captivity and were habituated to frequent handling. Of the four oldest tortoises, three were females (Wilhelmina, Moses and Alexandra) and one was male (Aldous) with plastron-lengths from 14 to 17 cm. The four smaller tortoises (Molly, Esme, Quinn and Emily with plastron-lengths between 9 and 11 cm) were of unknown sex. Six of the tortoises had previous experimental experience (e.g. Wilkinson et al. 2007; Wilkinson et al. 2009; Wilkinson et al., 2010; Müller et al., 2009) Three of the red-footed tortoises (Aldous, Wilhelmina and Alexandra) were kept together. They share their enclosure with a group of marmosets. The enclosure was 120 x 120 x 240 cm and included two houses where the tortoises could hide and sleep as well as a UVA/UVB ceiling light and a heat lamp at the right back corner. The remaining five tortoises (Moses, Molly, Esme, Quinn and Emily)

lived together in an enclosure measuring 125 x 60 x 31 cm next to the marmoset enclosure. They were also provided with hiding opportunities, UVB tube and a heating lamp.
As a substrate of bark mulch was used and both enclosures were equipped with a shallow pool of water where the tortoises could soak in and drink from. To keep the climate humid a water-disperser was installed. The daily light-cycle was set 12hours light/12hours darkness. Lights went on at 8 a.m and turned off at 8 p.m. Temperature was maintained at 29 ± 4°C.
The tortoises were not food deprived and were fed daily from Monday to Saturday, always in the afternoon after the experiments were finished. They received a starve day once a week on Sunday. Since these tortoises are omnivorous, they were fed a variation of vegetables and fruits like melon, plum, apple, pear, tomato, kiwi, rocket and also dandelions. Every three weeks they were given animal protein like egg or rehydrated cat food. Additionally, they received vitamins for reptiles twice a week.

Table 2: Subjects of both groups and their plastron length.

Group X (Non-Observer)	**Size (Length of Plastron)**	**Group Y (Observer)**	**Size (Length of Plastron)**
Emily	9 cm	Quinn	10.5 cm
Esme	11 cm	Molly	11 cm
Alexandra	14 cm	Moses	14 cm
Wilhelmina	16.2 cm	Aldous	17 cm

Testing room

The laboratory consisted of two adjacent rooms. In the first room the waiting arena was set up and the second room was used for running experiments. The waiting arena was 100 cm in length and width and had a height of 40 cm. The tortoises were provided with a heat lamp in the waiting area. The temperature in the laboratory was kept at approximately at 29°C.

Apparatus

The apparatus consisted of a V-shaped fence that was fixed onto a wooden plate, which fitted exactly into a test arena, which measured 120 x 120 x 40 centimetres (Fig.1). This ensured that the fence was stable and could not be moved. On the inside of the V-shaped fence was a food bowl. The two arms of the fence were 50 cm long and had a height of 40 cm. An

observer-cage was placed on the outside of the V-shaped fence 25 cm from it. This was close enough so that the tortoises could see the baited bowl. Three small pieces of melon (approximately 1cm x 1cm in size) were placed inside the bowl as a food reward. The fence had an intersecting angle of 110°. The edge of the fence was 25 cm away from the wall of the arena. This provided enough room for the tortoises to pass and turn around.

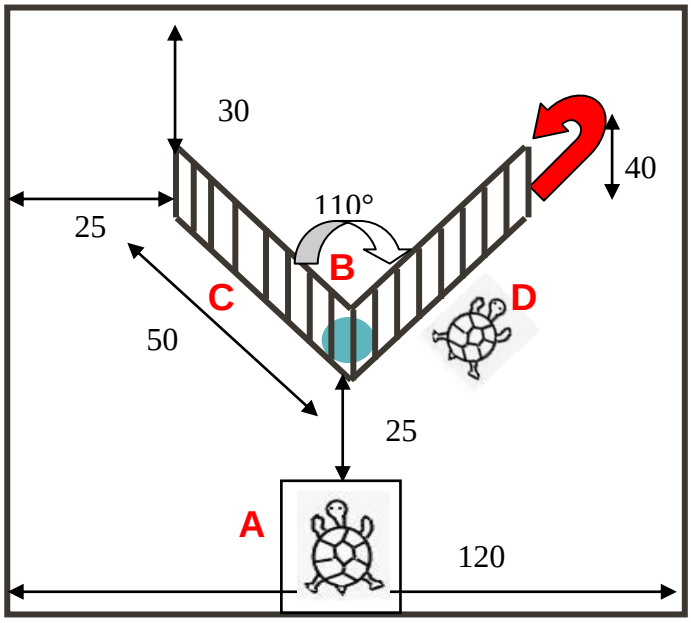

Fig.1: Experimental set-up with all measurements of the arena in centimetres. A: Observer cage; B: food-baited bowl; C: fence; D: demonstrator tortoise

Procedure

Pre-Training

Before the onset of the experiment, all tortoises were habituated to being handled. All animals received pre-training. In this pre-training they were placed in the observer cage for 30 seconds. They were then released and had to walk towards a baited food-bowl which was placed approximately 50 centimetres away from the animal. This served to habituate them to the cage and also allowed them to build an association between the bowl and the food. This pre-training took place in the same arena as the detour study, but before the fence was installed. Pre-training was considered complete when all tortoises had walked towards the bowl and had eaten from it in at least 3 of 4 consecutive trials. They did this readily.
Before starting with the detour experiment, every tortoise received thirty minutes habituation, during which each individual was placed inside the arena and was allowed to explore the whole area. The food bowl was not present and the tortoises received no food during the pre-exposure phase. All of them readily explored the arena.

All trials, both pre-training and experimental trials were recorded with a Canon video camera to allow later behavioural analysis.

Table 3: Overview of the study's three experiments and its participants.

Experiment 1		**Experiment 2**		**Experiment 3**
Non-Observer	**Observer**	**Non-Observer**	**Observer**	**Observer**
Group X	Group Y	Group Y	Group X	Group Y
N = 4 Wilhelmina Alexandra Esme Emily	N = 4 Aldous Moses Molly Quinn	N = 4 Aldous Moses Molly Quinn	N = 3 Alexandra Esme Emily	N = 4 Aldous Moses Molly Quinn

Non-Observers

The non-observers (Group X) consisted of four tortoises, two of them were subadults, the others juveniles. Each tortoise received one trial per day. Before they were allowed to run the trial, activity levels were increased by giving them a warm bath, or putting them underneath a lamp to ensure that they were warm.

The tortoise was then put inside the observer cage for thirty seconds. Subsequently the bark surrounding the fence was redistributed and then the tortoise was released. This was necessary in order to have the exact same procedure for both groups. As soon as the tortoise started walking, the two minute trial began. If the tortoise had not reached the goal (blue bowl baited with food) after two minutes the trial was terminated and the animal was removed from the apparatus. If it was close to the goal and moving in the right direction, the trial continued until the tortoise made an error, stood still again, or reached the goal. Each tortoise received 12 trials.

Demonstrator-Training

Following this, one of non-observer animals (Wilhelmina) was trained as a demonstrator. It would have been ideal to train one animal to navigate the detour in a rightward direction and one to do it in a leftward direction, however due to the small number of subjects, only one tortoise was trained in a rightward direction. We did this using a successive approximation procedure. When Wilhelmina made the detour in less than one minute for six consecutive trials, she was considered ready for the demonstration sessions. This took six weeks of training.

Observers

The observer tortoise was placed inside the observer cage, and then the demonstrator was put in front of the intersecting angle of the fence (see Fig.1). If the demonstrator was distracted by some noises coming from the other tortoise or outside the lab, or didn't start moving in the first minute, the trial was interrupted and was rerun later. Trials also were stopped when the observer tortoise spent less than 80% of the trial watching the demonstrator. This was judged as 80% of time with its head facing the direction of the demonstrator. When the demonstrator walked the detour and the observer was watching it, the former was allowed to eat the reward from the bowl (two tiny pieces of melon) before taken out and put aside. The bark was then redistributed at both sides of the fence to ensure that the tortoises could not complete the detour by following the odour cues of the demonstrator. The demonstrator was removed and the bowl was rebated with three pieces of melon. The observer tortoise was then released. In all other ways the observer trials were identical to those of the non-observer condition.

Scoring & Data analysis

For statistical analysis, successful trials, detour latencies, performance levels and types of errors were recorded. Different levels of success and errors of each trial were evaluated. The use of video recordings allowed exact measuring of latencies.

Performance Levels

To measure the performance of the tortoises on a detailed level, the behaviour was split into different categories. The scoring system gave a point for each correct part of the detour shown by the tortoise. After approaching the bowl (1 point, Fig. 2a), the subject must turn away and walk along the fence until the end to get another point (1 point, Fig. 2b), then turn around (1 point, Fig. 2c) and face the bowl again. If the tortoise then looked and moved towards the

bowl, it received the 4th success point (Fig. 2d). The final point was for reaching the bowl (Fig. 2e). If a tortoise received five points for a trial, it means that it successfully made detour and reached the bowl with the food reward.

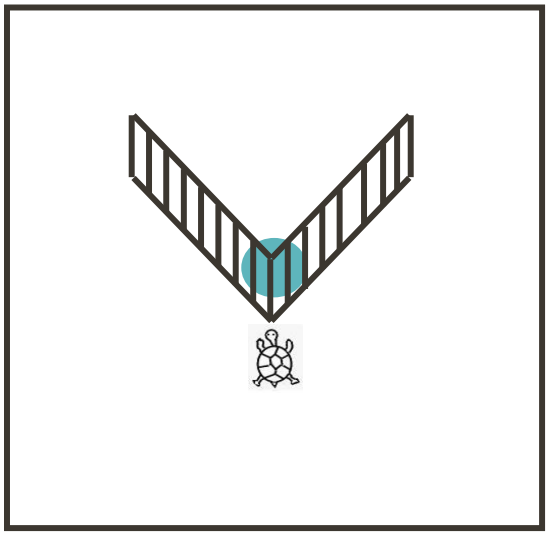

Fig. 2a: **Level 1**
"Approach of the bowl"

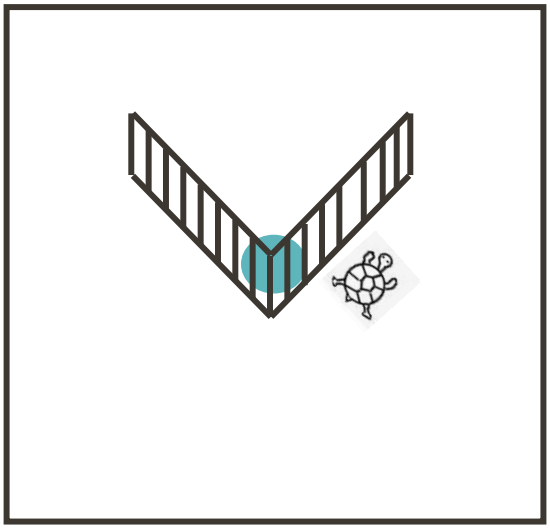

Fig. 2b: **Level 2**
"Moving away"

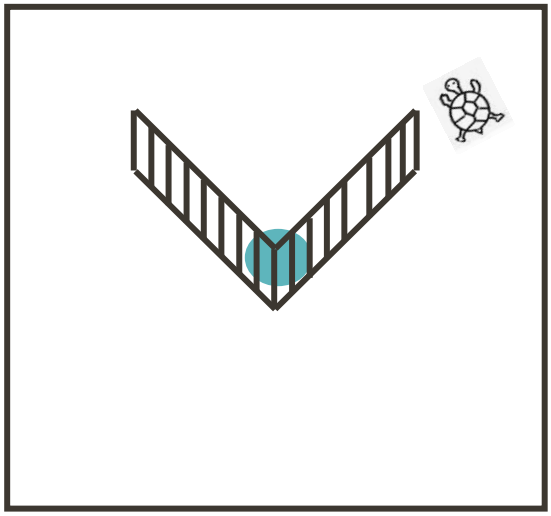

Fig. 2c: **Level 3**
"Turning around at the end of the fence"

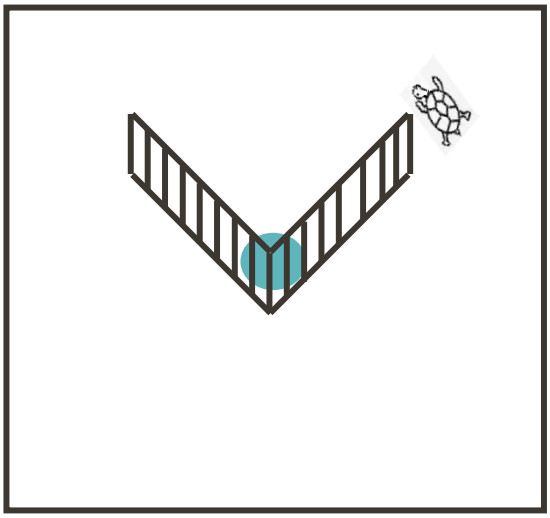

Fig. 2d: **Level 4**
"Facing the bowl, moving towards the bowl"

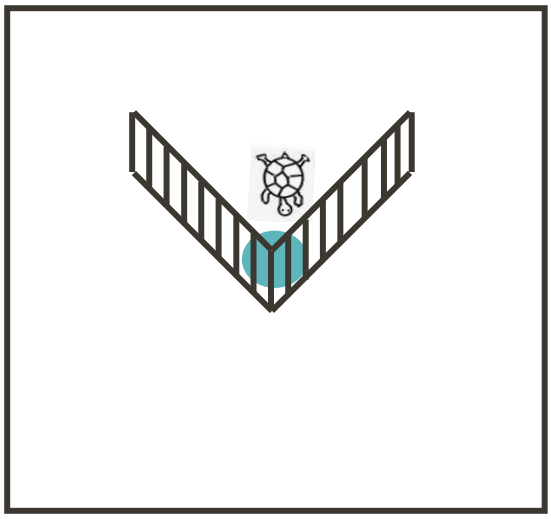

Fig. 2e: **Level 5**
"Reaching the bowl"

Types of Errors

Table 2: Five different types of errors during a detour

Type of error	**Definition**
1st: Refusal	The tortoise did not approach the intersecting angle, but moved around in the lower part of the apparatus instead (Fig. 3a)
2nd: Not moving away	The tortoise stuck at the wrong side of the fence, trying to squeeze through it to reach the blue bowl (Fig. 3b)
3rd: Walking back on the wrong side	A tortoise on its way to the edge of the fence turned around too early and hence walked back on the same (wrong) side of the fence (Fig. 3c)
4th: Corner	The tortoise did not turn around at the edge of the fence but went into the corner instead (Fig. 3d)
5th: Other side	The tortoise passed by the bowl and went till other side without even looking at it (Fig. 3e)

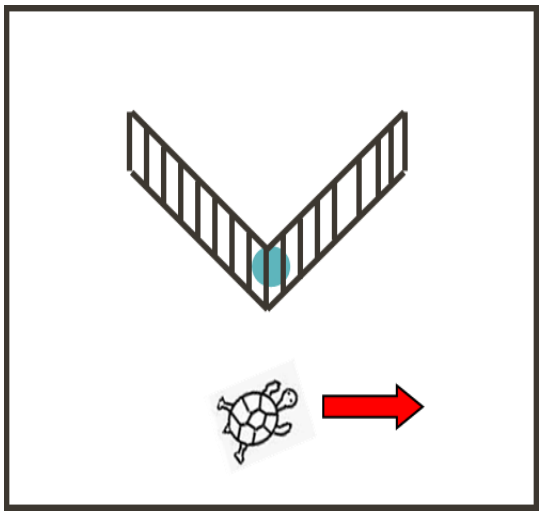

Fig. 3a: 1st type of error: "Refusal"

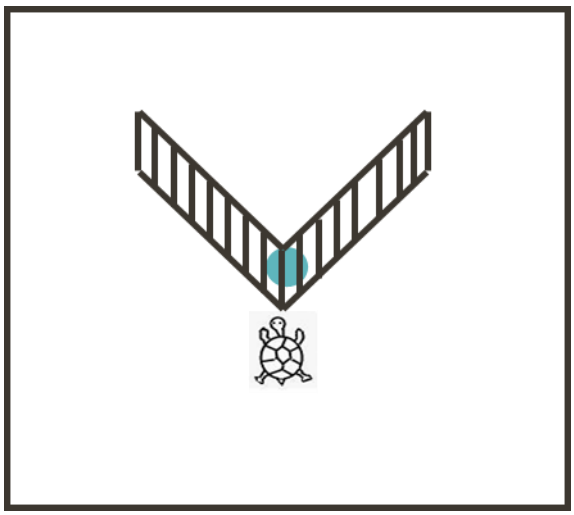

Fig. 3b: 2nd type:"Not moving away from the intersecting angle"

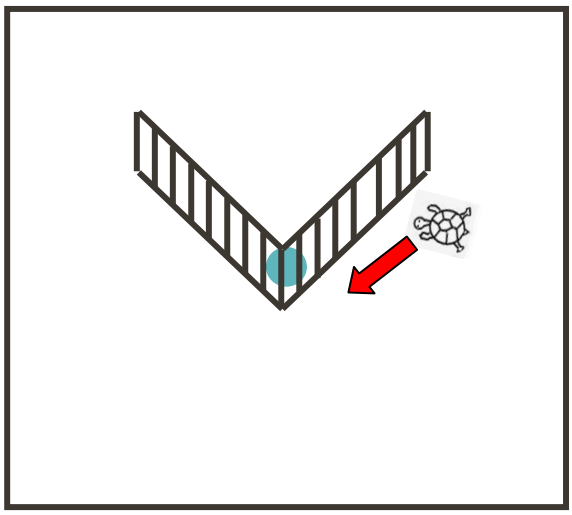

Fig. 3c: 3rd type: "Coming back at wrong side of the fence"

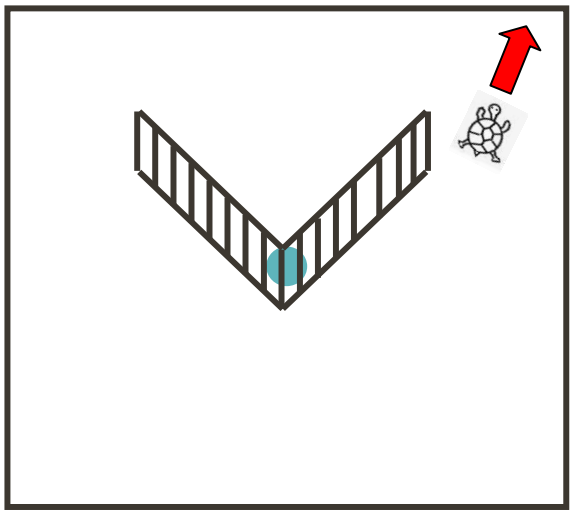

Fig.3d: 4th type: "Walking into the corner"

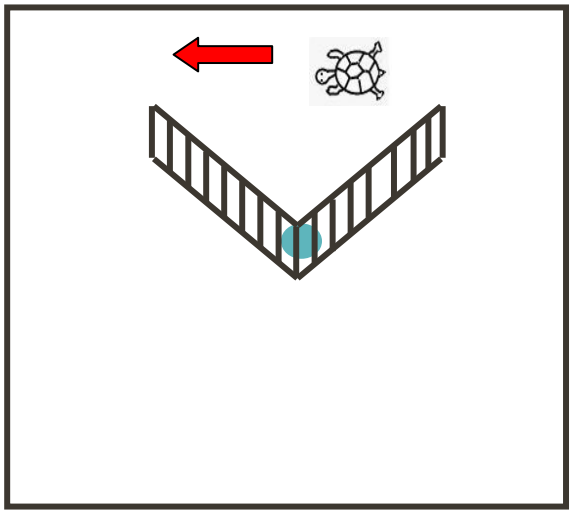

Fig. 3e: 5th type: "Passing bowl without looking at it and walking till other side"

Results

Success Rates & Direction of Detour

In experiment 1, two of the four tortoises of the experimental group successfully completed the detour on their first attempt and all completed the detour within the twelve trials. In contrast, none of the control group animals ever reached the goal during the twelve trials (Fig.4). There was a significant difference in the number of successful trials between the control and the experimental group ($t(6) = -2.678$; $p < 0.05$). Though all of the observers were successful in navigating to the rewarded bowl, inter-individual differences were high. The two older tortoises (Aldous and Moses) had a success rate three to four times higher than the two younger ones (Molly and Quinn).

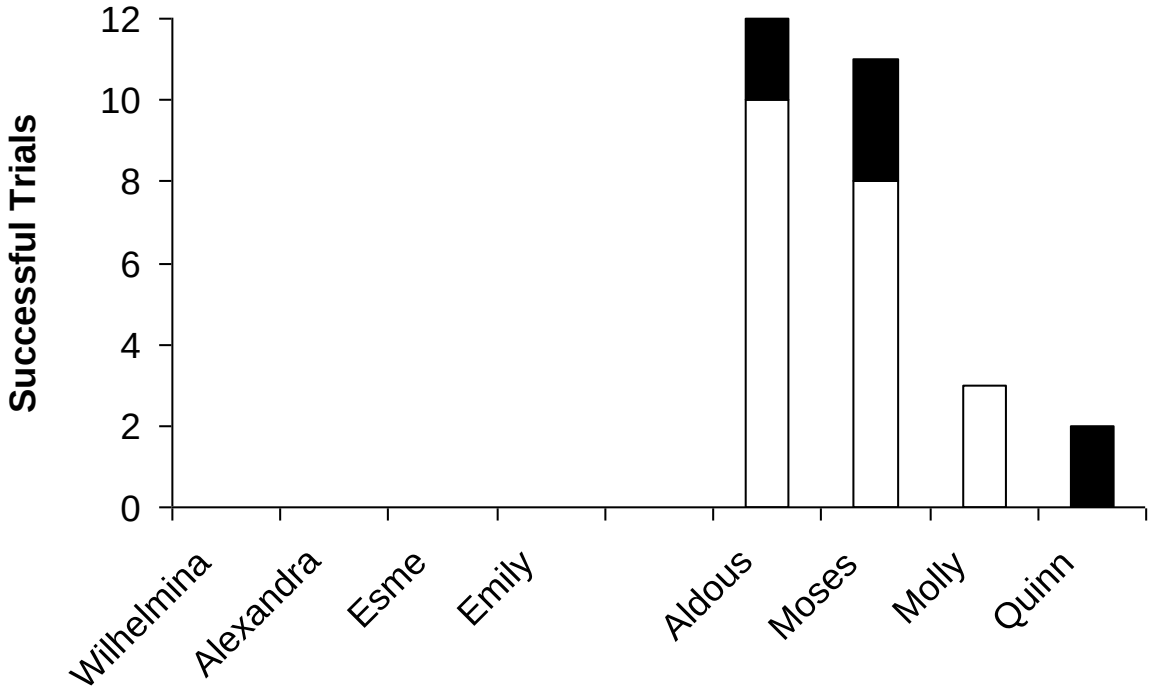

Fig.4: Number of successful trials of each tortoise of both the non-observers (left) and the observers (right) during Experiment 1. White bars represent rightward choices, black bars represent leftward detours.

Three of the four observer animals made their first correct detour in the same direction as the demonstrator, which means they made the detour in a rightward direction. Interestingly, one of the tortoises, Quinn only ever successfully completed the detour in a leftward direction. However, all tortoises, except Molly, also completed the detour in a leftward direction (see Fig. 4).

A binomial test, examining overall choice of directions, revealed that observers preferably chose the same direction as the demonstrator (p = 0.013). Overall, they showed 75 % rightward detours and in only 25% of the cases they went left.

Mean Level of Performance across All Trials

An independent samples t-test was performed to calculate the difference between the groups for the mean level of their performance, which is defined as the mean of reached levels for each trial, across all twelve trials (Fig. 5). The test revealed a significant difference between the groups ($t(6)$ = -3.281, p< 0.05), showing that overall the observer group was significantly better than the non-observer group. A within sample t-test of the non-observer group's first and last three trials revealed a significant difference; hence the performance of the tortoises got significantly better over time *($t(3) = 7{,}805$, $p < 0.05$).*

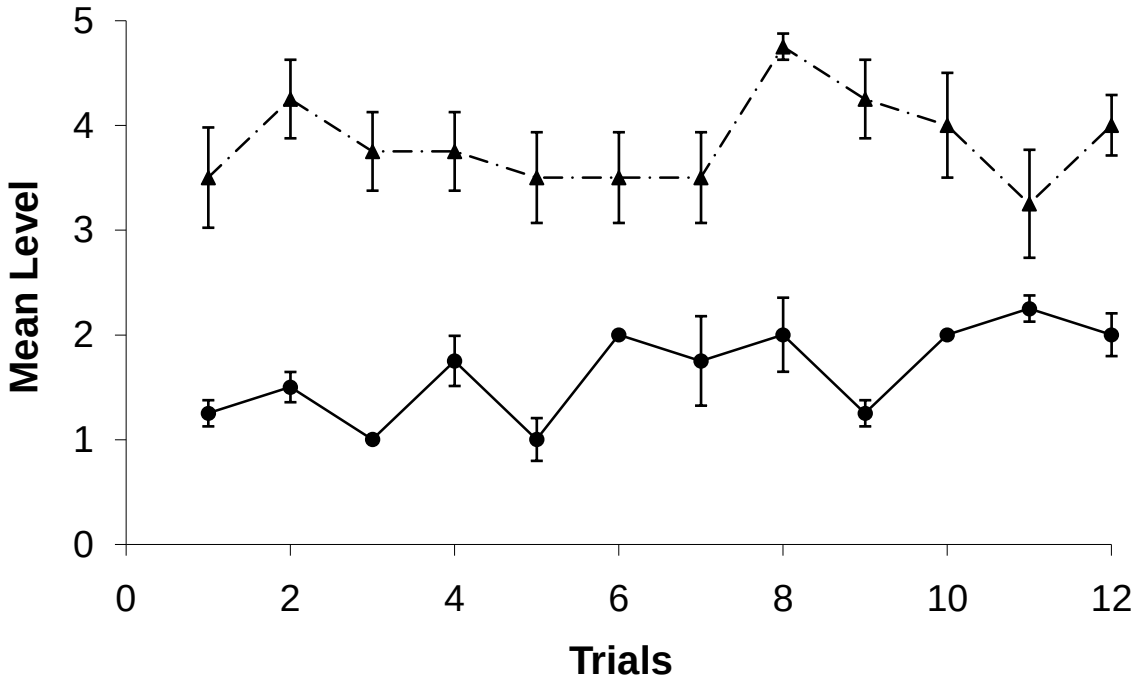

Fig. 5: Mean level of performance for all twelve trials (Experiment 1). The observer group (N=4) is represented by triangles, the non-observer group by circles (N=4). The whiskers represent the standard error.

Latencies

This analysis was only conducted for the observer group. The latencies for a successful detour (measured from the fence angle to reaching the goal) decreased significantly with the number of successful trials in two of four observer tortoises (Molly and Aldous). The relationship between these two variables is demonstrated as a linear regression function in Fig. 6 (*Aldous: r = -0,79; Moses: r = -0,13; Molly: r = -0,88; Quinn: r =1).*

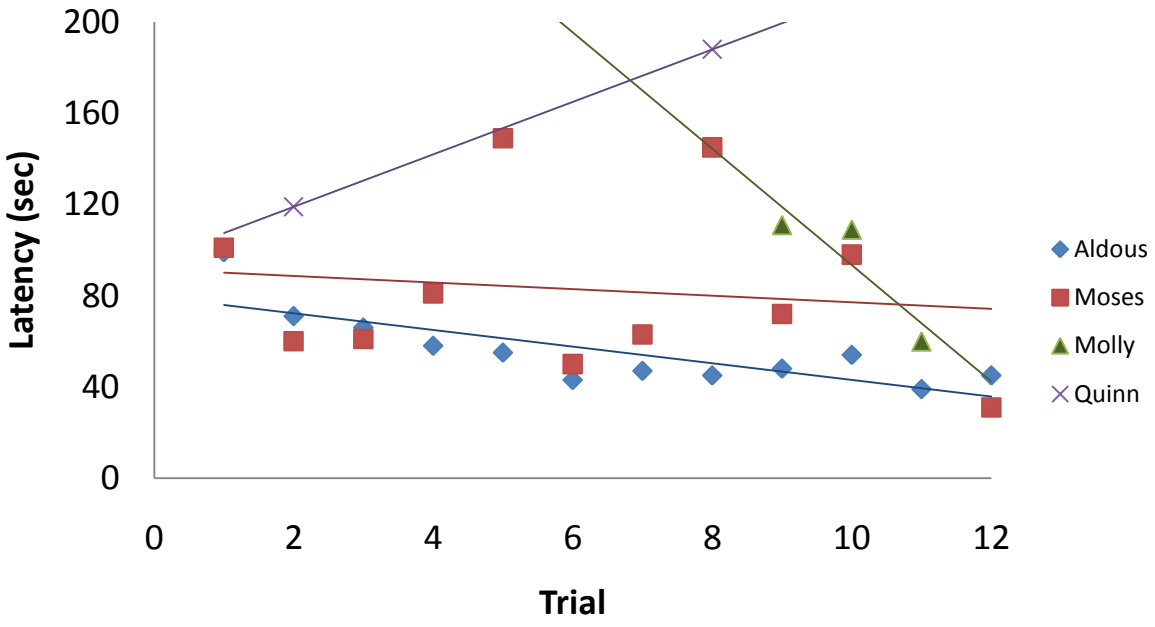

Fig. 6: This graph shows the relationship between the number of successful trials and the time the observer tortoises needed to complete the task.

Errors

The time that the control group animals spent at the intersecting angle before moving away was also measured. The linear regression graph (Fig. 7) shows a slight decrease in latencies for each tortoise, however the correlation effect is not significant (*r* = -0.69 Esme*; r* = -0.66 Wilhelmina; *r* = -0.49 Alexandra*; r* = -0.43 Emily*).*

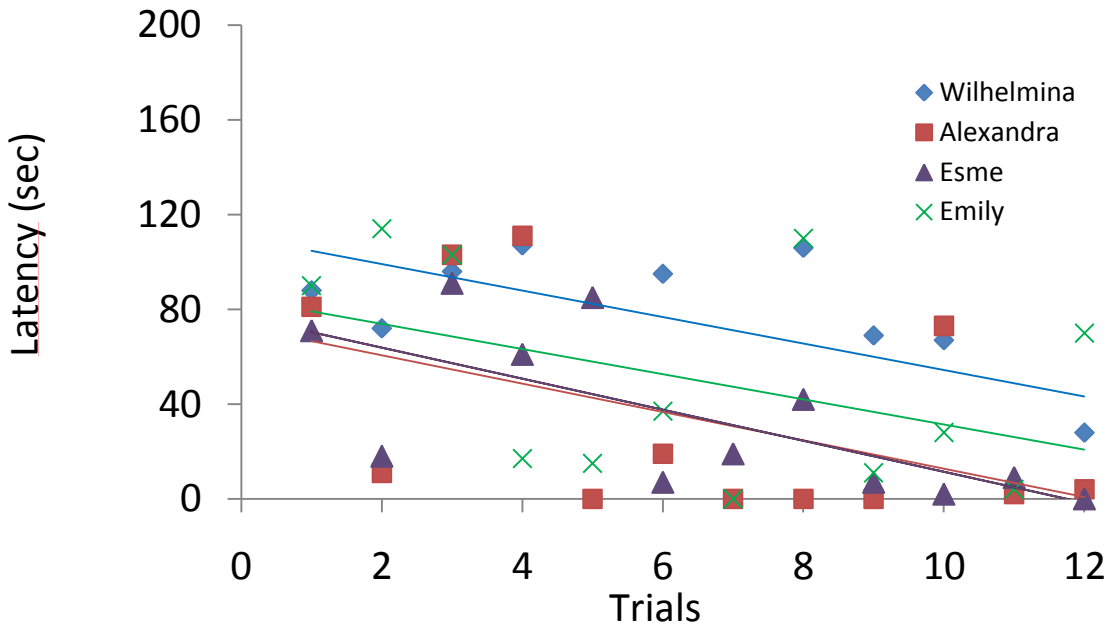

Fig.7: This graph shows the latency to leave the intersecting angle over trials.

During this experiment the observer tortoises made 21 errors, whilst the non-observers made twice as many (42, see Fig. 8). The distribution of the different types of errors demonstrates that when an error occurred, it occurred at the same point for both groups; they were not able to turn around at the end of the fence, but went into the corner instead. Furthermore the non-observer animals stuck significantly more often at the wrong side of the angle and didn't move away from it ($t(6) = 2.751$, $p < 0.05$). An independent sample t-test of the other types of errors did not reveal any significant differences between the two groups ($t(6) = 1.237$, $p > 0.05$ Corner; $t(6) = -0.330$, $p < 0.05$ Other Side).

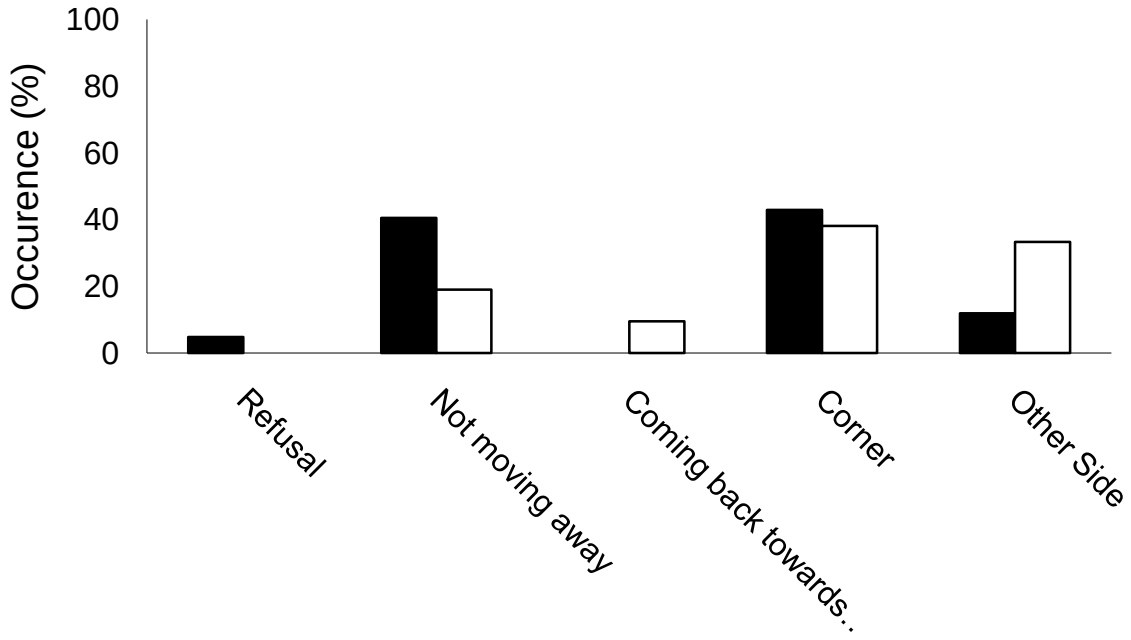

Fig. 8: The percentage of errors for the observer group (white bars, N=4) and the non-observer group (black bars, N=4) during Experiment 1.

Discussion

Success of Group Y – The observer group

The results of experiment 1 show for the first time that reptiles are able to solve a detour task through observation of a conspecific. The performance of the four non-observer animals suggests that solving the detour task through individual learning is not within the capabilities of the red-footed tortoise. Even training the demonstrator tortoise took over 100 trials. This fact makes it even more remarkable that all the observer tortoises successfully navigated the detour and two of them even reached the bowl already on their first trial. This suggests that the observer tortoises extracted some information, from the model's behaviour, which then allowed them to successfully reach the bowl.

Inter-individual differences in the observer's performances indicate that there might be some factors that influence the occurrence of social learning. Coussi-Korbel and Fragaszy (1995) suggested that the identity and characteristics of the demonstrator and the observer critically affect the probability of social learning. Could this account for the differences in the observer's behaviour?

Familiarity

Social rank, sex, age, and patterns of association frequently influence the likelihood of social learning. Studies have revealed that social learning does depend on the relationship between demonstrator and observer. Many social species have hierarchical or other types of social systems which define dyadic relationships. During social learning, the model has to tolerate an observer in close proximity, since they need to have good visual contact to extract important information. Therefore individuals that have a close social relationship with the model, like affiliates or kin, are most likely to be tolerated. Russon and Galdikas (1995), as well as Swaney et al. (2001), found that it often depends on the familiarity between the model and the observer how effectively a copying effect is elicited. The observer tortoises in this study had different levels of familiarity with the demonstrator. Of the two tortoises that were highly successful, one was familiar (Aldous) and one unfamiliar (Moses) with the demonstrator. Hence, the factor familiarity does not seem to influence the occurrence of social learning in the red-footed tortoise.

Sex

Although the sex is known for only half of the tortoises (N=4), the results suggest that this factor does not constrain the performance of the tortoises. Moses, a female, and Aldous, a male, were almost equally successful in navigating the detour. Though it seems unlikely that the sex of an observer affects its performance, the data set is too small to draw firm conclusions about this.

Age effect

The two highly successful tortoises were older than the two less successful tortoises. These results suggest that the age of the observer may have an impact on the social learning abilities of the tortoises. The two older tortoises, Moses and Aldous, were successful right away and their performance did not degrade, whereas the two younger ones, Molly and Quinn, were less successful in copying the model's actions. This might be a developmental effect, and suggests that some cognitive aspects of social learning, such as attention, memory of the model's action, reproduction of the body movements or other motivational factors, are not present in younger animals or just less accessible. Other studies have demonstrated an age effect from which observers are more likely to copy behaviours. Observers rather copied older, mature individuals than younger ones (Dugatkin and Godin, 1993; Galef et al., 2001). The age of the demonstrator tortoise might have been crucial for the successful learning. Wilhelmina is one

of the oldest tortoises and to investigate the effect of age of the model one must repeat the study with a younger tortoise as the demonstrator.

When comparing the sequence levels that both groups reached in Experiment 1, Fig. 5 reveals that both groups moved away from the intersecting angle. However the reason for this behaviour could be interpreted differently for each group. It may well be that the non-observer animals started to lose interest in reaching the bowl because they simply did not know how to get there, compared to the observer animals which were motivated by the demonstrator's performance to go the detour. This explanation can be probed by measuring the tortoise's behaviour right after leaving the angle. During observation of both groups in this detour task, the observer group tortoises looked back towards the bowl after they had moved away whilst the control animals did not. Unfortunately the video quality was too poor to measure this "looking back" behaviour in both groups.
The latency for moving away from the angle (Fig. 7) also decreased with the number of trials. However, instead of walking the detour, the non-observer animals mostly went to the corner and stayed there to rest.

EXPERIMENT 2

Introduction

To examine whether the control group could learn after a demonstration and whether the success of the observer group in the first experiment would continue even if no demonstrator was present, in the second experiment the conditions for both groups were switched. The former non-observers (Group X) now received twelve demonstration trials and the former observers (Group Y) now received twelve trials without a demonstration.

Methods

Subjects

All eight tortoises from Experiment 1 participated in this experiment. The keeping conditions were the same as in Experiment 1.

Apparatus

The experimental set-up was the same as in Experiment 1.

Procedure

Observer and non-observer trials were identical to those of the first experiment. The only difference was that the condition for both groups was switched.

Results

Success Rate & Direction of detour

Despite observing twelve demonstration trials, none of the three observer animals in Experiment 2 reached the goal. All non-observers were successful in navigating the detour at least once and again completed the detour by either going left-or rightwards. Quinn was again the only tortoise that only made the detour in the leftward direction (Fig. 9). Unlike in Experiment 1 statistical analysis did neither reveal a significant difference in the success rate between Group X and Y ($t(5) = -1.900$, $p = 0.098$) nor a significant rightward bias in choice of direction ($p > 0.05$; leftward:50%, rightward: 50%). Aldous' performance was considerably poorer than in Experiment 1. However, overall there was no significant difference between the performance with a demonstration and performance without of Group Y *($t(3)= 1,072$, $p > 0.05$).*

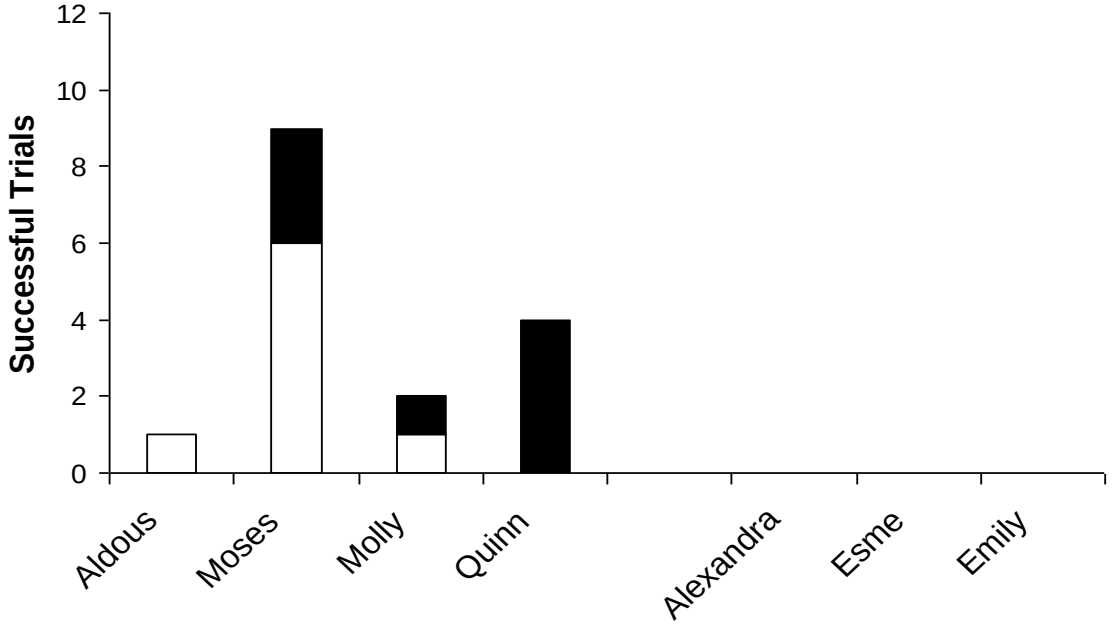

Fig.9: Number of successful trials of each tortoise of both the non-observers (left) and the observer tortoises (right) during Experiment 2.

Mean Level of Performance across All Trials

However, if comparing the mean level of performance across all trials, an independent t-test reveals a significant difference between both groups ($t(22) = -2.698$, $p < 0.05$). The non-observers performed significantly at a higher level than the observer tortoises (Fig.10).

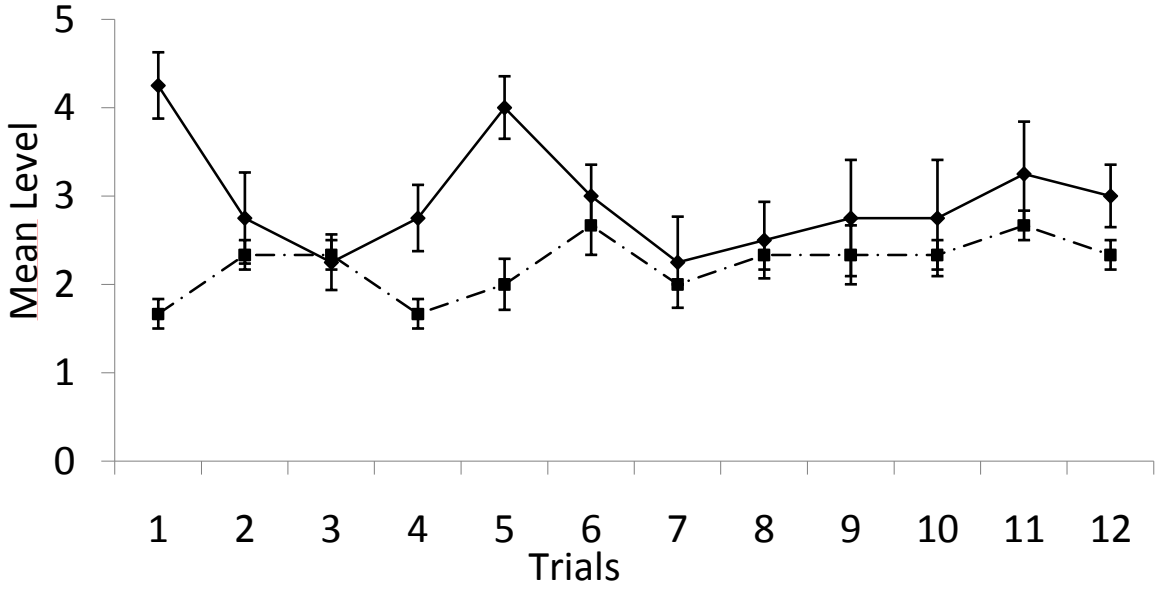

Fig. 10: Mean level of performance over all twelve trials in Experiment 2. The observer group (N=3) is represented by squares, the non-observer group by diamonds (N=4). The whiskers represent the standard error.

A within- subject comparison of the mean levels reached by Group Y between Experiment 1 and 2 revealed a significantly better performance of the tortoises in Experiment 1 ($t(11) = 2.563$, $p < 0.05$), when the animals were allowed to watch a demonstrator (Fig. 11).

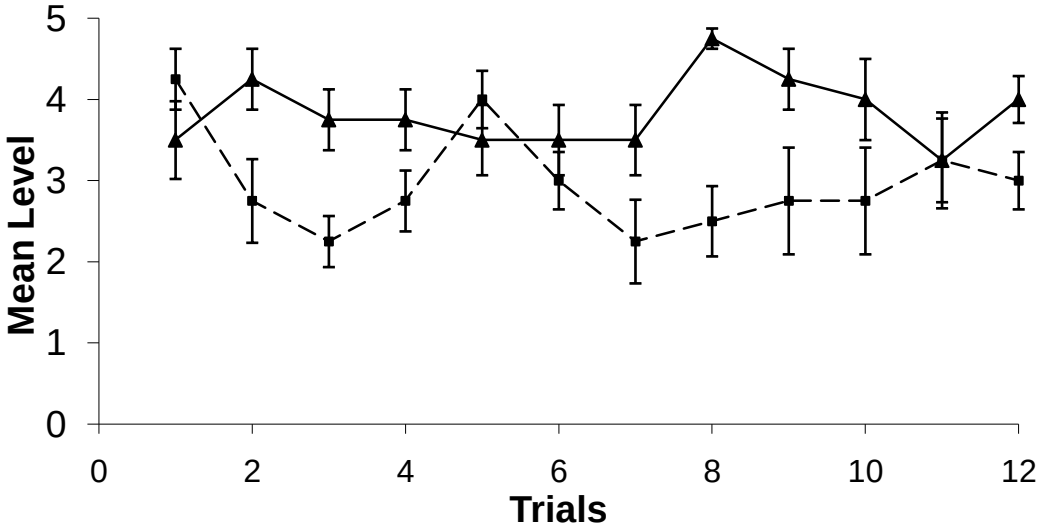

Fig. 11: Comparison of the mean level of performance over all twelve trials of Group Y. The performance of the group in Experiment 1 (N=4) is represented by triangles, the performance in Experiment 2 by squares (N=4). The whiskers represent the standard error.

A within- subject comparison of the mean levels reached by Group X between Experiment 1 and 2 revealed a significantly better performance of the tortoises in Experiment 2 ($t(11) = -2.816$, $p < 0.05$), when the animals were allowed to watch a demonstrator (Fig.12).

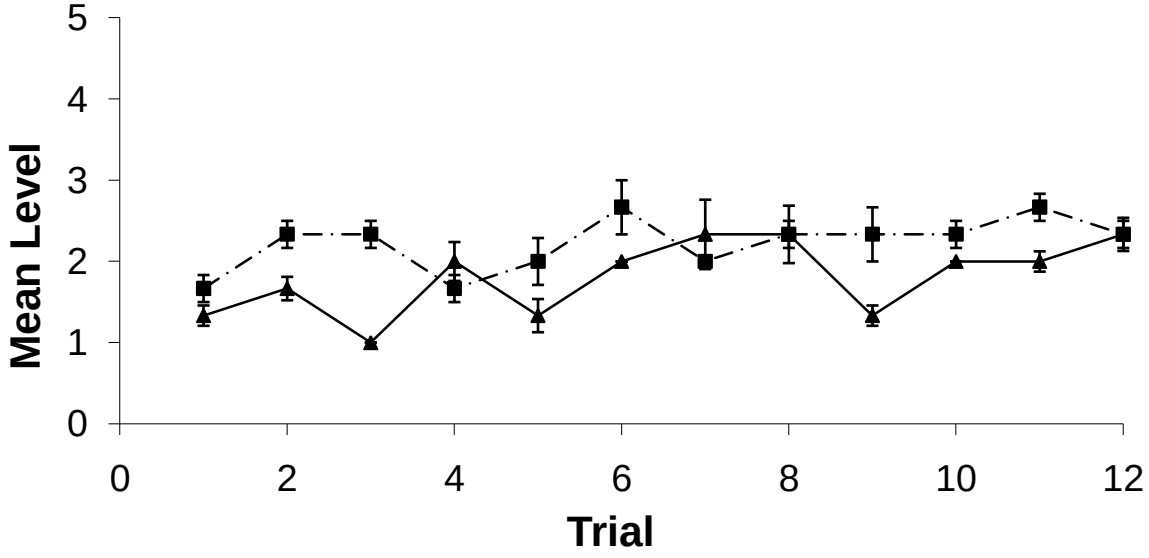

Fig. 12: Comparison of the mean level of performance over all twelve trials of Group X. The performance of the group in Experiment 1 (N=4) is represented by triangles, the performance in Experiment 2 squares (N=3). The whiskers represent the standard error.

Latencies

Fig. 13 shows the relationship between the number of successful trials and the time needed to complete the detour, measured from approach of the angle until feeding from the bowl. Since Aldous and Molly were only successful once and twice in all twelve demonstration trials, Moses' performance, i.e. the time she needed for navigating the detour, did not change significantly over trials. Quinn, who was successful four times during experiment 2, was the only tortoise that showed a decrease of latency over trials. (r = - 0.87).

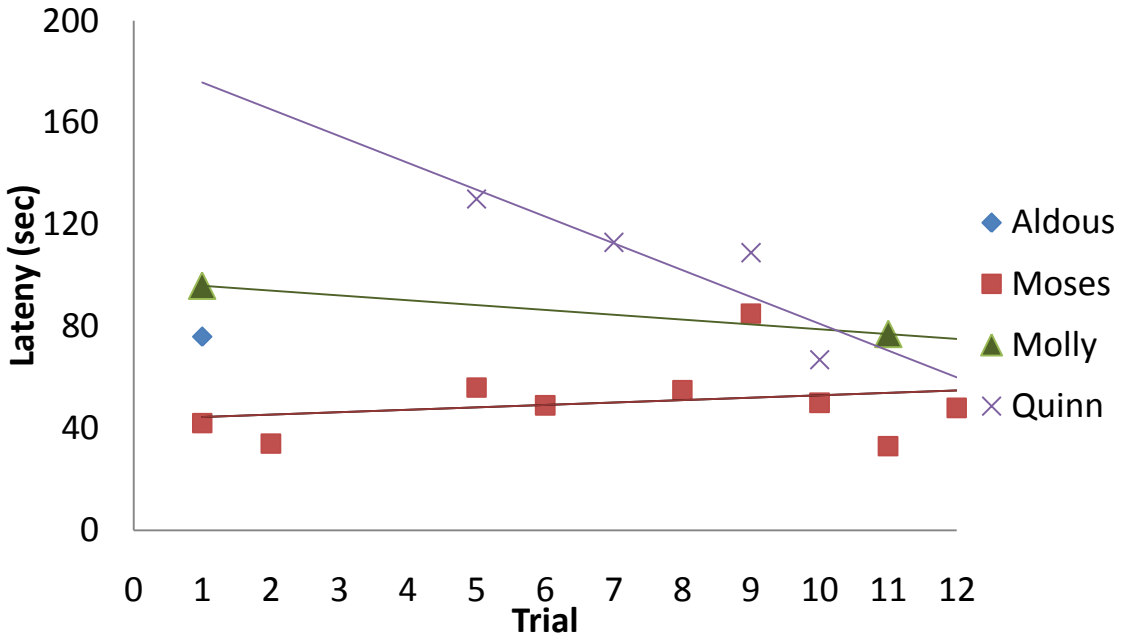

Fig.13: Latency for detour in Experiment 2 of Group Y (non-observers).

Errors

The error pattern of both groups during Experiment 2 shows a similar result as in Experiment 1. The non-observers (Group Y) now showed more Type 2 ("staying at angle") errors, just like Group X did during Experiment 1. However, the observer tortoises (Group X) went into the corners more frequently than the non-observers (Group Y) did. Nevertheless statistical analysis did not reveal any significant differences between both groups (NM: $t(5)= -0.572$, $p > 0.05$; CO: $t(5) = 1.840$, $p > 0.05$; OS: $t(5) = 1.660$, $p > 0.05$) (Fig. 14).

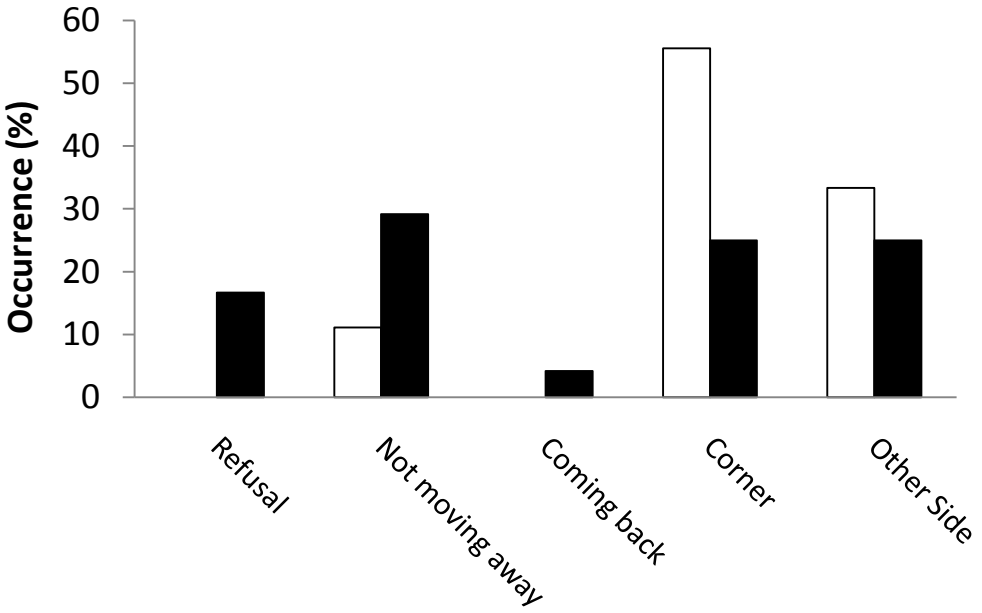

Fig.14: Comparison of occurred errors during Experiment 2 between observers (white bars, N=3) and non-observers (black bars, N=4).

Fig.15 shows the change in the error behaviour of Group X (non-observers in Experiment 1 and observers in Experiment 2) between Experiment 1 and 2. While moving into the corner was still the most frequent error, they now stayed at the angle much less. That means they moved away along the fence more frequently. Additionally, the occurrence of the error "walking past the bowl to the other side" (Type No.5) more than doubled.

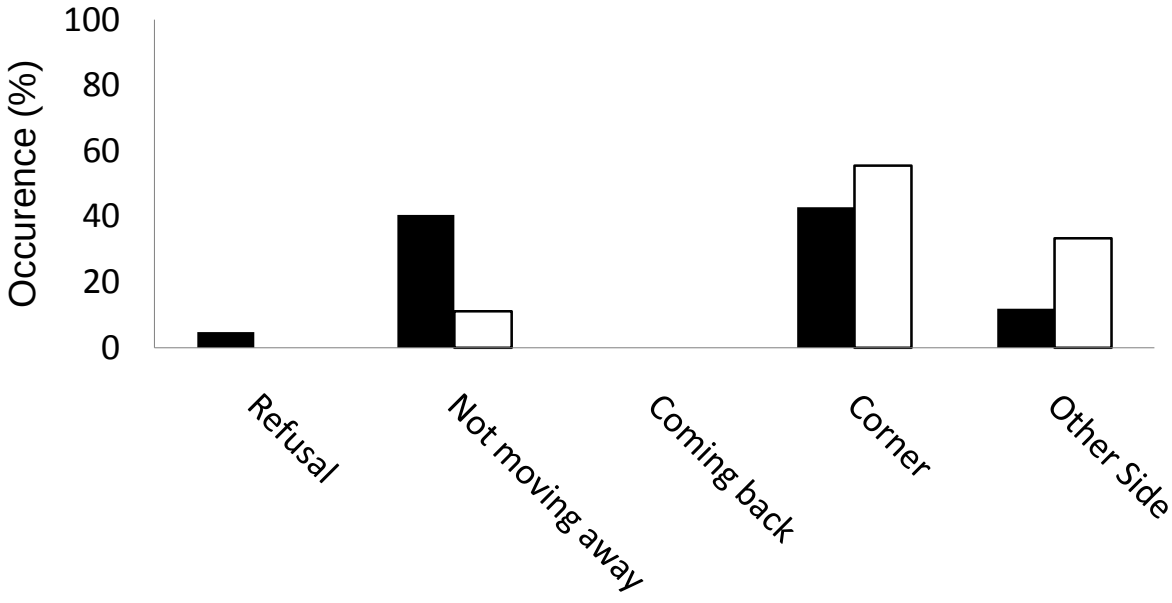

Fig.15: The percentage of occurred errors of Group X during Experiment 1(black bars, N=4) and Experiment 2 (white bars, N=3)

It is possible that the drop of error type No.2 (“not moving away”) in Experiment 2 is the result of the demonstration. However, a closer look at the errors of Experiment 1 reveals that this is not the case. If the errors of Experiment 1 are split into two phases (first six trials vs. last six trials), the same change in behaviour is seen. As demonstrated in Fig. 14, the occurrence of error type 2 (“not moving away”) already decreased during the second phase of Experiment 1. During the first 6 trials of Experiment 1, in over 60% of the errors the tortoises stayed at the angle, whereas during the second 6 trials the occurrence of this type of error dropped to about 20%, a similar level to that seen in Experiment 2. Statistical analysis revealed that the tortoises stuck significantly less at the angle during the second part of Experiment 1 *(t(3)=3,656 , p <0.05).*

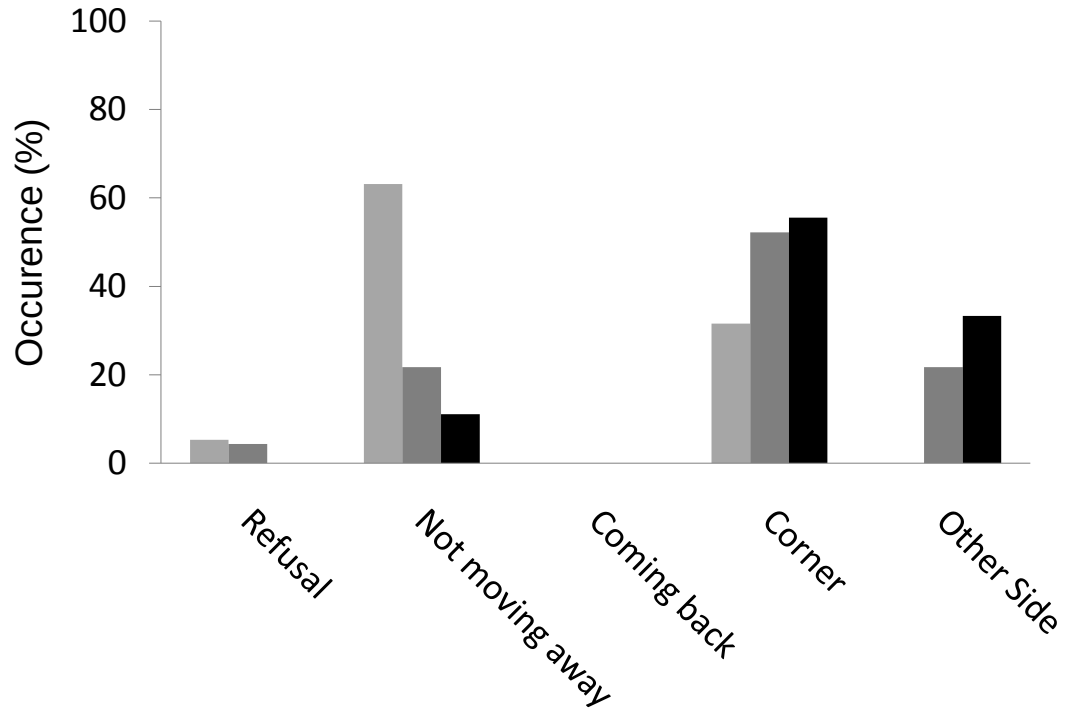

Fig.16: The percentage of occurred errors of Group X during the first 6 trials of Experiment 1 (Phase A, light grey); the second part of Experiment 1 (Phase B, dark grey); and Experiment 2 (black bars).

Discussion

Failure of Group X

The tortoises of Group X, which were non-observers in Experiment 1 and observers in Experiment 2, never reached the bowl, even after observing 12 demonstrations of the detour. This inevitably leads to the question: Why did the tortoises' performance not improve in Experiment 2? What caused this poor level of performance? It is possible (though unlikely) that this was the result of having accidentally selected a group of good learners and poor learners in Experiment 1. To entirely exclude this possibility we would have to switch initial conditions and ask them to solve a novel social learning task. The reason why I do not think that this is the case here, is the evidence of other experiments run in our lab using the same animals (Wilkinson et al. 2010, Müller et al., 2009), which have revealed no such difference. I would rather suggest that the difference observed was the result of different experience in the experimental setup which resulted in conditioned inhibition in the non-observer group. During their first twelve trials without demonstration, the tortoises initially tried to push past the fence to get to the food bowl and after a number of trials started to lose interest. This was indicated by them walking into the corners to rest, or walking along the arena walls. Even when they passed within 10 centimetres of the bowl, they did not look at it or approach it. It seems likely that the control tortoises had learned that they could not reach the goal. With every unsuccessful trial this association got stronger. The effect of watching a successful model was clearly too weak for the tortoises to overcome the original learning effect.

Taking a closer look at the error patterns of Group X during both experiments might clarify what was actually happening. A comparison between the errors of Group X tortoises in Experiment 1 and 2 (Fig. 15) revealed no difference. However, they tended to make fewer errors by staying at the intersecting angle (type No.2) during Experiment 2, but instead more frequently passed by the bowl and walked to the other side (type No. 5). With the decreased interest in the bowl (due to conditioned inhibition), they happened to come apparently closer to the target, but still did not approach it.

When splitting Experiment 1 into two phases (Fig. 16), the diagram shows that the error "not moving away" dropped to one-third in the second part of Experiment 1, and the tortoises rather went to the corners to rest. This could mean that even with a demonstrator the interest of the Group X animals in the food-baited bowl already decreased during Experiment 1 and remained weak during Experiment 2. This is supported by the fact that the tortoises continued

to go into the corners to rest and still did not show any “looking back” behaviour whilst moving away.

Success of Group Y

Although the Group Y tortoises did not receive any demonstration trials during this Experiment, all of them again successfully navigated the detour. However, there was a serious drop of performance in one animal, namely Aldous, with twelve successful trials in Experiment 1 and only one in Experiment 2.What could be the reason for this behaviour? And why did the other tortoises’ performance not drop? It might be the fact that he is a male tortoise and the demonstrator, Wilhelmina, a female. He might have been more interested in observing and following her movements and thus reached the goal in all twelve demonstration trials of Experiment 1.

The tortoises also successfully navigated the detour in both directions, which again supports the hypothesis that the tortoises learned to see the fence as an obstacle that can be circumvented left- and rightwards. Though the performance of Group Y slightly dropped between Experiment 1 and 2, the statistics did not reveal any significant difference.

EXPERIMENT 3

Introduction

A third Experiment was conducted to test further effects of demonstrations on the performance of the observer tortoises from Experiment 1 (Group Y).

To test whether the number of successful trials of the tortoises that have already proven to be able to reach the bowl, could further be increased, these four tortoises received twelve more demonstration trials.

Methods

Subjects

Only four tortoises (Group X: Aldous, Moses, Molly and Quinn) from the former experiments participated in this experiment. The keeping conditions were the same as in Experiment 1 and 2.

Apparatus

The experimental set-up was the same as in Experiment 1 and 2.

Procedure

Observer trials were identical to those of Experiment 1.

Results

Success Rates & Direction of Detour

A repeated-measure ANOVA revealed no significant difference of performance of Group Y over all three experiments ($F(2) = 0.88$; $p > 0.05$) (see Fig. 17).

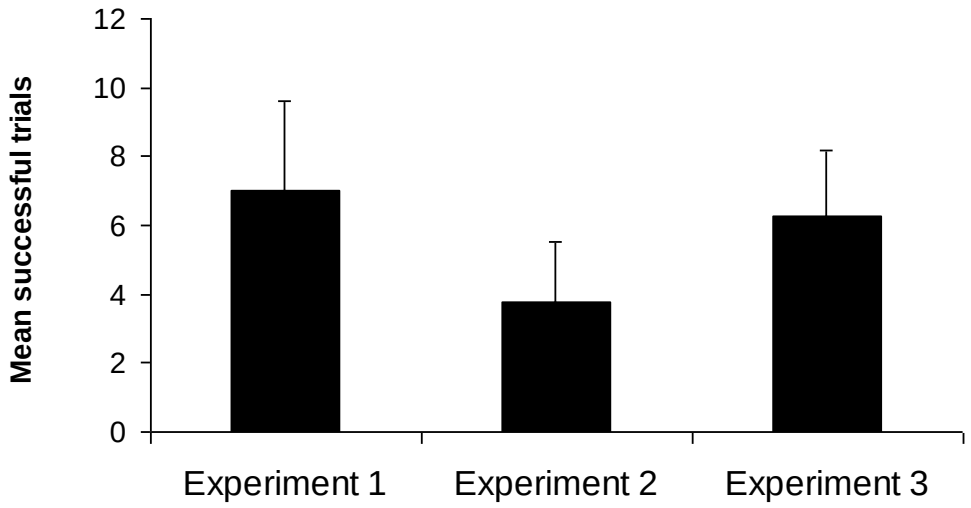

Fig 17: Comparison of mean successful trials of Group Y during Experiment 1, 2 and 3.

Fig. 18 shows the choice of direction of the observer tortoises in Experiment 3. Again, they showed significantly more rightward detours ($p = 0.036$), but one tortoise, namely Moses, went as many times left as right. Interestingly, Quinn started to switch directions, and in most of his trials walked away along the right side of the fence, compared to Experiment 2, where he unexceptionally went left. However, in all three successful trials, Quinn took the left detour.

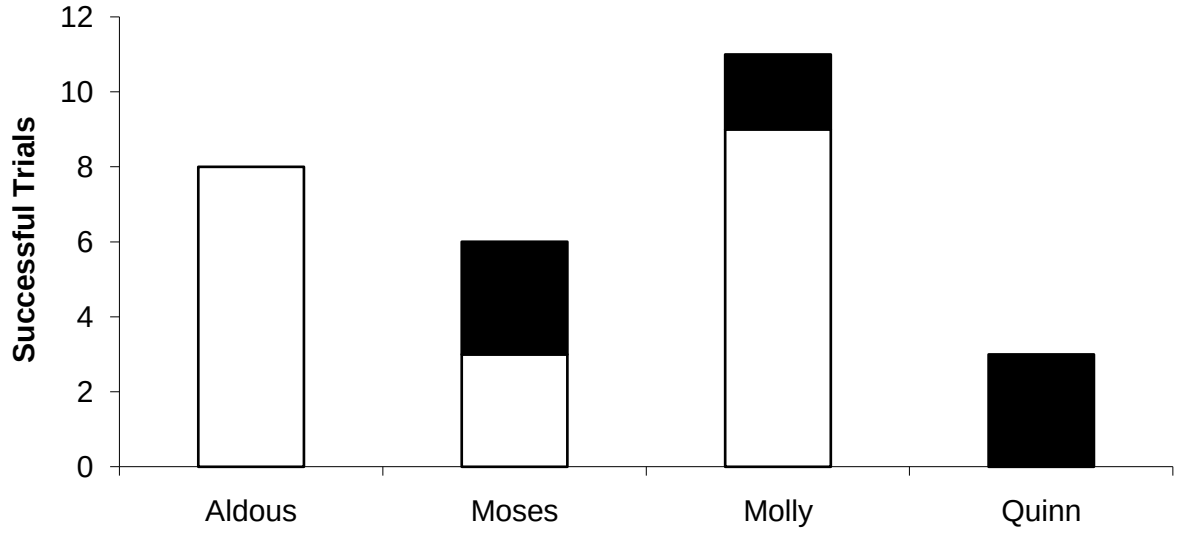

Fig.18: Number of successful trials of each observer tortoise group during experiment 3. Rightward detours are shown in white, leftward choices in black.

Mean Level of Performance

A repeated measures ANOVA of the mean levels reached by Group Y in Experiment 1, 2 and 3 revealed no significant difference of performance between all three experiments ($F(2) = 9.835$, $p > 0.05$), although there is an obvious drop of the performance during experiment 2, where the animals were not allowed to watch a demonstrator (see line with circles, Fig. 19).

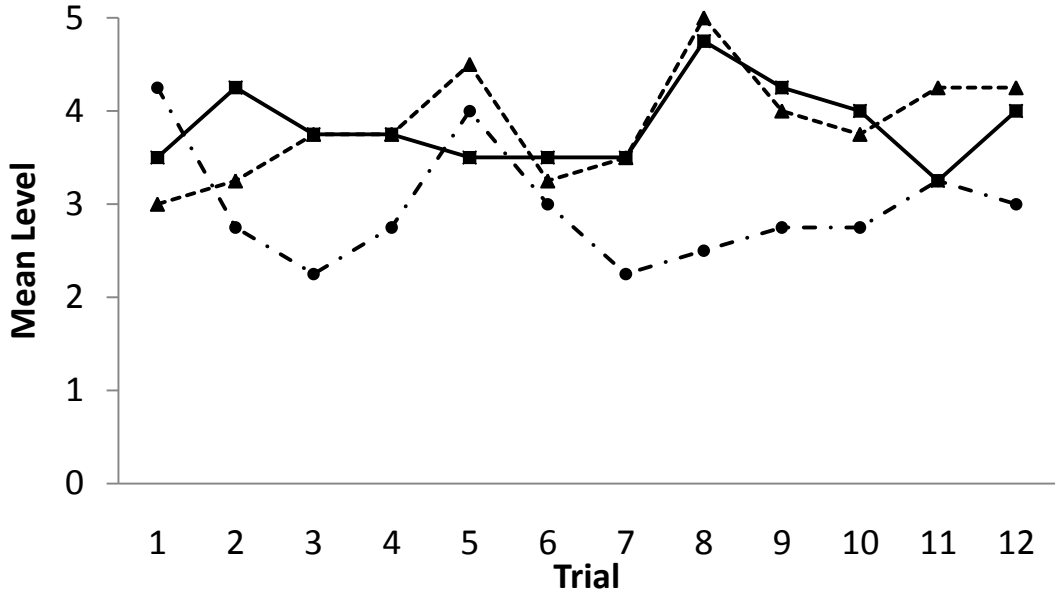

Fig. 19: Mean level of performance of Group Y for Experiment 1(squares), Experiment 2 (circles) and Experiment 3 (triangles).

Latencies

The time needed to complete the detour task in Experiment 3 differed between the individuals (Fig. 20). When Aldous and Quinn navigated the detour, they did it fast right from the first successful trial on. Molly showed an increased performance with the number of successful trials. In contrast to that, Moses was fastest in the first successful trials, but then her performance suddenly decreased (r = -0.21, Aldous; r = 0.33, Moses; r = -0.84, Molly; r = 0.09, Quinn).

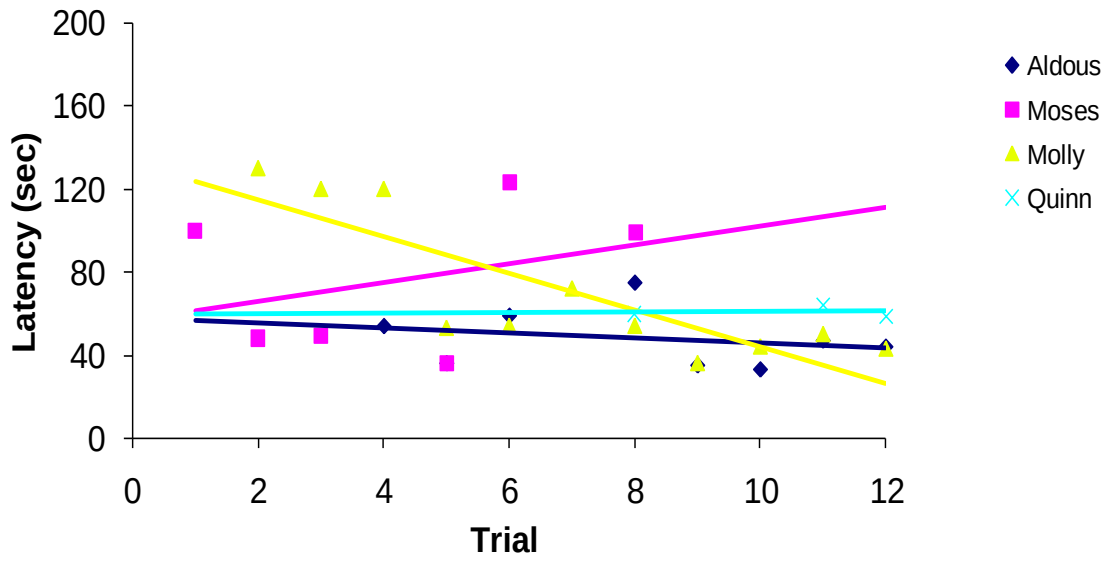

Fig. 20: This graph shows the relationship between the experience (more successful trials) and the time the observer tortoises needed to complete the task during Experiment 3.

Errors

The percentage of occurrence of error type No. 1 (“not moving away”) decreased in Experiment 3 compared to the first two experiments. Instead, another type of error (“walking till other side”) almost doubled (Fig. 21). Moses was the only tortoise that showed error No. 3 during this experiment.

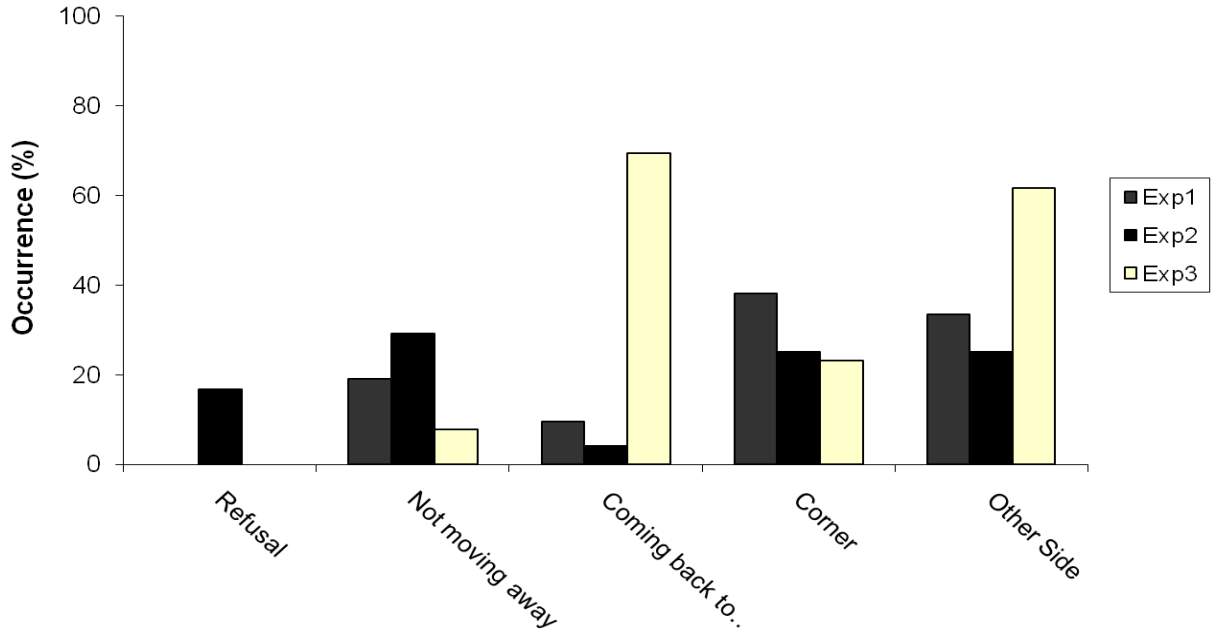

Fig.21: This bar diagram shows the occurrence of specific types of errors of Group Y during Experiment 1,2 and 3.

Discussion

Although a comparison of the performance between all three experiments did not reveal a significant effect, the individual performances of the tortoises show different patterns. Molly, one of the younger tortoises, learned the detour task in the last four trials of Experiment 1; however, a repetition of the demonstration trials in Experiment 3 increased her performance from 3 to 11 successful trials. This suggests that, once learned, it was easier for the tortoise to successfully copy the demonstrator's behaviour or it could be that it was the result of individual learning. However, Molly's performance did not increase during Experiment 2, where she/he had already learned how to reach the bowl, but showed a much better performance instead when having the possibility to watch Wilhelmina in Experiment 3.

Aldous' performance, which was perfect in Experiment 1, then surprisingly decreased down to only one successful trial during Experiment 2, but increased again during Experiment 3. The reason for this behaviour remains unclear. Interestingly, Aldous is our only tortoise that we know is male. It is possible that he focused more on the (female) demonstrator than the other observers. Though his success increased in Experiment 3 up to eight successful trials, his performance was not as good as in Experiment 1. Aldous' first successful trial in Experiment 3 was his fourth, but what happened during the first three? It could be that the

obvious insecurity during Experiment 2 continued inhibiting him also during the first part of Experiment 3, although Wilhelmina was present.
The pattern of errors made by Group Y tortoises was relatively similar between Experiment 1 and 2, but two types (No. 3 "coming back at wrong side of the fence" and No. 5 "walking to other side") clearly increased during Experiment 3. This was due to Moses, who was responsible for the increase of error type No. 3. She walked along the fence, but made the U-turn too early and hence came back to the angle at the wrong side of the fence. The reason why she started exhibiting this behaviour is currently not clear. It could be that Moses was a bit "overexcited", which made her turn around before even reaching the edge of the fence.
The most difficult part of the action sequence appears to be the part when the tortoises had to turn around at the edge of the fence and face the bowl again. This is also where most of erroneous behaviour occurred in both groups. In this specific position the tortoise looking straight forward do not see the baited food-bowl, but a tempting corner to rest instead.
If the tortoise made a turn at the edge, but it was not complete, it mostly ended up by walking till the other side of the arena without even looking at the bowl.
Furthermore, in Experiment 3 the tortoises made the detour significantly more in the rightward direction, as seen in Experiment 1 when they received their first twelve demonstration trials.

GENERAL DISCUSSION

Main findings

The results of this study show that solitary animals, like the red-footed tortoise, can learn socially. These findings argue against the *adaptive specialization hypothesis*, which claims that social learning only occurs in group-living and highly social animals. They rather suggest that the ability to learn through observation of a conspecific requires quite general cognitive abilities as is the case for associative learning. However, it is also possible that the ability to learn through observation of others was perhaps present in the amniotic stem reptile. This skill then might have been retained in all three amniotic taxa, namely reptiles, birds and mammals. However, if it is true that this ability was inherited from a more social amniotic ancestor, it would also support the adaptive specialization hypothesis.
This is the first evidence that a reptile species is capable of learning through observation. While demonstration of a conspecific improved the naïve tortoises' performance in making the detour, the absence of demonstration in the second experiment led to a slight (non-

significant) decrease of success in the observer group. However, the performance of this group did not differ significantly in all three experiments. Furthermore, in most cases the observer tortoises chose to go the same direction as the demonstrator, but also succeeded in sometimes going the detour leftwards, suggesting the tortoises had to learn about the detour and for most animals the latency to complete the task also decreased with the number of trials. On the other hand, the non-observer animals not only failed to reach the bowl in the individual learning condition, but could also not improve their performance when watching a demonstrator in the second experiment. Conditioned inhibition might have occurred during the first twelve trials in a sense that they learned that they could not access the bowl. Throughout Experiment 1, the tortoises spent less time at the intersecting angle, but instead of reaching the bowl, they mostly went into the corners to rest.

It is logical that animals living in social groups might encounter more possibilities to learn from others, and therefore more social learning events might be observed. But our findings show that being a social species is not a precondition for the occurrence of social learning. The only study that has shown that sociality may enhance social learning was a study by Templeton et al., (1999) with pinyon jays and Clark's nutcrackers. However, all other studies (see Reader and Lefebvre, 2001) have failed to find a correlation between sociality and social learning capability. Therefore, the answer to the question of what is the driving power behind this skill remained unclear. Reader and Lefebvre (2001) concluded that many possible variables for the evolution of social learning, e.g. sociality, phylogeny, dependence on parental care or simply cognitive capacity, may be involved and still need to be tested.

The red-footed tortoise used in this study, is neither a social animal, nor does it receive any parental care, however as it could still learn to solve a problem via observing a conspecific. This finding rather supports the theory that non-imitative forms of social learning should be considered as a subcategory of individual learning (Heyes 1994).

If the capacity to learn socially is really dependent of the general learning abilities of an animal, then differences in individual learning performances should predict similar differences in a social learning condition as has frequently been observed (Reader and Lefebvre, 2001).

According to purely ***experiential theories like the ASL model,*** (Heyes and Ray 2000) any animal which had appropriate prior experience would be able to learn socially. Our subjects had this experience. Therefore it is important to find out to which degree social experience is necessary for the tortoises to show social learning ability.

The role of the reward

Heyes (1994) suggests that observational learning can be regarded as a case of associative learning, and therefore explained by animal learning theory. According to this, an observer learns the R-S (response-stimulus) relationship not by experiencing it itself but via linking the model's behaviour with a specific outcome. This would then lead to a higher probability of matched behaviour in the observer. According to this, our observer tortoises might have associated the model's navigation of the detour with access to food. However, this explanation is restricted as it suggests that observational learning would only appear if a reinforcer is involved, as was the case in this experiment. Though we cannot exclude the hypothesis that the tortoises might have also navigated the detour when Wilhelmina would not have been rewarded, I believe it is rather unlikely. Miklósi (1999) points out that the role of the reward can influence the observer's behaviour in different ways. Firstly, reward may be generally necessary for copying to occur; secondly, the observer might be distracted by the presence of the reward. However, this did not appear to affect our tortoises. They attended to the model's actions and their head movements followed the demonstrator, as she navigated the detour.

Studies with birds (pigeons, Palameta & Lefebvre, 1985; Japanese quail, Akins & Zentall, 1998) have revealed mixed results of the effect of the demonstrator being rewarded for its action. Akins and Zentall (1998) exposed a quail to either a treadle-pecking or treadle-stepping demonstrator. For half of the quails in each group, the demonstrator's responses were reinforced, for the remaining quails, it was not. They found that only quails that had observed a rewarded model, showed significant evidence of imitation. However, in a slightly changed set-up McGregor et al. (2006) found evidence that pigeons even show imitation despite the demonstrators not being rewarded for their actions. Instead of testing the pigeons' imitative ability in an acquisition situation, McGregor and colleagues used an extinction testing condition. These results suggest that imitation in birds is rather blind than goal-directed. However, since the birds have learned in a pre-training to perform both actions, e.g. stepping and pecking on a plate, one could argue that blind imitation is more likely in such a context than when they observe new behaviours in an acquisition task. Since the tortoises were also confronted with an acquisition task, one might ask why they should copy a new behaviour that does not bring any benefits to them.

Underlying Mechanisms

There are four prerequisites that have to be fulfilled for social learning to occur (Bandura, 1977). One of these is *attention*. In order to learn something from a model the observer has to be attentive for a sufficient duration to perceive the action to be learned from. The amount of attention necessary depends partially on the relative novelty of the act. Paying attention to conspecifics might be unusual for solitary animals like tortoises, however our tortoises are group-housed and so may have learned that it is useful to attend to another tortoise through associative learning. The demonstrator normally needed approximately one minute to complete the task. However, sometimes she did not start to move right away, the result being that the observer tortoises had to wait in the small cage for a longer period of time. In these cases we frequently had to rerun trials, because the observers stopped watching.

Another important factor is the *motivation* of the observer to watch the demonstrator and reproduce its actions. Because all of the tortoises were rewarded with a preferred food, it was assumed and their behaviour indicated that they were motivated to get to the food. This was increased by not feeding them beforehand. First, they tried to push through the fence and then, in the case of the experimental group, circumvented the fence by copying the model. In this case the value of the reward might have been even greater, since they actually saw another tortoise feeding. The method used in this experiment, does not allow clarification of the social learning mechanism responsible for the tortoises' performance. Two of the observer tortoises, the smaller ones, were not able to reach the goal from the first trial on, but were successful at least twice. This contrasts with the control group animals, who all failed to reach the goal.

Which social learning mechanism could account for the tortoises' behaviour? We cannot entirely rule out the possibility that local or stimulus enhancement is responsible for the results. Only a two action procedure can rule out enhancement and facilitation effects. However, it seems unlikely that they account for our tortoises' behaviour. If stimulus/local enhancement would have occurred, then the tortoises should only have made the detour along the actual path of the demonstrator. Although three of four observers followed the demonstrator's path on their first successful trial, one tortoise, Quinn, went left on his first successful trial. Furthermore, although there was a significant preference for the rightward detour, three of the four observer tortoises also navigated the detour successfully in a leftward direction in Experiment 1. This means that the animals did not always follow the demonstrator's behaviour exactly, but found other similarly efficient solutions for the problem

that they were confronted with suggesting a more flexible strategy. They learned that they could get to the other side of the fence and hence to the bowl by either going right- or leftwards. Therefore social learning mechanisms like stimulus or local enhancement are unlikely to account for the tortoises' behaviour.

So, what were the tortoises doing? It is possible that they emulated the behaviour of the demonstrator. That they had learned about properties of objects or other aspects of the environment (Whiten et al. 2009). They may have come to understand the object's affordances, and having recognised these, the observer may then exploit them in their own behavioural strategies. In our tortoise's case, affordance learning would be the understanding of the fence as a barrier that can be circumvented by either going right- or leftwards, and by doing so they can reach the food-baited bowl on the other side of the fence.

Future Research

As this is the first study on this topic many questions still remain. It is important to examine what the tortoises had learned about the fence. This can be done by investigating the capacity to generalize to other detour situations. Are the tortoises also capable of generalizing the learned information about the detour to a different context? Experiments that address this question would include e.g. the same V-shaped fence but starting from an outward position or using a new shape of fence, e.g. a U-shaped detour. If the tortoise were successful in such modified detour conditions, then it would be very likely that the animals learned to see the fence as an obstacle that can be circumvented.

Other experiments should investigate the underlying mechanisms at work, to examine exactly how the tortoises learn from others. With a two-action procedure one might be able to investigate whether tortoises are actually imitating a model or rather find their own way to reach a specific goal. To understand the origins of this behavior, it is important to manipulate the experience of the tortoises. The subjects of this study were kept in groups and were experienced in watching others' behaviour and may have learned to associate this with a certain outcome. A critical test of this social experience hypothesis would examine whether these results only occur in group-housed tortoises. To find an answer to that question, the study would have to be repeated with another group of tortoises, which would be kept alone.

Another simple change in the experimental design could test the role of the model. Does it have to be a tortoise to learn how to navigate the detour? It could also be that any other animal or an artefact like a toy animal, or even a simple blinking light showing the observers the path to the goal, is sufficient to successfully navigate the detour. And finally, testing other solitary

reptile species in a social learning task, would further contribute to the understanding of the evolutionary origin of this skill.

Conclusion

In conclusion, this study has shown that the red-footed tortoise, a non-social species, is capable of learning how to reach a goal by observing the actions of a conspecific in an otherwise unsolvable detour task. None of the non-observer animals managed to navigate to the bowl, whilst all of the observer tortoises were successful. These findings provide striking evidence against the adaptive specialization hypothesis. It is clear that tortoises can learn something from a conspecific demonstrator; however, this study could not clarify exactly what social learning mechanisms were involved. Nevertheless, it provides a first step towards novel and exciting research into social learning in a non-social species.

The fact that the tortoises could use a conspecific as a cue to navigate the detour tells us that sociality is not a prerequisite for this type of learning and suggests that the ability to learn socially maybe a simple reflection of an animal's general ability to learn. Therefore, it is probable that a certain amount of social experience is necessary to be successful in learning from others. Future works should examine this.

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