MASTER'S THESIS

Titel der Masterarbeit/ Title of the Master's thesis

"Car versus Tortoise"
On the mechanisms of social and non-social learning

verfasst von/ submitted by

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angestrebter akademischer Grad/ in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2017/ Vienna, 2017

Studienkennzahl/ degree program course:	A 066 878
Studienrichtung/ degree programme:	Verhaltens-, Neuro- und Kognitionsbiologie
Betreut von/ Supervisor:	Univ.-Prof. Mag. Dr. Thomas Bugnyar

ACKNOWLEDGEMENTS

I would first like to thank Univ.-Prof. Mag. Dr. Thomas Bugnyar of the Department of Cognitive Biology at the University of Vienna for his academic support and for agreeing to supervise this project in the first place.

Furthermore, I would like to thank Dr. Anna Wilkinson for providing her research facilities at the University of Lincoln and for entrusting her cherished tortoises into my care. Beyond that, the door to Annas' office was always open whenever I ran into a trouble spot or had a question about my research or writing. She allowed this project to be my own work, but steered me in the right the direction whenever I was in doubt.

Special thanks belong to Paul Sheridan for his practical support in the lab and especially to Phil Assheton for his statistical input. Without your patience and endeavour Phil, I would have been lost.

Also, I am gratefully indebted to Eleonore Haussner for her very valuable comments on this thesis.

Finally, I must express my very profound gratitude to my parents who supported my decision to move to England and realise this project on so many different levels. I am forever grateful to Keith and Fiona Datchler, Chris Clarke, Luthia Merino and Madlen Schwaiger for providing me with unfailing support and continuous encouragement throughout the last year. This accomplishment would not have been possible without them.

Thank you.

Amelie

Table of Content

"Car versus tortoise"

On the mechanisms behind social and non-social learning

The ability to learn from conspecifics is adaptive, offering animals a shortcut to gaining access to resources. Whilst one line of research has focused on the strategies and benefits of social learning, the other has been concerned with the mechanisms producing those effects. Historically it has been argued that social learning mechanisms are distinct from other types of learning in both evolutionary origin and underlying process. Yet recent thought promotes the idea that social and asocial learning depend on a common set of mechanisms, namely associative mechanisms. To shed light on this issue, the present study investigates whether the solitary red-footed tortoise (*Chelonoidis carbonaria*) uses a conspecific and an inanimate object alike in order to solve a local enhancement task. For this purpose, one group of subjects was habituated to an in-animate, moving object, whilst the other was conditioned to it. Subjects were then tested in three different conditions, facing either the inanimate object, the conspecific or no demonstration. We found no evidence for differences between the two groups and their response to the two stimuli during testing. This finding is consistent with our expectation that the subjects would treat both stimuli the same, challenging the idea that social learning is distinct from asocial learning. On the contrary, our findings indicate that both types of learning are mediated by the same set of associative mechanisms.

1.   Introduction

Living in social groups offers non-human animals a variety of benefits such as access to resources, shelter and protection from predation. Moreover, it provides animals with an opportunity to learn from conspecifics, thus offering a shortcut to finding a solution. Whilst research in this field has largely focused on the adaptive functions and the results of social learning, little is known about the cognitive or neural processes producing those effects (Heyes 2012).

Two competing hypotheses exist concerning the processes underlying social learning: one proposes the existence of processes specific and exclusive to social learning, while the other suggests that social learning utilises the same processes as asocial learning. The former hypothesis, called adaptive specialisation hypothesis, has historically been dominant and proposes that the ability to learn socially has evolved as an adaption for group living (Klopfer 1961, Templeton *et al.* 1999). It conceptualises social learning as a process separate and independent from other already existent learning processes (Heyes 1994, Heyes 2016).

The more recent, alternative theory sometimes referred to as the associative hypothesis, proposes that social learning utilises the same processes as asocial learning. It conceptualises social learning as an instant of asocial, associative learning, in which merely the input happens to be socially derived, while the same mechanisms are used to process the information (Sterenly 2009, Heyes 2012).

The associative hypothesis receives support from both empirical and conceptual sources. Empirical findings of co-variation between social and asocial learning abilities in several species (Lefebvre and Giraldeau 1996, Reader and Laland 2002, Reader *et al.* 2011) cast doubt on the independence of the two abilities and instead suggest the existence of a link between the two. European starlings (*Sturnus vulgaris*)

for example are comparably consistent in their problem–solving abilities across non-social and social contexts (Boogert *et al.* 2008). Similar results were found in captive, wild-caught pigeons (*Columba livia*), reporting a positive correlation between performance in an innovation and a social learning task (Bouchard *et al.* 2007).

However, there is also evidence supporting the adaptive specialisation hypothesis (Lefebvre & Giraldeau, 1996; Munger *et al.* 2010; Shettleworth 1993) . A prominent example derives from a study by Templeton and colleagues (1999). The researchers presented two corvid species, that differ mainly in their sociality, with a social and an individual task. Whilst the more social Pinyon Jays performed better in the social tasks, Clark's nutcrackers performed equally well in both tasks.

The most clear-cut evidence in favour of the associative hypothesis rises from the study of social learning in non-social species. Considering that social learning mechanisms have supposedly evolved through selection pressures from the social environment, one would not expect solitary species capable of learning from conspecifics. However, several studies showed exactly this. Fiorito and Scotto (1992) found the non-social common octopus (*Octopus vulgaris*) capable of social learning in a colour discrimination task. Similarly, Wilkinson and colleagues (2010) presented another non-social species, the red-footed tortoise (*Chelonoidis carbonaria*), with a detour task which the animals failed to solve through individual learning, yet were able to succeed by observing the actions of a conspecific. Another example of social learning in reptiles comes from a field study at Aire Island in Spain (Pérez-Cembranos and Pérez-Mellado 2015) Field observations revealed that Balearic lizards (*Podarcis lilfordi*) show strong attraction towards foraging conspecifics and even towards immobile copper models. Interestingly they show a preference for groups of conspecifics even in absence of food. This suggests that non-social animals are able to use the presence of conspecifics as a social cue potentially providing them with

discrete information about the presence of food. Consequentially, this line of evidence weakens the main argument of the specialised adaptation hypothesis, namely social learning being an adaptation to group living.

The evidence presented suggests that social and asocial learning depend on a common set of mechanisms of shared decent. Yet, it remains unclear how these mechanisms work. Promoters of the associative hypothesis advocate that the traditional categories of asocial learning and the main categories of social learning coincide. This analogy offers a lead on how the processes operate, illustrated by the following examples.

First, stimulus enhancement, traditionally considered the simplest category of social learning (Spence 1937, Thorpe 1956, Kis *et al. 2015*) and single stimulus learning have been argued to coincide (Heyes 2012). One example comes from young black rats in Israeli pine forests who join adults when feeding, exposing them to partially stripped pine cones. Gnawing at these cones allows them efficient and easy access to the seeds underneath. Here learning occurs through trial and error when the rats continue stripping the cones by themselves (Terkel 1995). This process is social only by means of exposure as the adults create the conditions that are necessary for learning to occur (Shettleworth 2010).

Second, there is strong evidence for conformity of classical conditioning and observational conditioning (Heyes 2012, Mineka and Cook 1993, Suboski 1990) which has been considered the second traditional category of social learning (Cook *et al.* 1985). In observational conditioning, the observation of a conspecific' actions or affective state and behaviour towards one stimulus results in the building of an association between the two in the observer. As a result, the observers subsequently changes its own behaviour accordingly. Fear conditioning is a straight forward case of classical conditioning. Observing a conspecific's fear response towards a snake,

elicits a fear response in the observing monkey (Mineka and Cook 1993). Through classical conditioning the monkey builds an association between the snake and fear (Frith and Frith 2012).

Thirdly, observational learning, which is considered to be the third major social learning category, and S-R learning could be mediated by the same associative learning processes according to Galef (1988) and Heyes (1994). In the case of S-R learning, an animal builds a relationship between a stimulus and a response or an action and its outcome that occur selectively in the presence of the stimulus or action (Thorndike 1927). The same could be said in respect to observational learning in which the observation of a demonstrator exposes the observer to a relationship between a response and a reinforcer, causing the observer to form an association between them (Rendell *et al.* 2010).

The analogy between the three main social learning categories and the three main principles of animal learning theory further supports the idea that they are mediated by the same associative processes. These cognitive processes encode information for long term storage by forging excitatory and inhibitory links between event representations (Heyes 2012), independent of whether the information is provided by a social agent or through other (asocial) channels. In fact, a fMRI study in humans provides strong support for this theory. Behrens and colleagues (2008) showed that humans attend to social input via the same associative processes that mediate attention to non-social stimuli.

If social learning depends on asocial, associative processes as the evidence suggests, some have argued that social learning is neither really social nor special (Heyes 2012). The specifically social aspect of social learning might just lie elsewhere than previously thought: in the information input stage rather than the information

processing stage Specifically, a social input bias has been suggested, that provides animals with sensory, perceptual or motivational systems adaptively specialised for social cues, making them especially receptive to social information. For example, an animal may have a sensory system that makes it better at seeing affective displays, an attentional system that more accurately processes perceptual input from conspecifics, or a motivational system that predisposes attention toward the tracking of conspecific movements (Heyes 2012, Gustafsson 2013). The existence of a social input bias could potentially explain patterns of results previously thought to support the specialised adaptation hypothesis such as the formerly mentioned study by Templeton and colleagues (1999). The species differences reported could be a result of differences in perception, sensory or motivational capabilities between the two species (Heyes 2012, Gustafsson 2013).

Drawing on the evidence discussed, social cues could be learned through associative processes similar to other environmental cues (Heyes 2003). Consequently, this would predict that any species irrelevant of its sociality has the ability to learn socially as a consequence of exposure to conspecifics. The findings of Wilkinson et al. (2010) suggest that in the case of the red-footed tortoise this might be the case as the animals were able to learn socially and appeared to copy actions of a conspecific in a detour task despite being non-social. In order to investigate the processes mediating this ability, this project examines if tortoises treat conspecifics as cues just like any other cue. We investigate this by exposing two groups of animals to an inanimate, moving object over the course of a few weeks. The only difference between the two groups was that in the experimental group the car preceded the arrival of food whereas in the control group both events where temporally separated. As a result, the experimental group should become attracted to the stimulus whereas the control group should become habituated due to the temporal relationship and the contingency between the two events. Both groups were then presented with

three different conditions of a local enhancement task. Depending on the condition, subjects were presented with a demonstration by the in-animate object, or a conspecific or no demonstration. We expected to find a preference for the site of the conspecific in both groups in accordance with previous findings in socially housed red- footed tortoises (Wilkinson *et al.* 2010). Yet, it was anticipated that only the tortoises in the experimental group would show a similar bias in favour of the car. Such a consistent bias would be anticipated due to previous reinforcement through the course of training. If the tortoises treated both stimuli alike, it would suggest that they do so by means of associative learning.

2. Methods

2.1. Subjects and housing

Twelve red-footed tortoises (*Chelonoidis carbonaria*) participated in this study. All subjects were captive bred and are housed within and belong to the University of Lincoln. Their exact ages are unknown, however their plastrons reached a size of between 18.5 and 24.0 cm at the beginning of the study. The majority of the subjects had experience with cognitive research but were unfamiliar with the present task.

The animals lived in a heated room within the facilities of Lincoln University. The room was covered with wood chips and offered a variety of shelters such as wooden huts and moist pens and contained a variety of heat lamps. Water was available ad libitum. The temperature of the housing room was maintained at 29°C and approximately 60% humidity. The artificial room lighting was active from 8am until 8pm and windows were present to the outside. Subjects received their daily feeding after experimental sessions (a variety of fruit and vegetables).

2.2. Experimental room

The exposure as well as the experiment was conducted in a heated room (2.05m x 3.50m) that was adjacent to their holding room (Figure 1) and maintained at approximately 29°C. There were windows present to the outside and two standard fluorescent tube lamps (25W) provided additional light.

2.3. Exposure

For the purpose of this experiment subjects were randomly assigned to one of two training conditions, the experimental (n=6) and the control group (n=6). The groups were matched for size, age and experience. Both groups received training simultaneously and within the same room whereby the room was divided by a commercial flower bed wall (height: 39cm) separating both groups visually. The

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groups received exposure in one of the two compartments but were altered between the two every other day. Subjects received up to five days a week of exposure over a period of 6 weeks, each session lasting for two hours. Every session was recorded by a small Sony video camera (type: 42x.i. Zoom HD) that was raised by a tripod aiming to gain a view of both groups simultaneously. Subjects received their daily feeding amount throughout training, water was available ad libitum.

Both groups were exposed to a remote controlled car (Nissan, blue, 25x 7cm) during training. The number of encounters with the device was matched between the groups and varied daily between a minimum of three and a maximum of five exposures, the timing of events was pre-randomized. In the experimental group (n=6) the arrival of the car always preceded the immediate arrival of food. However, in the control group (n=6) the presentation of the car and the arrival of food were not contingent on one another but temporally separated. During exposure the car was held within a cardboard box and introduced to the subjects directly from the box to prevent the other group from observing. The experimenter remained with the other ("inactive") group and controlled the car via the remote-control to avoid acting as a cue. The car was moving around for about 30 seconds throughout the whole compartment before remaining in one place for 10 seconds. Depending on the group, food was then dropped around the car or it would be removed via the box after 10 seconds without the arrival of food. Subjects in both groups received the same number of exposures to the car and the same type, number and size of portions of food each day. The only difference between the two groups was that in the experimental group the car should predict the arrival of food whereas the control group should become habituated to the stimulus due to the temporal relationship and the contingency between the two events (Heyes and Pearce, 2015). Overall the tortoises received twenty-one trials over the course of seven weeks, with each one lasting for two hours and consisting of multiple exposures to the stimuli.
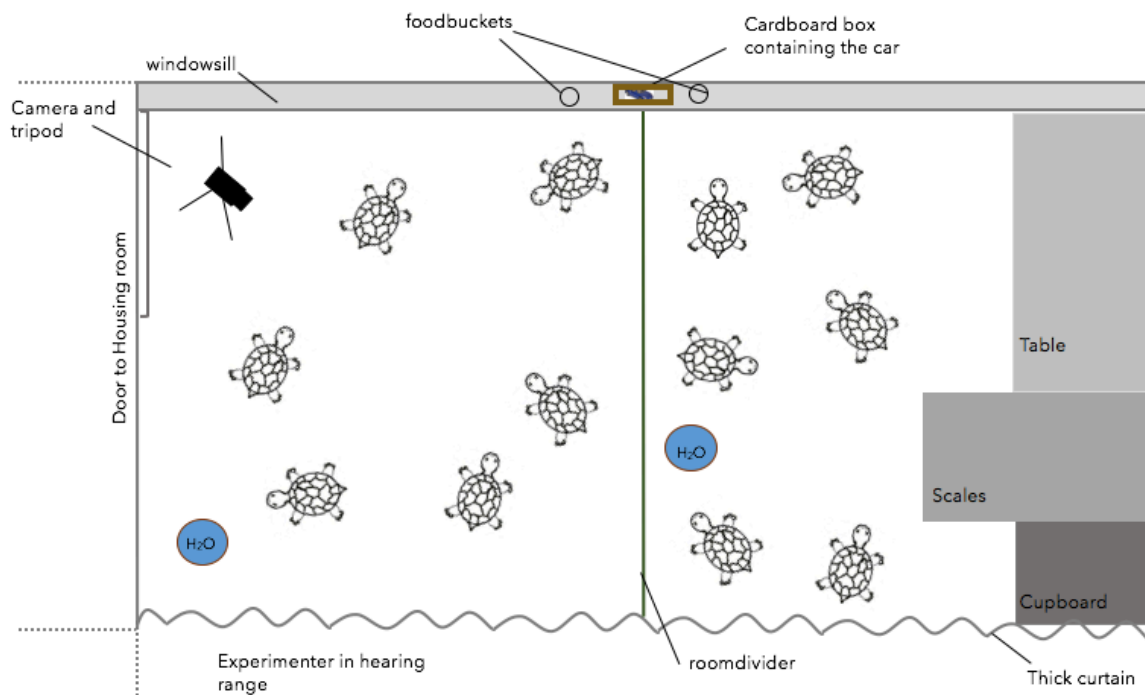
Figure 1: Sketch of the experimental room throughout exposure. Animals were carried into the room via the door on the left. Both groups were alternated in between the two separate spaces every other day. The experimenter was always in hearing range behind the curtain and entered the room through the curtain on the left side of the room. During exposure the experimenter remained within the space of the "inactive" group and food was provided by the bucket on the side of the "inactive" group to avoid any additional cues.

2.4.   Criteria to test

Behaviour during exposure was recorded by a Sony video camera and we recorded the subjects' behaviour towards the car during exposures. We counted the number of approaches per individual towards the moving car (focusing on and following the car) per session and per event. We compared the behaviour of both groups towards the stimulus after week 5 by plotting data from the last seven days. The experimental group showed significant interest in the car in contrast to the control group, testing was pursued.

The day before testing, subjects were habituated to the testing apparatus. All subjects were allowed fifteen minutes to explore the arena whilst being offered food in the centre of the arena.

2.5. Demonstrator

We chose Betty, a female red-footed tortoise, to act as a demonstrator. We were able to use her as a stimulus in the enhancement task in the same manner as we used the car.

2.6. Testing Apparatus

The testing arena was placed on the floor in the same room that was used for exposure. It was made of plastic and measured 158 x 108cm. The arena's floor was covered in bask chips. Two identical feeding wells were placed on one end of the arena 67 cm apart from each other and 30 cm from the back wall. A holding box (56x 50x 30 cm) was placed at the opposite end of the arena facing the two wells. The box provided test subjects with a clear view of the arena through a wire mash trapdoor. In order to block the view an opaque trapdoor was inserted. A Sony video camera was placed on a tripod behind the opposite end of the arena facing the holding box. The experimenter remained behind the holding box in order to place and remove the trapdoors and record the subjects' choice.
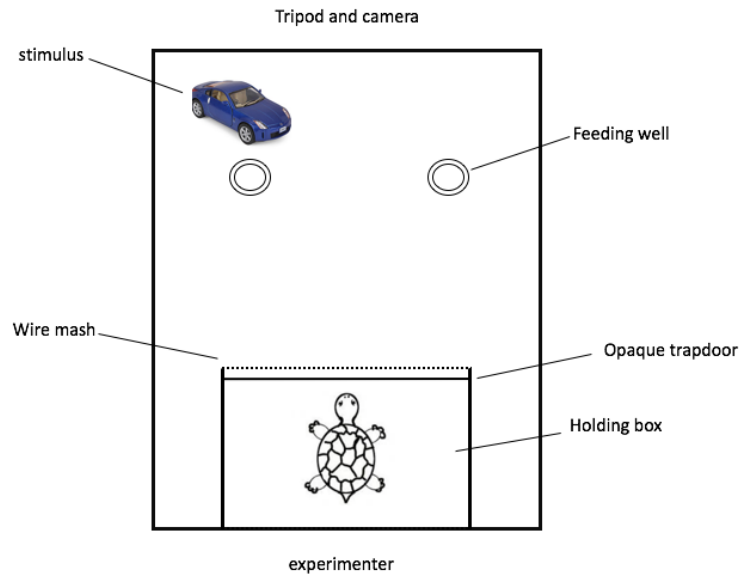
Figure 2: Testing apparatus: Tortoises were placed in the holding box with the opaque trapdoor down, after placement of stimulus the trapdoor was removed and tortoises were given 30seconds to watch the arena before the trapdoor would be placed again whilst the stimulus was removed and the reward was placed in both wells. At last both trapdoors were removed and the subject was able to make its choice.

2.7. Testing Procedure

All subjects were presented with three different testing conditions in a pseudo-randomized block design (Figure 3). Subjects received four trials of one condition before being tested in the next. The order of conditions was randomized as well as the testing order of the subjects. Depending on the testing condition, subjects were presented with either a conspecific (social condition) or the car behind one of two feedings wells (non- social condition). In the third condition subjects were released after 30 seconds without any additional cues available (non-stimulus condition). The order of the conditions in which the animals were tested as well as the position of the stimuli were randomized within the groups and matched across groups.

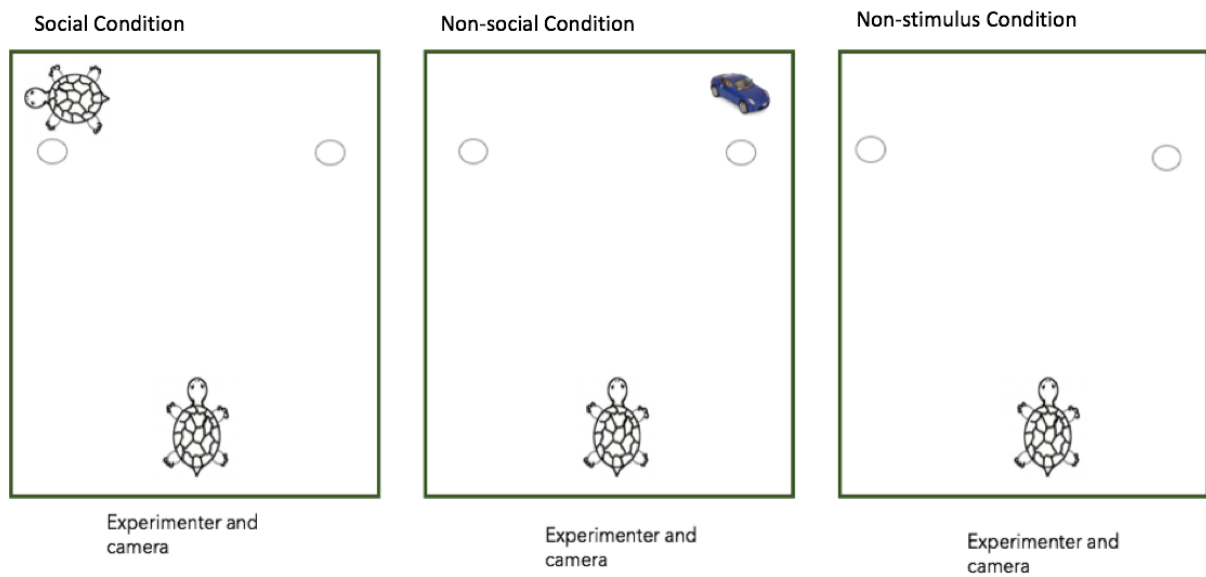Subjects received up to three trials a day with long breaks in-between.

Figure 3: Subjects were presented with three different conditions in which they were presented with Betty, a conspecific, a remote controlled car or no stimulus, thus no demonstration. The tortoises received four trials each.

Table 1: Subjects were presented with three different testing conditions in a pseudo-randomized block design. The order of conditions was pre-randomized and matched across groups.

Experimental Group	Control Group	1st .Condition	2nd .Condition	3rd .Condition
T-19	Mozart	car	tortoise	control
Aldous	Savina	control	car	tortoise
Alexandra	Patty	tortoise	car	control
Ranieri	Wilhelmina	tortoise	control	car
Gerard Butler	Moses	control	tortoise	car
Darwin	Seisou	car	control	tortoise

2.8.   Procedure

During test trials each subject was placed in the holding box with the opaque trapdoor down whilst the stimulus was placed. Next the opaque barrier was removed and subjects were allowed 30 seconds to watch the demonstrator through the wire mesh trapdoor. After 30 seconds the opaque trapdoor was reinstalled before the stimulus was removed, the bark was rearranged and both feeding wells were filled with one piece of fruit each (strawberries or mango). Finally, both doors were removed allowing the subject to move freely and approach one feeding well. The

tortoises were allowed 30 seconds to start moving and given 2 minutes to solve the task after starting to move. Subjects were allowed to visit one feeding well and consume the food within. A choice was defined when the animals' beak came within 5cm proximity of one of the wells and was reinforced irrelevant of choice. After the animal finished eating it was carried back to its housing room and received a break until all the other subjects finished their trials. Before collecting the next subject, the experimenter rearranged the bark, emptied and cleaned the feeding wells using "Safe" 4 Disinfectant spray as well as swapping them in position to extinguish potential scent cues.

Any trial in which the observer did not watch the demonstrator for at least 15 seconds or in which the subject did not make a choice was repeated.

2.9. Data collection

Trials were marked as being either *correct* in case the position of the stimulus and the subjects' choice matched or *fail* in case they differed. If subjects did not pay attention whilst being presented with either the car or their conspecific, the trials were marked as *repeat* and were repeated after a long break. Latency of approach was recorded using stopwatches (type: Brannan England sports timer).

2.10. Data analysis

2.10.1. Analysis of Training

In order to assess the progress of training a Wilcoxon Mann Whitney Test was conducted, comparing the behaviour of both groups towards the car during their fifth week of training. Here, we calculated the number of approaches towards the stimulus per individual over the course of week five. Consequently, we compared the overall participation (percentage) of the individuals from the experimental group with the participation of the control group by running a Wilcoxon Mann Whitney Test in R.

2.10.2. Analysis of Testing

We used a Generalized Linear Mixed Model to assess the ability of the tortoises to choose the correct feeding well. Group (experimental vs control group) and stimulus (car vs tortoise) were coded as fixed effects. Changes in behaviour as the trials progressed were measured by adding time as a covariate. All interactions were also included in the model. We used R (version 3.3.1) and Lme4 (package version 1.1.12). Our outcome variable was a binary response variable: trials were coded as correct if the subject's choice matched the position of the stimulus and as failure if they did not match. As random effects we had intercepts for each tortoise. Our predictors were trial, group and the two stimuli car and tortoise. Group and stimulus were effect coded, trial was treated as a covariate with the first trial coded as zero in order to focus the main effects on performance at time zero (start of testing) and to look at performance over time. Hence, a form of centering was conducted by shifting trial one to trial zero. Collinearity was not an issue as the order of subjects and the order of conditions were pre-randomized and a correlation matrix for stimulus effect and group effect revealed no correlation either. P-values were based on the standard Wald tests. The main assumption of our analysis was of a linear relationship between trial and log odds.

Additionally, we conducted a number of analyses to test for potential side biases. An intercept-only GLMM (with animals as random effects) was used to test whether side choices (left=1, right=0) tended more on average to one side than the other, and a Generalized Linear Model (with animals as *fixed* effects, and no intercept) was used to test whether individual animals had a preference to the left or right. Here, we modelled the choices (left or right) of the subjects of all three conditions (car, tortoise, no stimulus). Furthermore, a chi-square test was used to test whether we see more side biases than we would expect according to chance.

3.   Results

Despite the fact that both groups responded significantly different towards the stimulus during training (W=0, P-value=0.004772), no significant two- way interactions between the two groups and their preferences for either stimuli were found during testing (GLMM: Coefficient Estimate= 0.0.4918, SE= 0.40072, P-value= 0.9023; Table 2). Moreover, we did not find any significant three-way interaction. Thus there is no evidence for differences between the two groups and their response towards the two stimuli and for this pattern to change over time (GLMM: Coefficient Estimate= 0.07379, SE= 0.22605, P-value= 0.744; Table 2)

Table 2: Results from the GLMM illustrating interactions. Positive coefficients represent the experimental group and the stimulus car, negative coefficients represent the control group and the stimulus tortoise. Asterisks mark interactions and highlight statistical significance (Pr(>(>|z|).

Fixed effects	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.54784	0.40072	-1.367	0.1716
Stimulus Effect	0.63001	0.40072	1.572	0.1159
Group Effect	0.94586	0.40072	2.360	0.0183*
trial	0.53037	0.22605	2.346	0.0190*
Stimulus Effect* Group Effect	0.04918	0.40072	0.123	0.9023
Stimulus Effect* trial	-0.46781	0.22605	-2.070	0.0385
Group Effect* trial	-0.50021	0.22605	-2.213	0.0269*
Stimulus Effect* Group Effect* trial	0.07379	0.22605	0.326	0.7441

There was, however, a significant effect of trial depending on two factors: stimulus and group (GLMM: Coefficient Estimate= -0.50021, SE= 0.22605, P-value= 0.0269; Tab.2). Independent of which group they were in, subjects showed an increasing preference for the tortoise through the course of testing. Preference for the car, on the contrary, remained constant across trials (Figure 4).
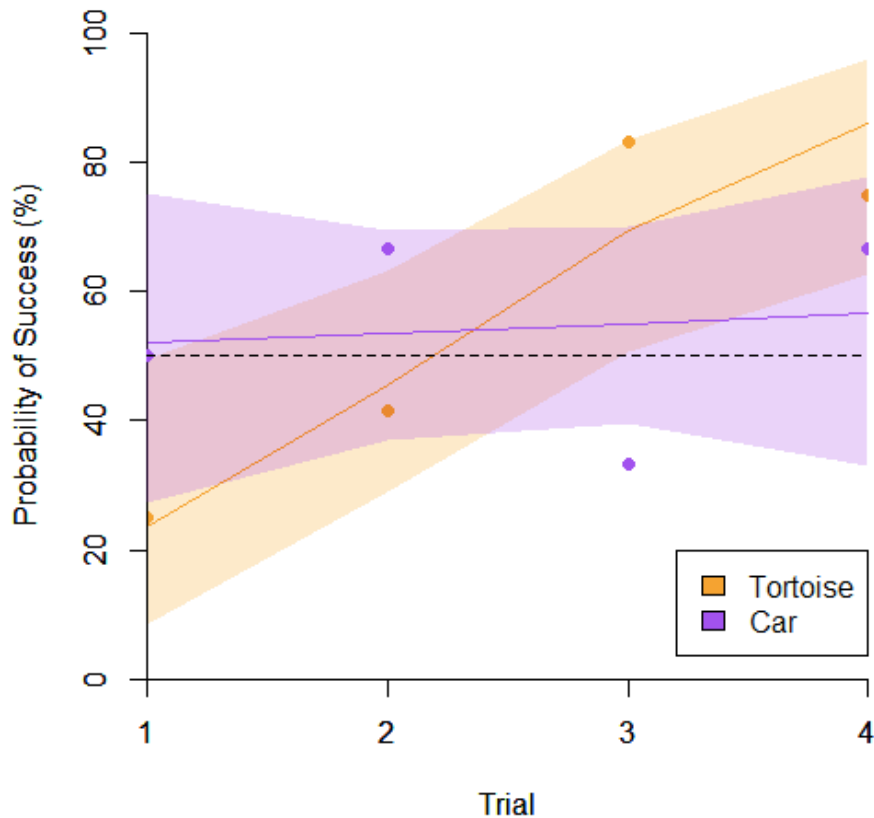
Figure 4: Percentage of correct choices across groups per trial and per stimulus: lines represent the best fit, dots represent the actual percentages and the coloured regions represent the CI of the model, chance level is illustrated by the dotted line.

Looking at each group separately, we found that the experimental group's choice for both stimuli stayed constant and non-significant over the course of four trials (Figure 5). However, the control group avoided both stimuli significantly in the beginning, yet showed a steady increase in preference, reaching significance in trial four (GLMM: Coefficient Estimate= -0.50021, SE= 0.22605, P-value= 0.0269; Table 2; Figure 5).
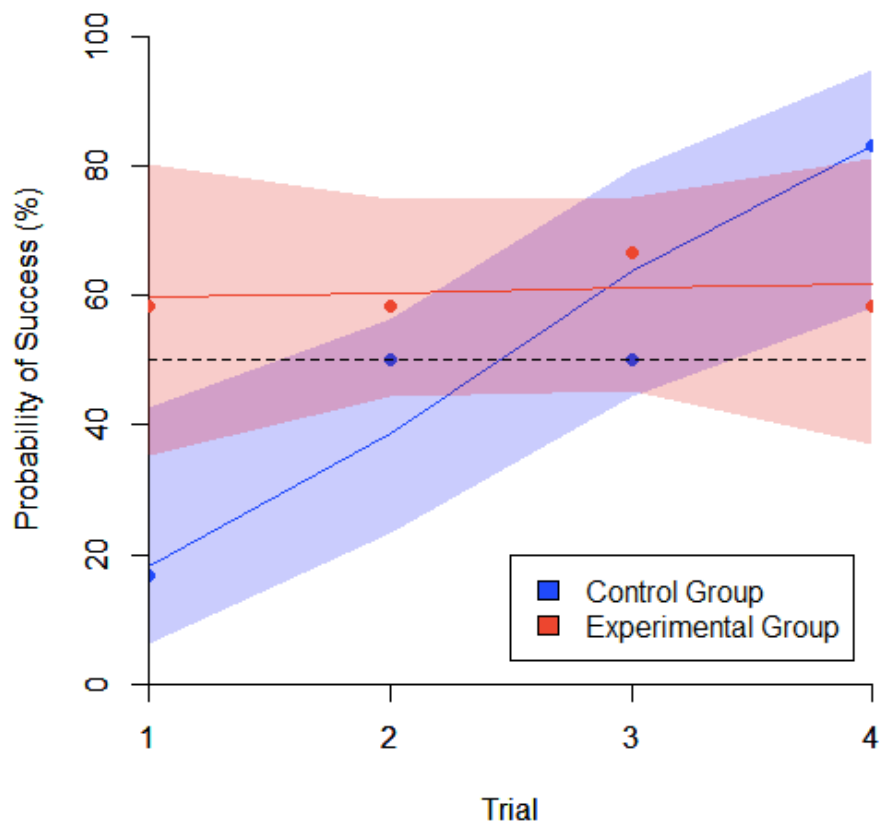
Figure 5: Percentages of correct choices across stimuli per trial and per group: lines represent best fit of the model, dots represent actual percentages and coloured regions represent the CI of the mode, chance level is illustrated by the dotted line.

Both groups choose the demonstrator increasingly over time (Figure 6). However, we only have evidence for significance in the control group. In the beginning of the study, the control group avoided their conspecific significantly yet in the end they showed a significant preference for Betty.
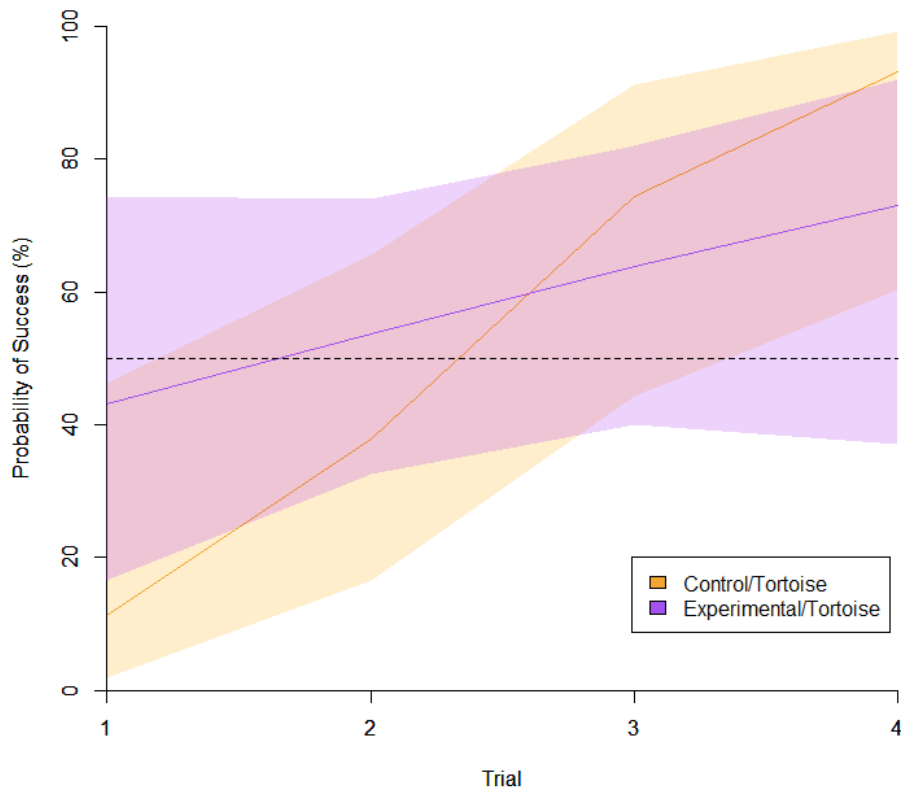
Figure 6: Percentages of correct choices in the social condition per trial and per group: lines represent best fit of the model, dots represent actual percentages and coloured regions represent the CI of the mode, chance level is illustrated by the dotted line.

When presenting subjects with the inanimate stimulus, no differences were found between the two groups (GLMM: Coefficient Estimate= 0.04918, SE= 0.40072, P-value= 0.9023; Table 2; Figure 7)
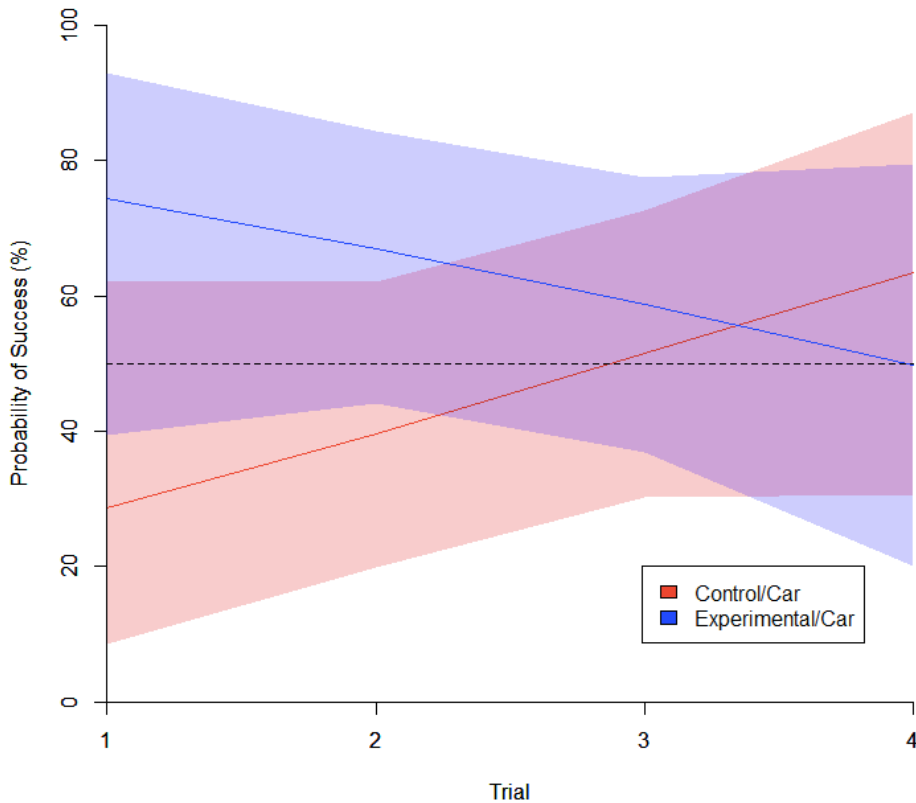
Figure 7: Percentages of correct choices in the non-social condition per trial and per group: lines represent best fit of the model, dots represent actual percentages and coloured regions represent the CI of the mode, chance level is illustrated by the dotted line.

3.1. Non-stimulus Condition

To test for potential side biases a Non-stimulus condition was performed. Overall, the GLMM revealed no significant biases towards one specific side (Intercept: Coefficient Estimate= 0.2031, SE= 0.3882, P- value= 0.601). However, at an individual level it appears that Savina, Mozart and Moses have a preference for going to the right whereas Aldous and Alexandra have a tendency to go to the left (Tab.2). Running a chi-square test on the individual p- values revealed that we see significantly more side biases than would be expected by chance (x^2= 33.965, df=1, P-value=5.611e^{-09}).

Table 3: Results from the GLMM illustrating individual side biases: positive coefficients are coded for the left side, negative for the right, Asterisks highlight statistical significance. Dark shaded rows represent individuals from the control group, light blue represents subjects from the experimental group.

Subject	Estimate	Std. Error	z-value	Pr(>|z|)
Aldous	-2.3979	1.0445	-2.296	0.0217*
Alexandra	-1.6094	0.7746	-2.078	0.0377*
Darwin	0.3365	0.5855	0.575	0.5655
Gerard B.	0.3365	0.5855	0.575	0.5655
Moses	2.3979	1.0445	2.296	0.0217*
Mozart	1.6094	0.7746	2.078	0.0377*
Patty	-0.3365	0.5855	-0.575	0.5655
Ranieri	1.0986	0.6667	1.648	0.0994
Savina	1.6094	0.7746	2.078	0.0377*
Seisou	-1.0986	0.6667	-1.648	0.0994
T-19	-0.6931	0.6124	-1.132	0.2577
Wilhelmina	1.0986	0.6667	1.648	0.0994

4.   Discussion

The results show a clear difference between the two groups and their response to the stimulus car during training. Thus we believe that the training was successful, resulting in attraction towards the object in the experimental group and habituation in the control group. However, when presenting the subjects with the inanimate stimulus during testing, neither of the two groups showed a preference for the car. Given the extensive habituation to the stimulus, this behaviour was to be expected in the control group, suggesting that the effect of training was still present and subjects were able to generalise across contexts. Yet, interestingly the experimental group did not show a significant interest in the car either.

The lack of effect in the experimental group could be due to two reasons: either the experimental group failed to generalise across settings or the design of the experiment obscured any trainings effects.

The most apparent limitation of our study lies in the schedule of reinforcement. We did not use differential reinforcement, instead any approach by the subjects was rewarded. Thus subjects are likely to have learned that they would get rewarded regardless their choice. We know that tortoises use context specific information- if available (Mueller-Paul et al 2014). Hence it is possible that the tortoises adapted their behaviour to the experimental conditions by relying on the most recent info obtained and consequently abandoned previous knowledge. However, we did aim to reduce this possibility by limiting the number of trials in advance.

It is also worth considering that evidence for social learning in red- footed tortoises originates from a study where the task was very difficult. Only after observing a demonstrator perform the detour, the subjects were able to circumvent the barrier (Wilkinson *et al.* 2010). Yet the present task was simple and there was no risk of error due to non-differential reinforcement. Hence previous knowledge was no longer

required given that any approach resulted in access to rewards. Whilst the experimental groups responded to the car during training yet not during testing suggests that this might have been the case. On the whole it looks as if individual learning, provoked by continuous reinforcement, interfered with social learning and habituation resulting in a lack of effect in both conditions.

In respect to the social condition, we expected to find a preference for the site of the conspecific in both groups in accordance with previous findings in socially housed red- footed tortoises (Wilkinson *et al.* 2010) and lizards (Stamps 1988, Stamps 1991, Pérez-Cembranos and Pérez-Mellado, 2015). On the contrary, it seemed as if the tortoises, in the control group especially, were avoiding their conspecific in the beginning, yet gaining interest in Betty through the course of testing. There is a number of potential reasons, that can explain this initial suspicion-all suggesting that the tortoises did not consider Betty as a predictor of food initially. First, it might have to do with the fact that Betty was only introduced to the group recently. We know that movement and activity of conspecifics attracts conspecifics (Rand *et al.* 1975) and that familiarity between observer and demonstrator may help the observer to attend to and recognize significant changes in the animals' behaviour (Coussi-Korbel and Fragaszy 1995). Therefore, it is possible that the subjects did not consider her a reliable cue in the beginning of the study.

Furthermore, it is worth considering that subjects did not observe Betty feeding which might have complicated learning. Animals that see food (i.e. eating) after a novel motor act are much more likely to build a causal link between the behaviour pattern and the food. Palameta and Lefebvre (1985) showed that pigeons were only able to solve a food-finding problem (piercing a paper lid on a box concealing food) when they were exposed to both the decision (pierce) and the cue (eating) simultaneously. Those that witnessed either the piercing of the lid, or a demonstrator feeding were

unable to learn the task during subsequent testing sessions.

Another potential reason for initially choosing the opposite well is that the subjects expected the food source already emptied by Betty. This behaviour, known as the depletion effect (Templeton 1998), has been found in a few species such as rhesus macaques who chose the opposite food container after demonstration by a conspecific (Darby and Riopelle 1959). However, sofar reptiles such as lizards have been found to be naturally attracted to the sites of conspecifics (Stamps 1988, 1991, Pérez-Cembranos and Pérez-Mellado, 2015). Tortoises in the previous study were able to learn how to circumvent a barrier and gain access to food even though they did not observe the demonstrator feeding (Wilkinson *et al.* 2010).

Despite their initial avoidance, the control group seemed to develop a preference for the demonstrator with time. Interestingly however, we only have evidence for a significant preference in the control group. We know that mammals, birds and humans (Miller and Dollard 1941; Galef 1981, Dyer *et al.* 2005, Mui *et al.* 2007, Klein *et al.* 2008, Behrens *et al.* 2008) become more attentive to social stimuli as a consequence of experiences in which these stimuli provided reliable information about the availability and location of resources. Hence, it seems plausible that the tortoises learned to associate their conspecific with food as a result of continuous reinforcement during testing. However, they did not learn to choose the inanimate stimulus. This finding is likely to be a result of habituation during training.

The general pattern of our results reports no effect. Neither did we find evidence for differences between the two groups in their preferences for either stimulus, nor did this behaviour change over time. Thus, we do not have any evidence that the tortoises, regardless of which group they were in treated the inanimate object differently than their conspecific. However, we know that the way the subjects'

behaviour changes over time differs between the two groups as the control group developed a significant preference for the conspecific in the end.

Taken together these findings show that reptiles use the presence of conspecifics as indirect cue for food, suggesting that social cues can be learned through associative processes similar to other environmental cues (Heyes 2003). Thus our study partially supports the theory that social and asocial learning depend on the same cognitive mechanisms. Conceptual evidence promotes the idea that single stimulus learning, such as habituation and sensitization, coincides with the social learning strategy of local enhancement (Heyes 2012). Yet the results presented here, in combination with previous findings in reptiles and other taxonomic groups provide empirical support. Considering that the three basic types of learning, single stimulus learning, classical conditioning and stimulus-response learning are defined by associative processes points towards the possibility of social learning being mediated by associative processes also (Heyes 2012).

Several origins of social learning in asocial species have been suggested in the literature. Empirical evidence agrees that in most cases public information is advantageous (Templeton & Giraldeau 1995, 1996; Smith et al. 1999; Valone & Templeton 2002, allowing social animals to acquire information, fast, reliable and at low cost (Clark & Mangel 1986, Giraldeau 1997; Galef & Giraldeau 2001). Whilst the majority of the scientific community implicitly attributes these benefits to social animals, evidence of social learning in solitary species challenges this assumption. Alternatively, it has been proposed that social learning might be a result of foraging ecology and opportunism rather than social ecology. Promoters argue that social learning is most evident in species that forage on limited resources, all at the same time, also referred to as scramble competition (Lefebvre *et al.* 1996).

If social learning indeed originates from scramble competition, it would help explain evidence of social learning in reptiles in the field and the lab (Wilkinson *et al.* 2010, Pérez-Cembranos and Pérez-Mellado, 2015). Even in non-social species, foraging conspecifics can provide reliable information about food resources (Valone and Templeton 2002) by attracting conspecifics, whereby the presence of a group is interpreted as indirect cue for the presence of food. This can lead to high population densities that aggregate around rich food patches and may thus increase foraging success (Pérez-Cembranos and Pérez-Mellado, 2015).

Drawing on the conceptual and empirical evidence presented it seems that on a mechanistic level, there is nothing special about social learning. Social learning seems to be a label we assign to cases of learning where information is supplied through a social channel, such as the observation of conspecifics. It may be social by means of input mechanisms that provide animals with sensory, perceptual or motivational systems adaptively specialised for social cues making them especially receptive to social information. It may be that animals prioritize social stimuli. Yet the cognitive processes that encode information that is gained via the observation of conspecifics or through the animals' own interactions with the world seem to be just be the same.

Future work might focus on investigating if social learning is distinct from asocial learning by means of a socially biased input mechanism. In case evidence for such a bias emerges, it would be worth examining if it is of perceptual, attentional or motivational nature. Furthermore, knowing if the origin of such a bias was phylogenetic or ontogenetic-evolved by natural selection or by learning would help shed further light on the mechanisms involved and their evolutionary development.

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6. Appendix

6.1. Abstract (German)

"Auto versus Schildkröte"

Über die Mechanismen von Sozialem und Non-sozialem Lernen

Die Fähigkeit, von den Artgenossen zu lernen, ist adaptiv und bietet Tieren einen schnellen Weg um Zugang zu Ressourcen zu erhalten. Während sich eine Gruppe an Wissenschaftlern auf die Strategien und Vorteile des sozialen Lernens konzentriert hat, beschäftigte sich die andere mit den Mechanismen, die diese Effekte hervorbringen. Historisch gesehen wurde argumentiert, dass soziale Lernmechanismen sich von anderen Arten des Lernens sowohl im evolutionären Ursprung als auch in den zugrunde liegenden Prozessen unterscheiden. Doch jüngstes Gedankengut fördert die Idee, dass Soziales und Non-soziales Lernen von einer gemeinsamen Reihe von Mechanismen abhängen, nämlich assoziativen Mechanismen. Um dieses Thema genauer zu beleuchten, untersucht die vorliegende Studie, ob die solitäre Köhlerschildkröte (Chelonoidis carbonaria) einen Artgenossen und ein unbelebtes, fahrendes Objekt verwenden, um einen Local Enhancement Task zu lösen. Zu diesem Zweck wurde eine Gruppe von Tieren auf einen beweglichen Gegenstand habituiert, während die andere darauf konditioniert wurde. Die Tiere wurden dann unter drei verschiedenen Bedingungen getestet, wobei sie entweder mit dem unbelebten Objekt, ihrem Artgenossen oder keiner Demonstration konfrontiert wurden. Wir fanden keine Beweise für Unterschiede zwischen den beiden Gruppen und ihrer Reaktion auf die beiden Reize während des Testens. Diese Ergebnisse stehen im Einklang mit unserer Erwartung, dass die Tiere beide Reize gleichbehandeln und hinterfragen somit die Idee, dass Soziales und Asozialen-Lernen verschieden sind. Im Gegenteil, unsere Erkenntnisse deuten darauf hin, dass beide Arten des Lernens durch dieselbe Reihe assoziativer Mechanismen vermittelt werden.