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Social learning via vertical transmission in Kune Kune pigs (*Sus scrofa domesticus*)

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1. Introduction

1.1. Social learning in non-human animals

The evolution of social learning

There are to date several hypotheses attempting to explain the evolution of advanced cognitive abilities. In contrast to explanations based on technical skills, like tool-use and other manipulations of the environment, called the "physical intelligence hypothesis" (Byrne, 1997), the "social intelligence hypothesis" (Humphrey, 1976; Byrne & Whiten, 1988; Whiten & Byrne, 1997) proposes that the evolution of intelligence is a result of the necessity to cope with problems arising by living in social settings. The advantage of being able to interpret social cues in terms of the goals and desires of conspecifics thereby led to the development of sociocognitive abilities. These abilities can be used by social animals to apply the knowledge acquired to their own behaviour in order to improve the living conditions, not only within the social domain but also in terms of locating food sources or identifying predators. The abilities extend to the part where more experienced individuals can serve as a model for naïve individuals. Inexperienced conspecifics can, for example, observe and adapt food choices and learn new food extraction techniques. One example for the latter is the roof rat (*Rattus rattus*) living in the forest near Jerusalem. The rats are specialized in extracting the seeds from pine cones. However, to get the seeds is difficult since the scales of the pine cone are only removable if the process is started from the base of the pine cone. Terkel (1996) found that this technique is unlikely to be acquired by the young rats if they are not able to watch their mothers during extraction. This process of being able to learn through observation of others, or interaction with them or their products, is called "social learning" (Galef, 1988).

The functions of social learning

Instead of learning by experiencing the consequences of their own behaviour ("asocial learning") it is profitable under certain circumstances for animals to learn via observation of others. Animals that only independently learn by trial and error, can be confronted with, sometimes fatal, disadvantages (Zentall, 2006), especially when it comes to choosing the non-poisonous food or avoiding specific predators. Next to species-typical behaviour and trial and error learning animals have to find a way to survive by being flexible, when changes in the environment impair living conditions. Observational learning is therefore thought to provide animals with more behavioural flexibility (Boyd & Richerson, 1988; Zentall, 2006).

When and who to copy?

Copying another's behaviour might not always be favourable. Theoretical models have attempted to determine when to copy behaviour and have revealed that individuals should adopt the strategy of

copying when independent learning is costly, even though it might be more accurate (Boyd & Richerson 1985, 1988). In addition, animals should be selective, not only about when to copy behaviour, but also about from whom to copy (Laland, 2004). Choosing to copy the majority can be influenced by conformity (Galef & Laland, 2005). Day and colleagues (2003) could show that guppies (*Poecilia reticulata*) living in larger shoals located hidden food faster than in small shoals. Additionally, large numbers of fish at a food site attracted conspecifics faster than small aggregations. However, Pesendorfer and colleagues (2009) found in common marmosets (*Callithrix jacchus*), that behavioural patterns within groups can also be explained by habit formation instead of conformity. Another strategy, namely copying successful or older individuals, can be a good alternative. In the case of young animals it is sometimes vital to observe and copy the behaviour of older, more experienced individuals. Schiel & Huber (2006) found that wild young marmosets pay more attention towards foraging behaviour of older group members; and especially in the foraging context mothers serve as models for their offspring (Dell'mour et al., 2009). Völkl and colleagues (2006) additionally provided evidence for socially influenced behaviour towards novel food locations in marmosets. Krakauer (2005) showed that infant aye-ayes (*Daubentonia madagascariensis*) avoid novel foods until their mothers or even others have tried them. Rats, too, avoid foods which are not being eaten by others, and instead focus on the foods which are being eaten (Galef & Whiskin, 2001).

The direction of the transmission of information can be distinguished between learning from parents, or from individuals of that generation (vertical, or oblique transmission) and learning from peers (horizontal transmission). If social learning appears on a larger scale than just between a few individuals, it can contribute to population-specific behaviour, which ultimately can lead to traditions and culture (Huber, 2011). In different parts of Africa some chimpanzee (*Pan troglodytes*) groups use sticks to fish for insects (Sugiyama, 1985) whereas in other parts the chimpanzees instead crack open nuts with stones and wood hammers (Whiten et al., 1999). However, learning a specific behaviour in the first place can be due to several different mechanisms of varying complexity.

1.2. Social learning mechanisms

Imitation

Researchers have attempted to categorize the different classes of social learning (see Galef, 1988; Whiten & Ham, 1992; Heyes, 1994; Whiten et al. 2004; Zentall, 2006), nevertheless, the study of social learning has been dominated in the past by the research on the ability of animals, mainly primates, to imitate one another (Galef, 1988; Whiten & Ham, 1992). Other mechanisms than imitation have been identified for being responsible for learning, many of which are not mutually exclusive from one another (Heyes, 1994). Imitation itself is viewed by different researchers as either a basic mechanism to scrounge problem solving behaviour, or a highly cognitively demanding process (Huber et al., 2009). In the latter case the observer copies the behaviour of the demonstrator by not

only gaining information about a new technique, but also by acquiring insight into the demonstrators' goals and intentions. Previously only thought to be accomplished by humans and great apes, non-ape primates like marmosets were as well shown to be able to truly imitate (Müller & Cant, 2010; Völkl & Huber, 2000). Even bearded dragon lizards (*Pogona vitticeps*), living solitary for most of the year, were able to learn trough imitation (Kis et. al, 2015).

Goal emulation

Another cognitive mechanism called emulation was originally described by Tomasello and colleagues (1990). Here, the observer does not copy the exact motor pattern, as would be necessary for action imitation, but reproduces similar results as the demonstrator (Huber, 2011) by learning about the change that occurred in the environment (Custance et al., 1999; Kendall, 2005). If the observer learns about the goal of the conspecific's action, which can be achieved by manipulating the object, without using all the demonstrated behaviours, especially if these are not necessary to solve the task, it is known as goal or end-state emulation. Horner and Whiten (2005) found out, that chimpanzees emulate, whereas three to four years-old human infants over-imitate, when presented with an opaque box and both a necessary and an irrelevant behaviour. Dogs (*Canis lupus familiaris*) were also able to infer the necessity of an observed behaviour (Range et al., 2007). They selectively copied pressing a bar down with the paw, when the mouth of the model was free. If however the mouth was blocked with a ball, observers used their mouth to pull instead.

Affordance learning

Affordance learning is a mechanism, where the observer learns the properties of an object and how it can be manipulated, rather than the goal of the demonstrator (Whiten et al., 2004; Kendall, 2005). This might be the reason for the increased manipulation rate on a multi-lock box by kea (*Nestor notabilis*), when the birds were able to watch a demonstrator before given access to the box compared to non-observing subjects (Huber et al., 2001).

Object movement re-enactment

Another process called object movement re-enactment (OMR) should be considered, if an observer only reproduces the demonstrated movement of an object (Custance et al., 1999). The observer does not necessarily understand the outcome of the task or the goal of the demonstrator, but can recreate the movement of an object with relation to its surroundings (Whiten et al., 2004). Rigamonti et al. (2005) compared the social learning mechanisms of pig-tailed macaques (*Macaca nemestrina*) and human infants and found that whereas children were able to learn socially in four different tasks, the pig-tailed macaques only showed a weak effect of OMR.

Local and stimulus enhancement

A simpler way to explain social learning might be if it depends on perceptual effects. The attention of the observer hereby gets shifted by a model to either a specific place (local enhancement: Thorpe, 1956) or a certain object or stimulus (stimulus enhancement: Spence, 1937). In the latter case, observers pay more attention to either the whole class of objects or to particular parts of an object (localized stimulus enhancement: Caldwell & Whiten, 2004). The observer does not learn about the behaviour or its consequences, but acquires the technique or motor pattern on its own. Wilkinson and colleagues (2010) found that tortoises (*Geochelone carbonaria*) use local or stimulus enhancement when being tested in a detour task. Lorenz (1935) described that ducks (*Anas platyrhynchos domesticus*) are more likely to pass through a hole in the fence themselves, if they are near another duck while it escapes. Seeing the duck passing through might allow the observer to notice the location of the hole in the first place, which can be explained by local enhancement. However, if the observing duck would watch the escape from another enclosure, with yet another hole, and the observing duck would escape through it, the mechanism used is rather stimulus enhancement.

Social facilitation

It is possible however, that the action of the demonstrator simply leads to an enhanced motivational level in the observer and thereby immediately elicits an increase in the frequency of the same responses in their own behavioural repertoire. Clayton (1978) described this process as social facilitation ("Coaction": Zajonc, 1965). Dindo and colleagues (2009) report that capuchin monkeys (*Cebus apella*), in the presence of a feeding conspecific, were over three times faster in a novel foraging task than monkeys who were alone with the apparatus, due to social facilitation.

1.3. Test methods

Bidirectional control procedure

Generally, to test for social learning, a sample of animals (called 'observers') is exposed to a skilled conspecific (called 'demonstrator') performing a specific behaviour on an object. The test is called bidirectional control procedure (Dawson & Foss, 1965), if the object can be manipulated to move in two directions. The animal is tested for its ability to learn the change in the environment. Kis and colleagues (2014) let bearded dragon lizards observe a model slide a door open to either the left or right side in order to be able to leave the enclosure. In order to rule out simpler mechanisms like enhancement, facilitation or even goal emulation, a ghost control, where the door opened without a conspecific manipulating it, provided evidence for imitative learning in this species.

Two action procedure

In an early study on imitation, Heyes and colleagues (1992) compared the performance of a non-observer control with that of animals allowed to observe a demonstrator performing an action on an object. If the observer animals performed the action faster or more efficiently than the non-observers (Zentall et al., 1996), social learning via imitation was concluded. However, to control for non-imitative effects, Dawson and Foss (1965) recommended the two-action procedure. Two groups of animals observe a demonstrator using either one or another action on an object, resulting in the same outcome. If the observer groups show a significant difference between the two actions possible, and if they show a bias towards the demonstrated action, imitation is likely to have occurred. Völkl & Huber (2000) exposed two groups of marmosets to demonstrators removing the lid of a film container either with their mouth or their hand. As only mouth observers used their mouth to open the canister on test, the authors concluded that at least those observers imitated the observed opening technique.

Two object procedure

In contrast to the two action procedure, it is also possible to let the observers choose between two objects, or parts of one object, of which one was manipulated by the demonstrator. Campbell and colleagues (1999) tested European starlings (*Sturnuns vulgaris*) in a combination of two-action and two-object tests. Observers were able to watch a demonstrator removing one of two differently coloured plugs by respectively either pulling it out or pushing it in with its beak, in order to get to the reward inside of the hole. For both groups, observers chose the same plug and performed the same action as their demonstrator.

Deferred Imitation

Being able to benefit from learning socially requires an observer to have the opportunity to observe a demonstrator performing a behaviour which the observer has not yet performed before. The observer then has to be able to recreate the behaviour later, without the demonstrator being present (Shettleworth, 2010). Some have argued that 'true' imitation can only be assumed if observers are able to perform the copy in the absence of the demonstrator and after a considerable time has elapsed since the last presentation, that means if the observer is able to enact the copy from memory ('deferred imitation'; Piaget, 1962). Enculturated chimpanzees, for example, could produce the copy after 24 hours (Tomasello et al., 1993).Therefore to test for social learning, instead of using the duplicate chamber procedure (Warden & Jackson, 1935), where the demonstrator and the observer have simultaneous access to an apparatus, the deferred imitation setup should be used. Here, there is only one apparatus in use, and the model and the observer cannot work simultaneously. The observers' response can therefore not derive from response facilitation, in which one response from the individual's repertoire may be enhanced or primed by seeing it done, thereby causing a higher probability of the response occurring consequently (Byrne, 1994).

1.4. Pigs in science

Pigs as a model animal

Domestic pigs (*Sus scrofa domesticus*) have been investigated in biomedical research, to fill the gap between rodent and human clinical testing (Gieling et al., 2011). However, studies on animal cognition in farm animals in general have been scarce whereas research on rodents, primates, birds and, increasingly, dogs has produced a lot of information (Marino & Colvin, 2015). Especially pigs have been subject to few studies in respect to their cognitive abilities (for a review see Kornum & Kundsen, 2011). The research on pig cognition could help to corroborate concerns about animal welfare in industrial farming. Improving animal welfare, not only in industrial farming, but also in the laboratory setting, will allow researchers to get to know the true nature of pig behaviour and cognition. However, it is likely, that only with an increasing amount of knowledge about the cognitive abilities of an animal, its living conditions in captivity will be of concern to the public (Broom, 2010). In order to make an impact on the living conditions of industrial farming, tests need to be performed on healthy and unimpaired pigs, which live long enough to investigate developmental effects (Gieling et al., 2011). One key factor, next to housing, is the social setting in which the pigs live in. Since the behavioural traits of the domestic pig are very similar to the ones of their ancestors, the wild boars (*Sus scrofa*) (Stolba & Wood-Gush, 1989), it can be assumed that living in a long term socially stable herd consisting of sows and their offspring, like those found in wild boar populations (Graves, 1984), is most advantageous. This setting allows researchers, for example, to investigate the social intelligence hypothesis. In order to determine the evolutionary development of intelligence, different social systems across different species need to be studied to gain insights into the distribution of the cognitive abilities of social living animals. Additionally the effects of domestication can be studied. Pigs, like dogs, can be compared to their wild ancestors. Thereby, researchers are able to find domestication effects arising from living in close proximity to humans.

Ecology and Behaviour

The domestication of wild boars began about 9.000 years ago (Giuffra et al., 2000) and led to many different domestic pig breeds. Given the opportunity, domestic pigs show the same behaviours concerning foraging and socialising as their wild ancestors (Stolba & Wood-Gush, 1989; Held et al., 2001b). Both, wild and feral pigs forage in groups, consisting of sows and their offspring (Graves, 1984). They search wide areas for edibles because their food is irregularly scattered (Held et al., 2001a; Mendl et al., 2010). Pigs use their highly tactile snout not only for rooting, carrying and pushing but also to engage in social interactions (Stolba & Wood-Gush, 1989). Their strong exploratory behaviour makes pigs suitable for technical test settings, whereas their natural exposure to social dynamics might have led to cognitive abilities comparable to other heavily studied animals.

Cognitive research on pigs

Research on pigs has covered both non-social (e.g. sensory capacities, spatial learning and memory and object recognition) and social cognition (e.g. individual recognition, observational learning, perspective taking, mirror self-recognition and emotional contagion) (for reviews see Gieling et al., 2011; Kornum & Knudsen, 2011; Marino & Colvin, 2015). Pigs rely heavily on olfactory cues and can learn discrimination tasks faster in the olfactory than the visual domain (Croney, 1999). Additionally, Tanida and colleagues (1991) found that pigs can only discriminate blue from red, green and grey, but are red-green colour blind. It is therefore not surprising, that visual cues are usually used in combination with other senses (Arave, 1996), but if these are absent pigs can also discriminate objects simply by vision (Koba & Tanida, 2001). Pigs have shown the ability to discriminate between novel and familiar objects. Researchers used different stimuli exposure durations and delay intervals between first- and re-exposure, which led to different results. Longer pre-exposure might have increased habituation to the object, which might have led to decreased interest of the presented objects. On the other hand, longer inter-phase delay may have weakened the memory which would have led to decreased discrimination between the familiar and unfamiliar object. Moustgaard and colleagues (2002) found that pigs can memorise familiar objects for at least one hour, whereas Kornum and colleagues (2007) reported object recognition in pigs only in delay intervals of less than one hour. Another study showed that pigs can even remember objects for at least five days, under the restriction of object exposure of less than two days (Gifford et al., 2007). The latter has been interpreted as evidence for the capacity of long-term memory (Marino & Colvin, 2015). Additionally, Kouwenberg and colleagues (2009) provided evidence for episodic-like memory in pigs by performing a novel object recognition task where pigs recalled time, location and context. Pigs also distinguish between conspecifics (urine samples: Mendl et al., 2002; Y-maze: McLeman et al., 2005) and can even exploit knowledge about food locations by observing others (informed forager paradigm: Held et al., 2000). Non-informed dominant individuals scrounged on their subordinate informed group members. The subordinates, however, altered their foraging behaviour depending on the behaviour of the dominants. If subordinates were able to arrive at the food source before their exploiters, they were more likely to show food-directed behaviour (Held et al., 2002). Furthermore, there is weak evidence for perspective taking abilities, when pigs were tested for the ability to discriminate between individuals who can and cannot see where food is being hidden (knower-guesser paradigm: Held et al., 2001a). With regard to social learning, Nicol & Pope (1994) found that pigs use their siblings' knowledge of feeding sites, but not novel foods. Additionally, pigs showed an observer effect in terms of higher interaction frequencies with an apparatus than non-observers, but did not prefer to copy the action that led to a reward. The authors conclude that learning from relatively naïve siblings might not be ecologically relevant since even young pigs are efficient foragers. However, the authors propose to continue further investigations with regard to social learning via vertical transmission and longer delays between observation sessions and observer testing.

Study question

Piglets, like many other young animals, follow their mothers' example when choosing food sources (Oostindjer et al., 2011) and might even prefer their foraging sites and techniques. Based on the results of the Master's thesis projects of Ricke (unpublished, 2013) and Burin (unpublished, 2015) on stable housed domestic pigs, this study investigates the ability of young Kune Kune pigs to learn via observation. In Ricke's study dominant peers were chosen to slide a door open to either the left or right side by inserting the snout into a hole in the middle of the door. However, the subjects were not able to copy the door opening behaviour of their demonstrator. In a follow-up study, Burin could show, with a slightly modified apparatus, that domestic pigs use local or stimulus enhancement to learn about opening the sliding door. The present study focuses on a vertical transmission setting where, instead of using the most dominant peers, the mothers of the test subjects were chosen as demonstrators in an observational learning task. Kune Kune piglets of half a year of age were exposed to one of two demonstrators performing on a two object / bidirectional control procedure. Animals were technically able to push a sliding door either to the left or to the right side (bidirectional) using a blue or white bar (two objects), positioned on the left or right side of the door respectively. It was of interest, whether observer piglets would learn via observation to use one specifically coloured bar of the door to slide it to the demonstrated side. In addition, the observer piglets had to perform in different delay conditions. It was thereby possible to get a grasp of how long pigs can memorise information which is not acquired directly via learning through experience with the object itself, but only through observation.

Predictions

In accordance with results provided by Burin's master's thesis (2015) on domestic pigs of a common hybrid-breed used in industrial farming, the Kune Kune pigs were also expected to show social learning mediated by local or stimulus enhancement. Observation quality during demonstration sessions might have thereby influenced the success ratio positively. Additionally, pigs were expected to show the ability to memorise and to reproduce the demonstrated behaviour up to at least one hour, if not for a whole day. The subjects of the non-observer control group were expected to take longer than the observing piglets to acquire the most sufficient technique on their own, in order to open the sliding door, as was shown by Heyes and colleagues (1992). As demonstrators were chosen with regard to kinship to the observers, no effect of demonstrator identity was expected.

2. Methods

2.1. Animals

2.1.1. Housing

Free-ranging pigs of the New Zealand breed Kune Kune were used to conduct this experiment. At the time of the experiment the group consisted of three sows and their offspring, 18 piglets (10 females, 8 males). The Kune Kune pigs were housed in semi-natural conditions on an 8 hectare sized pasture. They found shelter in a forest patch of 1 hectare, where three A-shaped insulated wooden huts, water dispensers and the wallow were located. The animals had free access to the pasture, where a special clover-grass mixture was cultivated to provide fresh roughage ad libitum. Additionally, they were fed once a day with varying amounts of vegetables, fruits, bread and whole grain. Fresh water was supplied ad libitum. The piglets were weaned naturally by their mothers until the age of 13 weeks.

2.1.2. Social structure

The three sows were sisters of the same litter, grew up together and were never separated. They raised their offspring together in a combined kinder garden. Their litters consisted of five, six and seven piglets, respectively. One litter was born one month later than the other two. Two of the piglets had to be partially hand-raised until the latest farrowing sow took over and raised three piglets of her sister in addition to her own litter. The sow Zora was the highest in rank at the time.

2.1.3. Demonstrators and test subjects

In previous research demonstrators were chosen with regard to the highest rank in hierarchy. In this study we instead used the two most active adult sows as demonstrators. All 18 piglets were equally divided into three groups, one non-observer group and two observer groups (Tab. 2.1.1). The group members were semi-randomly chosen, taking into account the sex ratio and the kinship to their own demonstrator to avoid genetic or relationship effects on the results from unbalanced grouping. Each observer group consisted of three first degree relatives (mother-piglet) and three second degree relatives (aunt-piglet). The non-observer group was made up by the six remaining piglets.

Tab. 2.1.1. List of animals.

	Name	Abbrev.	Sex	Date of birth	Raised by
Non-observer Group	Blume	BL	F	26.09.2014	Beauty
	Rasputin	RS	M	30.08.2014	Hand/Beauty
	Ronja	RJ	F	30.08.2014	Rosalie
	Rudi	RU	M	30.08.2014	Rosalie/Beauty
	Zafira	ZF	F	28.08.2014	Zora
	Zoe	ZO	F	28.08.2014	Zora
Observer Group Beauty	Bella	BA	F	26.09.2014	Beauty
	Benjamin	BE	M	26.09.2014	Beauty
	Bessy	BS	F	26.09.2014	Beauty
	Rapunzel	RP	F	30.08.2014	Rosalie
	Zacharias	ZC	M	28.08.2014	Zora
	Zazou	ZU	M	28.08.2014	Zora
Observer Group Zora	Bibi	BI	F	26.09.2014	Beauty
	Bijou	BJ	F	26.09.2014	Beauty
	Romeo	RO	M	30.08.2014	Hand/Beauty
	Zampano	ZP	M	28.08.2014	Zora
	Zerberus	ZE	M	28.08.2014	Zora
	Zwetschge	ZW	F	28.08.2014	Zora

2.2. Procedure

2.2.1. Apparatus

The apparatus [76 cm height; 91 cm width; 28 cm depth] (Fig. 2.2.1) consisted of a box with a sliding door [56.5 cm height; 38 cm width] in front of a reward hole. A metal handle was connected to the top part of the sliding door reaching over the edge of the apparatus. The experimenter stood behind the apparatus to move the door back to its default position, in front of the hole, by using the metal handle. The apparatus, previously used in Master thesis projects on stable housed domestic pigs of Danika Ricke (unpublished, 2013) and Sandra Burin (unpublished, 2015), underwent some modifications. In Ricke's experiment the animals had to push the door sideways by inserting their snout in a hole in the middle of the door. This setup was changed for the following study of Burin. The hole was covered with a grey board, and two wooden bars were installed on each side of the board. To make the bars visibly distinguishable from one another the right bar was painted white, and the left bar was painted blue. Pigs were found to have dichromatic colour vision, where blue is the only colour they can distinguish from grey (Neitz & Jacobs, 1989; Tanida et al., 1991). It is therefore reasonable to assume that both bars would be perceived as different both in terms of brightness and colour. The only alternation for the present study was to let the door slide more easily compared to the studies with stable housed domestic pigs. Since our test subjects live as free-ranging pigs, they are not as impeded in their need to explore the environment as domestic pigs living in production sufficient housing conditions, and are therefore not as vigorous when presented with new objects. Additionally, Kune Kune pigs are a small, slow growing breed, and not as strong and vigorous as common fattening pig breeds.

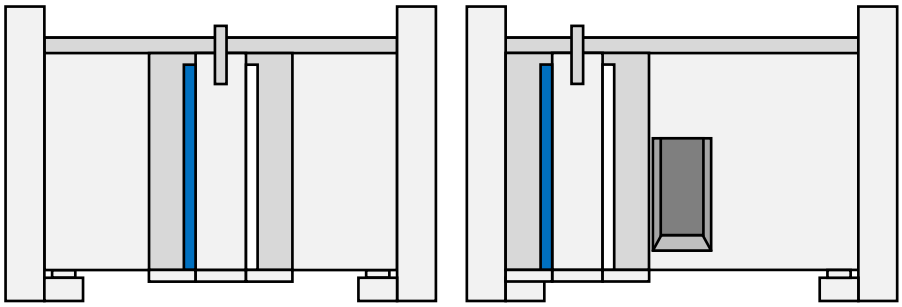


Fig. 2.2.1. Schematic drawing of Apparatus: Default position (left) and with the door opened (right).

2.2.2. Experimental Environment

The wall of the experimental hut [15.5 m^2] provided the left barrier next to the apparatus. On the right side of the apparatus two connectable metal fence-segments were installed, one of which contained a door to let the demonstrator or the test subject pass through. The observer had a direct view through the fence to the demonstrator from any place of the compartment (see Fig. 2.2.3). On the right side connected metal fence segments were installed, covered with an opaque plastic tarpaulin, to avoid the observers getting distracted. In addition, another curtain was installed on top of the apparatus around the experimenter 1 (E1) so the observers would neither see E1 handling rewards nor sliding the door back to its default position. The test subjects and their demonstrators were usually let into the test compartment through doors 1 and 3 by experimenter 2 (E2) (see Fig.2.2.2).

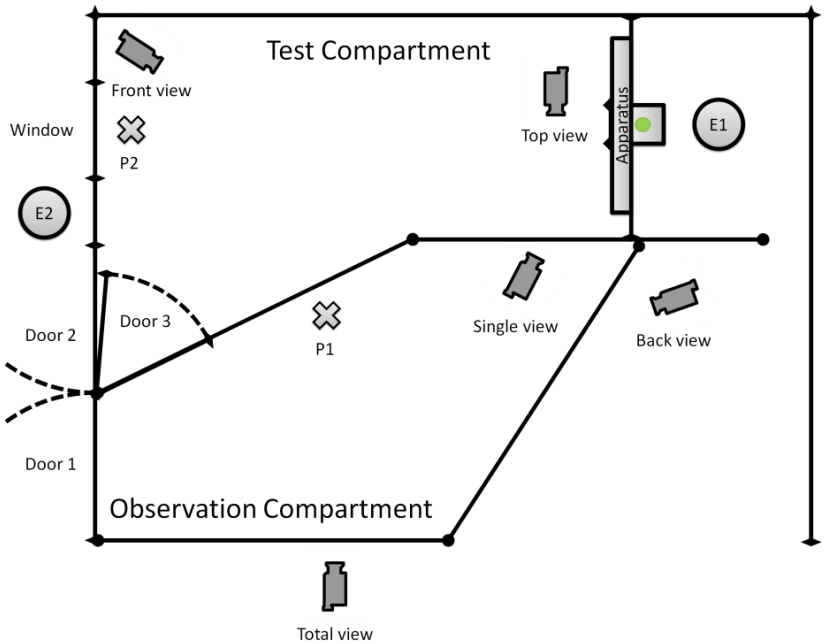


Fig. 2.2.2. Schematic drawing of experimental compartment. The test compartment is also used for demonstrations. E1: Position of experimenter 1. E2: Position of experimenter 2 during observation and open box sessions, and during observer testing. P1 / P2: Position 1 / 2 of E2 during non-observer testing. Cameras: single view – used for demonstrator training and non-observer testing; front and back view – used for observation sessions; top and total view – used for observer testing.

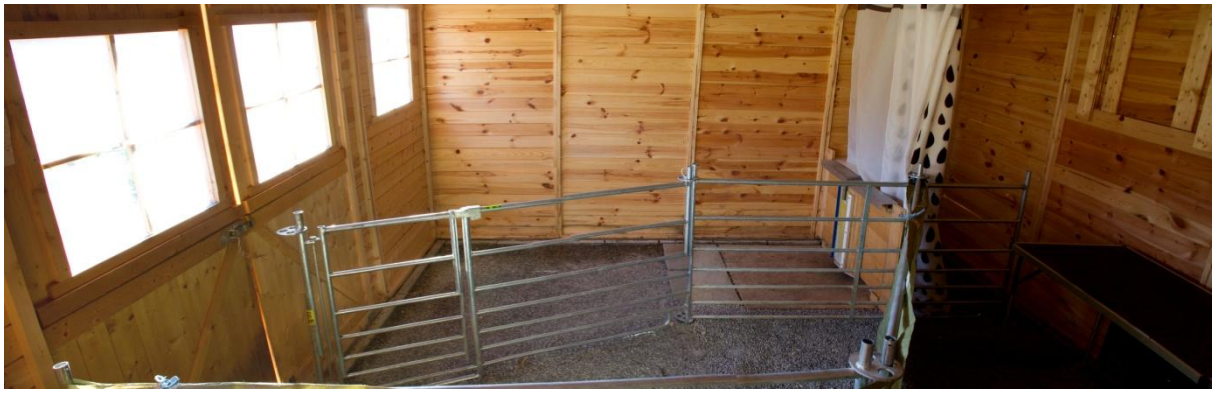


Fig. 2.2.3. Picture of experimental compartment.

2.2.3. Demonstrator Training

The demonstrators were first introduced to the apparatus without the door, so they would learn about the recess and the reward placed inside it. During their second training session, they were already confronted with the door covering the hole. Demonstrators were trained twice a week for 9 weeks, where they had to learn to slide the door open in the assigned direction using the correct bar. The movability of the door was impeded by a screw, to make sure the door would only open into the desired direction. After the demonstrators learned how to open the apparatus, they were trained to step back at least 50 cm after each opening. This was done to allow the observers to more easily distinguish the movement produced by the demonstrator from the movement in the opposite direction produced by E1 when closing the door again. Demonstrator training ended after 19 Sessions, when 20 consecutive trials were completed without any mistakes, such as trying to open the door handling the other side, not stepping back or closing the door by themselves.

2.2.4. Observation Sessions

During the observation sessions the observer piglets were separately exposed to at least 20 door openings per session. In total 20 sessions were conducted. A screw always prohibited the door to slide open in the other direction. However, we could not prevent the observers from watching the closing of the door by E1. All piglets were 27 ½ weeks old when observation sessions started. Since the offspring of Beauty were born one month after the other piglets, they started 4 weeks later, when 10 out of 20 sessions had already been completed for the older piglets. After the observer piglets completed 20 observation sessions, the testing phase started.

2.2.5. Observer Testing

Part 1 – Fixed Sliding Door

The first part of the observer testing consisted of 13 tests in four conditions. Since Burin (2015) found in her study that pigs can learn socially via observation the setting was modified in two ways. First, we tried to find out whether pigs would be able to remember and replicate the solution observed 24 hours

before (condition 1d – 1 day delay), or one hour before (condition 1h – 1 hour delay), or if the testing needed to follow immediately after the demonstration (condition 1m –1 minute delay). Another set of tests was added, where the blue and white coloured bars were interchanged (condition Sw – switched bars, 1 minute delay), to be able to distinguish between local and stimulus enhancement. Provided the subjects would choose the correct bars in the previous conditions, it could be determined whether they based their choice on the colour of the bar (stimulus enhancement) or the side of the sliding door (local enhancement). Secondly, the movement of the sliding door was always disabled during testing, to make sure the subjects learned as little as possible by trial and error about the task. Only then it was possible to test the subjects repeatedly. Before every test the apparatus was washed off with a sponge and clear water to remove visible mud stains and to spread the smell of the demonstrator from one specific spot all around the apparatus, so the test subject would not be able to only follow the olfactory trail to the correct bar.

Test subjects were let into the testing compartment via the observation compartment, allowing them to view the apparatus first from the right side, as they were used to from the observation sessions. The same procedure was carried out for all tests. The testing phase for the observers started in the same offset manner as described for the observation sessions to allow the same development for all subjects. We therefore began testing with seven piglets and continued testing for the remaining five one month later. The first testing started one day after the 20th observation session (condition 1d). One test was conducted in condition 1d, whereas in conditions 1h, 1m and Sw four tests were carried out. Before every test an observation session (OS) was carried out – in condition 1d one day and in condition 1h one hour before testing, in conditions 1m and Sw immediately before testing. The piglets always had to leave the experimental hut before being tested, to give E1 time to clean the apparatus, and switch the bars in condition Sw. Observation sessions prior to tests of condition Sw were conducted in the usual setting. Bars were changed immediately before testing. Open box sessions (OB) were introduced with the second 1 hour delay test to enhance motivation to work on the apparatus, as the test subjects were never able to actually succeed in opening the sliding door because of the fixation, (see appendix Tab. 7.1). Open box sessions were always performed prior to the OS of the respective tests. The door was removed from the apparatus; observer subjects were separately let into the test compartment and were consecutively fed six pieces of apple inside of the box. After the OB, subjects were led outside again and were later exposed to 20 demonstrations and were tested after the respective delay. The order of the individuals during the open box session was not always the same as for observation sessions and tests. For each test, the subjects were randomly asked to participate.

Part 2 – Movable Sliding Door

The second part of the observer testing was conducted six weeks after the last test of condition Sw. The sliding door was now movable in both directions. The test subjects were reintroduced to the procedure by one observation session followed by an open box session. After two days break an

observation session was carried out, followed by the '1 day delay test'. Subjects which successfully opened the sliding door, by using the demonstrator matching technique, were not tested any further. Subjects which used a non-matching technique but managed to open the door and retrieve the reward were retested in the next shorter delay condition, whereas subjects which did not open the door were retested in the same delay condition. If subjects did not interact with the apparatus for five consecutive tests, they were also tested in the next lower delay condition.

2.2.6. Non-observer Testing

Part 1 – Test for side bias

We conducted 13 sessions in total, starting in the 20th week of the piglets' life. The six piglets were individually introduced to the apparatus with the movable sliding door. During the first three sessions, if no interaction was observed after two minutes, we increased interest in the apparatus by putting favourable food in the centre beneath the door. The piglets would then try to reach the food pieces, which was only possible if they moved the door. If no further interaction with the apparatus was observed by the experimenters, the subject stayed in the testing compartment for up to three minutes in total and was then released. If the door was opened fully, another reward inside of the apparatus could be obtained. In most cases the initial reward, which was placed under the door, was removed by E1 from behind the apparatus when the piglet opened the door, so only the reward inside the hole would be available. This procedure was necessary in order to keep them interested in the task, and in the apparatus, respectively. The first three test subjects were not additionally motivated in their first test. These motivation sessions included mostly five, but up to six trials. In the following 10 sessions 10 consecutive trials were conducted with the only reward being inside the apparatus. One trial consisted of a subject opening the door to either side. After the reward was retrieved the subject was called back by E2 (P1, see Fig.2.2) and was being fed one or more pieces of reward. While the subject was turning its back on the apparatus, E1 closed the door again. This method was used to prevent the subject from seeing the door being moved in a different direction than they themselves moved it in. If the subject did not open the door fully and turned away from the apparatus, E1 also moved the door back to the centre of the apparatus. After the first 7 sessions the position of E2 was changed from inside the observation compartment next to the metal fence, to the wall inside of the testing compartment opposite of the apparatus (P2, see Fig.2.2). The subject thereby had to leave the apparatus in a straight line instead of being attracted to the right side of the testing compartment by E2.

Part 2 – Memory Test

Five months after the last test on the non-observers was conducted, we reintroduced the subjects to the apparatus in order to determine their long-term memory of the task and their preferred technique. One test á 10 trials was carried out.

2.3. Data Collection and Analysis

2.3.1. Data collection

Video cameras (JVC® Everio GZ-EX515BE) recorded every individual's encounter with the apparatus. Demonstrator training sessions, non-observer test sessions and open box sessions were recorded by a single camera, whereas observation sessions and observer test sessions were recorded by two cameras from different angles, using back and front view for the first 20 observation sessions, and top and total view for the following observation and test sessions (see Fig.2.2).

2.3.2. Data coding

Video recordings were coded using Solomon Coder© beta 15.11.19, as well as VLC® Media Player 2.0.3 for playback and Microsoft® Office Excel® 2007 for data organization. Each interaction with the door was coded for all tests of all subjects, divided into two main categories: touch and push. A touch was coded when the snout touched the door. A push additionally resulted in the movement of the door. For both categories the location of the snout on the door was coded using seven different areas (L / LM / ML / M / MR / RM / R), which were later simplified in data analysis into three areas: left bar (L / LM / ML), middle (M) and right bar (R / RM / MR). The bar area included all sides of the blue (or white) bar and the left (or right) area of the door, the middle lay in between both bars (Fig. 2.3.1). The direction of the movement was also coded if the door was moved by the snout of the subject. Three directions were coded: left and right direction, as well as an upward movement, where the test subject would either put the snout under the door and lift it up, or push the door straight ahead so the apparatus would tilt backwards. However, in analysis only pushes in either the left (*L) or the right (*R) direction were included. First pushes in an upward motion were replaced with the next push. This procedure replaced two and erased four data points for both side choice and direction. The first push was analysed for each of the test trials, and the push which opened the door, if applicable. In addition, to estimate the observation quality of each observer piglet, the ratio between "observed" and "not observed" door openings per observation session (observation ratio) was calculated. Door openings by the demonstrator were counted as "observed" if the observers' head was directed towards the apparatus during the opening of the door, otherwise it was counted as "not observed".

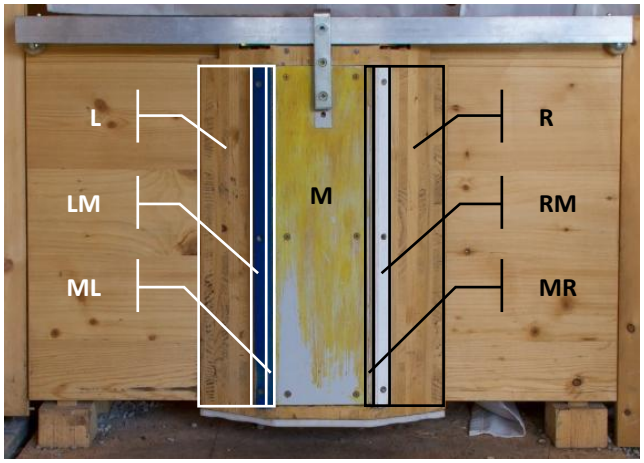


Fig. 2.3.1. Schematic picture of the door being divided into seven areas. Areas around the left (blue) bar, framed in white: L – left side of the left bar, including area of the door left of the blue bar; LM – front part of the left bar; ML – right side of the left bar. Areas of the right (white) bar, framed in black: R – right side of the right bar, including area of the door right of the white bar; RM – front part of the right bar; MR – left side of the right bar. The middle area (M) lay in between both bars.

2.3.3. Data analysis

In order to define the bias for a specific technique used by the non-observer group, a χ^2 test was used. To test for a difference of the observation ratios between both observer groups a Mann-Whitney-U test was used. Additionally, a χ^2 test was used to find a difference between the participation of the observer groups. A binomial test was carried out using different probability values for the respective techniques, to calculate whether the demonstrator matching technique (DMT: matching bar and matching direction) was used significantly more often than other techniques. The probability of touching one of the three areas of the door by chance was set to be one third (P = 1/3). Since only two of three observed pushing directions were used in the analysis, the probability of pushing in the matching direction was therefore set to 50 % (P = 1/2). In total, 14 techniques were possible (seven areas with two pushing directions each). However, the percentage of using the DMT per chance was calculated by assuming 6 techniques (three areas with two directions to push to) and was then calculated at 16.67 % (P = 1/6). The binomial test was used with afore mentioned probabilities to determine whether the observer subjects preferred the matching bar or direction over the non-matching one. Since the first push data of the observers was analysed twice, first for using the demonstrator matching technique (DMT) and second for choosing the matching bar and pushing into the matching direction separately, we applied a Bonferroni correction, setting the α value for the binomial tests to $\alpha = 0.025$, whereas all other test had $\alpha = 0.05$. A success score was created per observer individual, which represents the average preference for the matching bar or direction over all participated tests of the "fixed door" condition. A Spearman correlation was calculated in order to investigate the influence of the individual observation ratio on the respective success scores.

Data analysis was carried out using SPSS Statistics 17.0 and Microsoft Office Excel 2007.

3. Results

3.1. Observation Sessions

The average observation quality (observation ratio) over all sessions and individuals was found to be 57.5 % (N = 384, min. = 0, max. = 1, $\bar{x}$ = 0.575 ± 0.214 SD). Five of the six observers of Beauty's observer group paid above average attention, whereas five of the six Zora observers paid below average attention to the demonstrated door openings (Fig. 3.1.1). There was a significant difference between both observer groups over all observation sessions (N = 192, U = 14508, p < 0.001).

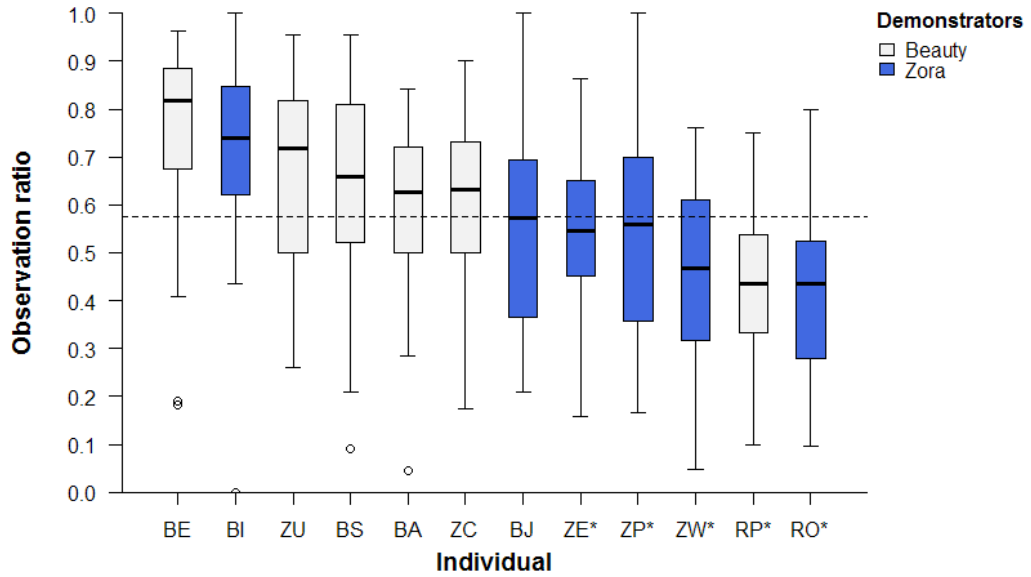


Fig. 3.1.1. Box-Whisker-Plot of the observation ratio per individual. The boxes depict the values between the first and the third quartile, the line inside each box marks the median; whiskers depict maximum and minimum values. Dots show outliers. Individuals are sorted by their mean observation ratio. Dashed line at 0.5747 depicts overall mean observation ratio. Asterisks mark individuals which were bitten at by their demonstrator during observation sessions.

During observation sessions Zora bit at four of her six observers and Beauty at one observer piglet (Tab. 3.1.1). This might have interfered with the individual observation quality. Those five individuals showed the least interest in the demonstrations. Their observation quality was below average, indicated with asterisks in Figure 3.1.1.

Tab. 3.1.1. Amount of bites against observers during observation sessions (OS).

Demonstrator	Ind. Abbrev.	Total bite sum	Amount of OS	Mean amount of bites per OS
Zora	RO	83	18	4.611
	ZE	13	8	1.625
	ZP	1	1	1.0
	ZW	11	2	5.5
Beauty	RP	7	7	1.0

Over the course of all OS an increase of observation quality within the first 5 observation sessions was found (Fig. 3.1.2). The following sessions underwent some fluctuations around 60%, showing steady increase after testing started (1d) until the last test of the 1 hour delay tests (1h4), where a sudden decrease of the mean observation ratio occurred, followed by more fluctuations.

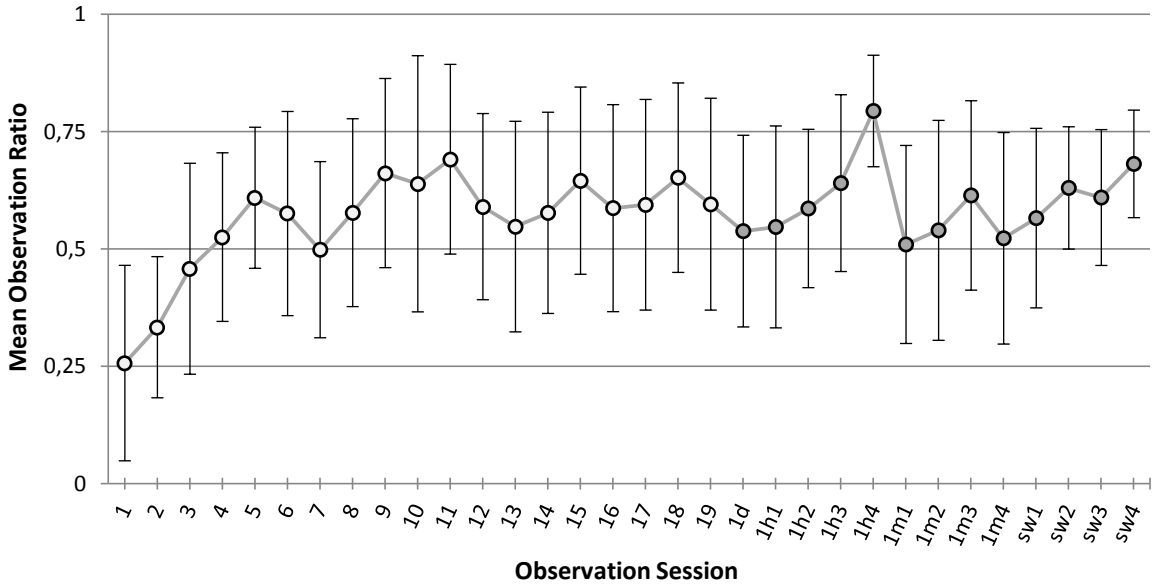


Fig. 3.1.2. Mean observation quality over observation sessions. Circles depict mean observation ratio over all individuals per observation session (OS). Light circles mark OS before start of testing (1-19), dark circles mark OS prior to each respective test (1d, 1h1-4, 1m1-4, sw1-4). Error bars show ± standard deviation.

3.2. Observer Testing

Part 1 – Fixed Sliding Door

When analysing the techniques of the observers per condition, by combining the chosen bar and the direction pushed, the highest percentage of "demonstrator matching technique" (DMT: matching bar and matching direction) was found in the first observer test, condition 1d (Fig. 3.2.1, for a detailed table of techniques per test and individual see appendix Tab. 7.2). A binomial test confirmed a significant preference for the usage of DMT over other techniques (binomial test: $P = 1/6$, $p = 0.02$, $\alpha = 0.025$). As is depicted in Fig. 3.2.1, the percentage of DMT decreased rapidly over the course of all tests. During the 1 hour delay test still a tendency for the DMT was shown (binomial test: $P = 1/6$, $p = 0.03$, $\alpha = 0.025$). The frequency of only matching the direction increased over the first three conditions, whereas only matching the bar was not used as much by the observers. In the switched bars condition none of the techniques were favoured, however, the percentage of pushing the matching bar was higher than in the other conditions (Fig. 3.2.1). The frequencies of using the non-matching technique ("non-mt": pushing the non-matching bar into the non-matching direction) decreased over the first three conditions and was lowest in condition 1m.

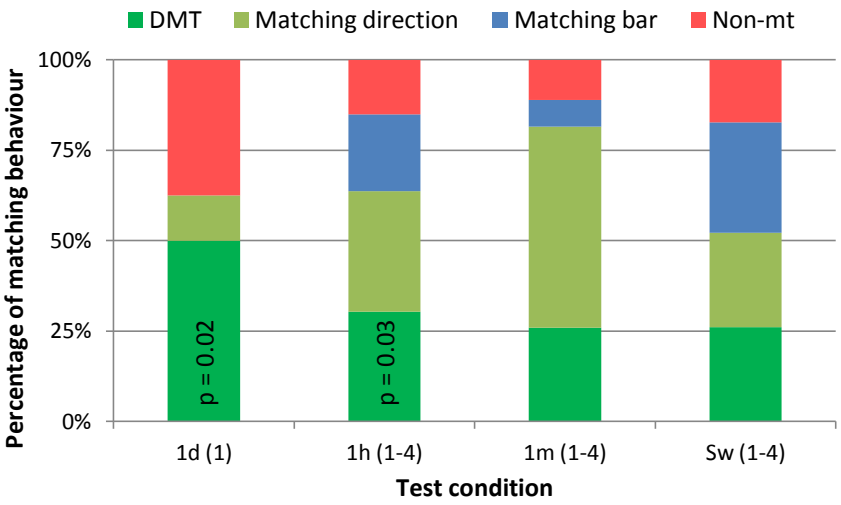


Fig. 3.2.1. Percentage of matching behaviour per test condition. The percentage of four possible techniques is depicted per test condition. "Demonstrator matching technique" (DMT = matching bar and matching direction), "matching direction" (but non-matching bar), "matching bar" (but non-matching direction) and "non-mt" (non- matching technique). P-values were calculated using the binomial test (P = 1/6), to test for significant usage of the "DMT" per condition.

In order to review the change of techniques over the four conditions, Fig. 3.2.2 shows the percentage of the bar used being the matching bar, and the direction used being the matching direction. There was no significant preference for either the matching bar, irrespective of the direction, and no significant preference for the matching direction, irrespective of the bar choice, in the 1 day delay test. This discrepancy to the results of the significant preference for the DMT was due to higher probabilities of the occurrence of the matching behaviour ("DMT": P = 1/6 versus "matching bar": P = 1/3; "matching direction": P = 1/2). During the 1 hour delay test the preference for the matching bar was found to be significantly higher than for the non-matching behaviour (binomial test: P = 1/3, p = 0.021, $\alpha = 0.025$). On the other hand, observers did not push significantly more in the matching than the non-matching direction (binomial test: P = 1/2, p = 0.082, $\alpha = 0.025$). However, when test 1h1 is excluded from analysis, due to low participation (four out of 12 individuals, see Fig. 3.2.3), there is a tendency for pushing in the matching direction after all (binomial test: P = 1/2, p = 0.032, $\alpha = 0.025$). During the 1 minute delay tests the matching bar choices dropped by a third, on the other hand, pushing in the matching direction reached the highest percentage out of all conditions (binomial test: P = 1/2, p = 0.001, $\alpha = 0.025$). In order to explain this behaviour, whether the subjects may have been pushing in the matching direction by choosing the matching side of any bar was analysed. Subjects indeed chose the matching side of either bar significantly more often than other areas of the door (binomial test: 1m: P = 1/3, $p < 0.001$, $\alpha = 0.025$). When bar and direction choice are combined into a technique, again there was a highly significant usage of the demonstrator matching technique in terms of pushing the matching side of either bar in the matching direction during the 1 minute delay condition (binomial test: P = 1/6, $p < 0.0001$, $\alpha = 0.025$). Additionally, in the 1 hour delay test, some of the matching bar

and some of the non-matching bar data combine to a significant choice for the matching side of either bar (binomial test: P = 1/3, p = 0.021, α = 0.025).

As described before, the choice for the matching bar had almost doubled between condition 1m and the switched bars condition. Subjects did choose the matching side of the door again significantly more often than other areas of the door (binomial test: Sw: P = 1/3, p = 0.016, α = 0.025), meaning that animals did not push at the side of the matching coloured bar. In turn, pushes towards the matching direction were fewer than in any other condition.

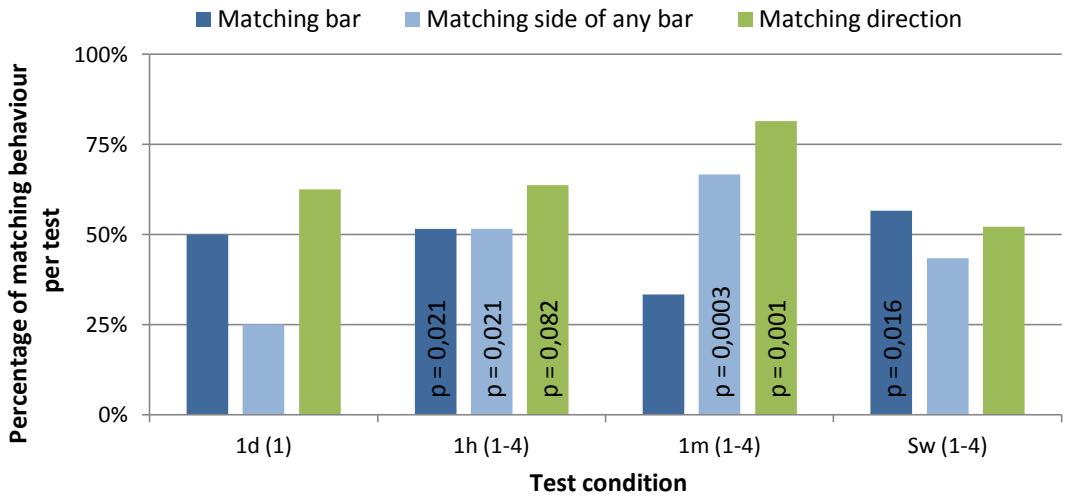


Fig. 3.2.2. Percentage of matching behaviour per test condition. The percentage was calculated by adding up all tests with matching behaviour, dividing it by the sum of all tests participated by the subjects. Three possible techniques are depicted per test condition: "matching direction", "matching bar" and "matching side of any bar" (left side of left or right bar / right side of right or left bar). P-values were calculated using the binomial test (bar choice: P = 1/3; direction: P = 1/2), to test for significant usage of the matching behaviour per condition.

In order to put the significance of the binomial tests into perspective, it needs to be considered that condition 1d included only one test, whereas conditions 1h, 1m and Sw included four tests. Additionally, the participation varied a lot between the tests (Fig. 3.2.3). Participation was lowest after the first test, in test 1h1, but rose again for tests 1h2 and 1h3, and was highest in test 1h4. These were the three tests where the open box sessions were introduced. After that participation dropped to a minimum of five subjects pushing the door. In total, more Beauty-observers participated per test than Zora-observers (χ^2 test: $\chi^2 = 10.56$; d.f.: 1; $p < 0.01$).

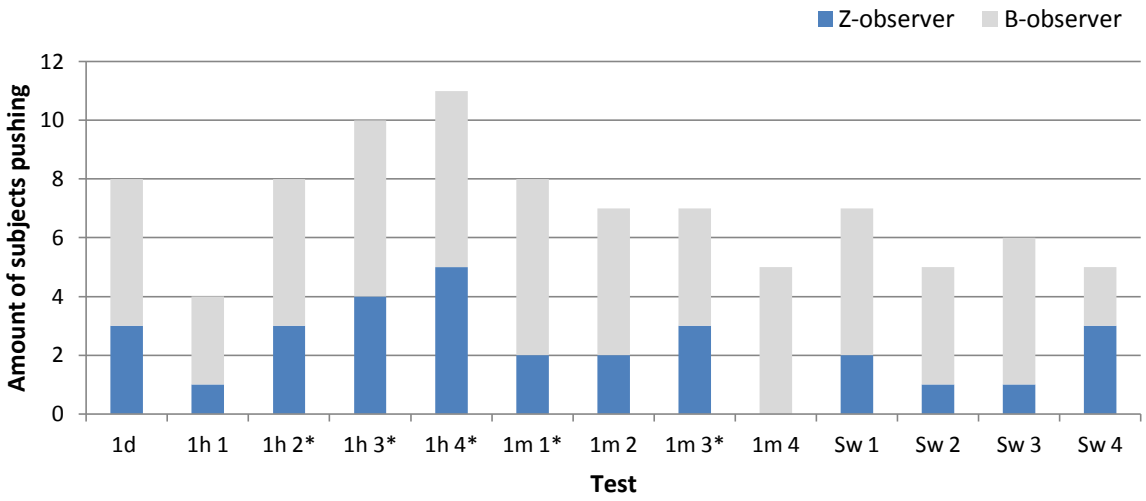
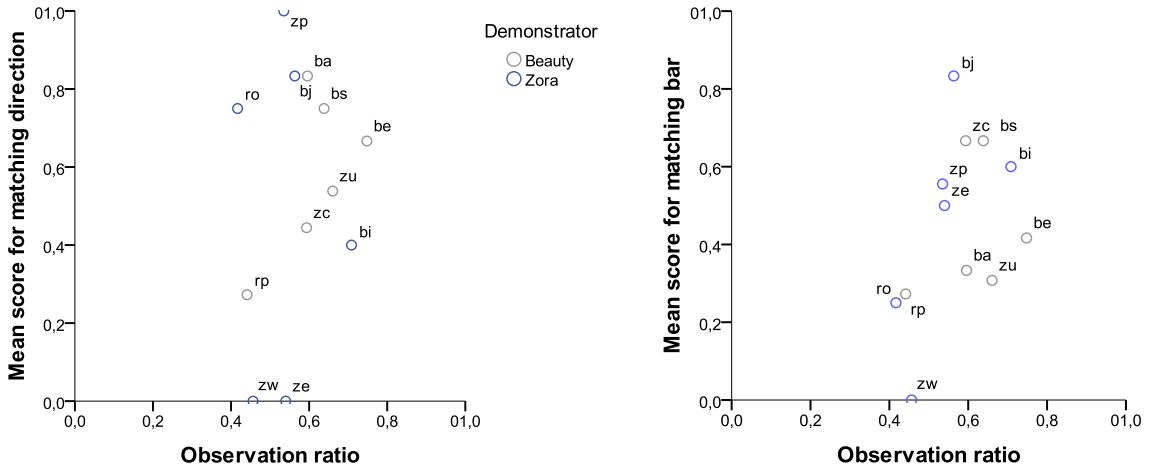


Fig. 3.2.3. Amount of participating subjects of each observer group per test. Participation was counted if the subjects pushed at least once. Asterisks mark tests with open box sessions prior to the observation sessions.

Over all tests a success score per individual was created which represents the average preference for the matching bar or direction. These scores were plotted against the respective observation ratio of the individual (Fig. 3.2.4. a and b). No significant correlation was found between the observation quality and choosing the matching bar or pushing in the matching direction. However, there was a tendency for a higher score of matching the bar when observation quality was higher (Spearman's rho, 1-tailed: corr. coeficent = 0.434, p = 0.079). Even though there was a difference between the observer groups with regard to observation quality and participation during the tests, there was no difference in the performance of both observer groups.



a) b)

Fig. 3.2.4. Scatter plots of success score and observation ratio. Mean success score of matching the direction (a) and bar (b) over 13 tests plotted against the mean observation ratio over 32 observation sessions.

Part 2 – Movable Sliding Door

When being retested in the 1 day delay test, five subjects immediately opened the door by using the demonstrator matching technique (BI, ZP, BE, BS, ZU), three subjects used the opposite technique (RO, RP, ZC) and four subjects did not push at all (BJ, ZE, ZW, BA). Consequently, the three non-matching subjects were retested in the 1 hour delay condition, where one subject changed its technique to the DMT (ZC) and was therefore not tested again. The remaining two subjects continued with the non-matching technique for the 1 hour and the 1 minute delay test (RO, RP). These were the only subjects which were offspring of the third sow Rosalie, which was not chosen to be a demonstrator. Additionally, both subjects were the ones with the lowest observation ratio and were the ones being bitten at the most by their demonstrators.

Out of the four subjects who did not participate in the first and second 1 day delay test (BJ, ZE, ZW, BA), one subject successfully opened the door with the DMT in the third 1 day delay test (ZE), whereas two subjects used the non-matching behaviour to open the door (BJ, ZW). One of these subjects changed its technique to the DMT after being retested in the 1 hour delay condition (ZW). The remaining fourth subject did not open the door for six 1 day delay tests and was therefore retested in the 1 hour delay test, where she successfully opened the door using the DMT (BA).

As Table 3.2.1 shows, nine out of 12 subjects opened the door using the DMT. Of these nine, seven were successful in their first test in which they participated (1 day: BI, ZP, BE, BS, ZE, ZU; 1 hour: BA) and two subjects changed to the DMT in their second test in which they participated (1 hour: ZC, ZW). Three subjects did not change their technique and used the non-matching technique in all conditions (BJ, RO, RP). Six out of 12 successful subjects provided evidence for the preference to open the door with the DMT in the 1 day delay condition (binomial test: P = 1/6; p = 0.00024).

Tab. 3.2.1. Timetable of the techniques used by the observers in the movable door tests.
Techniques: **"**DMT" = demonstrator matching behaviour marked in dark green, "non-mt" = every other technique than DMT marked in red. Tests: 1d1/2/3 = 1 day delay test 1/2/3, 1h = 1 hour delay test, 1m = 1 minute delay test.

Ind	1d1	1d2	1d3	1h	1m	total
BI	L*R					1d DMT
BJ	no push	no push	R*L	R*L	R*L	Non-mt
RO	R*L			ML*L	R*L	Non-mt
ZE	no push	no push	L*R			1d DMT
ZP	L*R					1d DMT
ZW	no push	no push	R*L	L*R		Change
BA	no push	no push	no push	R*L		1h DMT
BE	R*L					1d DMT
BS	R*L					1d DMT
RP	L*R			L*R	L*R	Non-mt
ZC	MR*R			R*L		Change
ZU	R*L					1d DMT

Additionally, observer subjects only changed their push direction between first push and opening push in 10 % of the cases (two changes out of 20 cases), but were less accurate with their bar choice (eight changes out of 20 cases).

3.3. Non-Observer Testing

Part 1 – Test for side bias

Three non-observer piglets were able to open the door from the first test day onward. However, those subjects received motivational enhancement (reward beneath the door). The first three subjects, which were tested without motivational enhancement in the first test, did not open the door. For the first three tests the amount of techniques used to open the door increased from five to nine techniques and decreased again for the following tests (Fig. 3.3.1). In the first three tests no preference for a specific technique was observed. Pushing in the right direction was above chance level during test one but decreased rapidly. Overall, there was a preference for opening the door by pushing the right bar in the left direction, over any other technique possible (χ^2 test: $\chi^2 = 331.655$; d.f.: 2; $p < 0.001$).

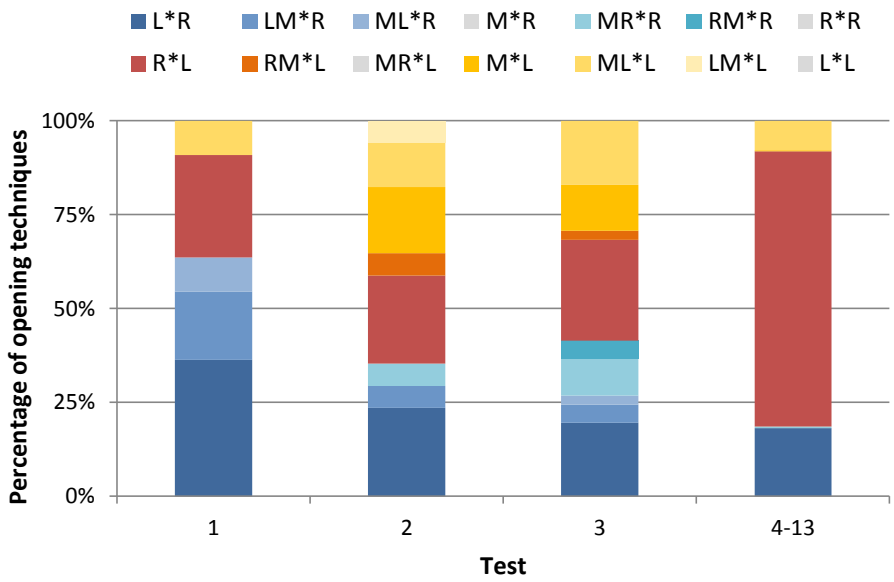


Fig. 3.3.1. Percentage of techniques used to open the door. Techniques are described by "area of the door" * "direction". Blue colours depict pushes to the right and red/orange colours depict pushes to the left. Grey colours depict techniques never used by the non-observers.

Depicted in Figure 3.3.2, the door openings increased over the first four tests to up to 10 openings per individual with a total of 60 openings from the fourth test session onwards. As mentioned before, in the first test only three subjects participated. These were the ones which received additional motivation enhancement in order to elicit an interaction with the apparatus. The other three subjects did not receive motivational enhancement and hence did not interact with the door.

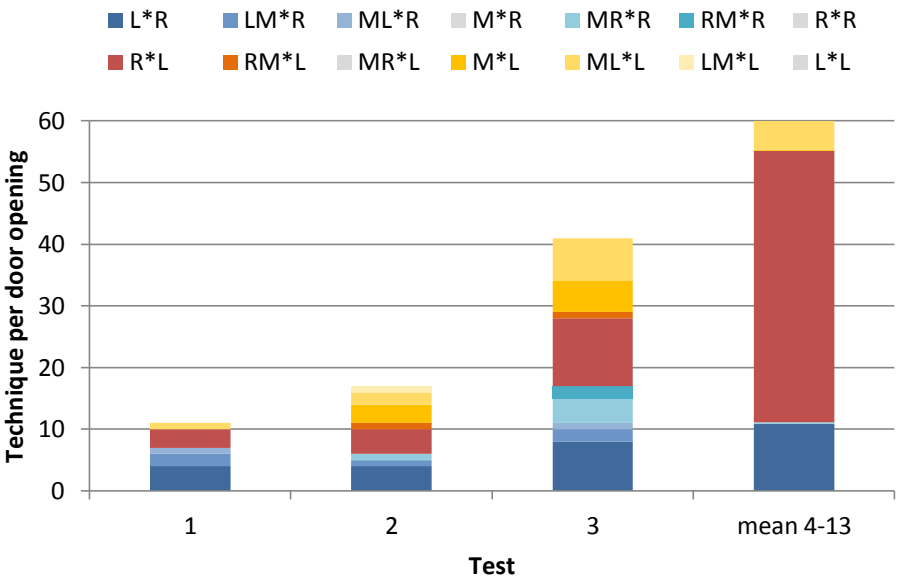


Fig. 3.3.2. Amount of techniques used to open the door. Techniques are described by "area of the door" * "direction". Blue colours depict pushes to the right and red/orange colours depict pushes to the left. Grey colours depict techniques never used by the non-observers. Techniques per trial (door opening) of tests 4-13 were averaged.

Part 2 – Memory test

In the memory test four out of six non-observer subjects repeated the same technique at least nine out of 10 times, whereas two subjects were indecisive and interchanged their techniques. One of these two subjects pushed the door nine out of 10 times in the same direction, and was in this respect coherent with its previous preference. Both subjects interchanging their techniques did so also during the first six tests (part 1), whereas the other four subjects had shown a preference for one opening technique from the fourth test onward.

3.4. Comparison non-observer versus observer

Four out of 12 observers (30%) did not participate in the first test, whereas three out of three (not additionally motivated) non-observers (100%) did not try to open the door.

If all 21 possible techniques (seven areas with three directions to push) are being considered, the mean total amount of techniques used per individual was significantly higher in the non-observers than in the observers during the first three tests (t-test, 2-tailed: $t = -6.658$; $p = 0.014$; see Fig 3.4.1). Non-observers tried more techniques in order to gain access to the reward than observers during each one of the first three test sessions. However, if the amount of techniques used by the non-observers is divided by the amount of trials within one test session, no difference can be found (Fig. 3.4.2).

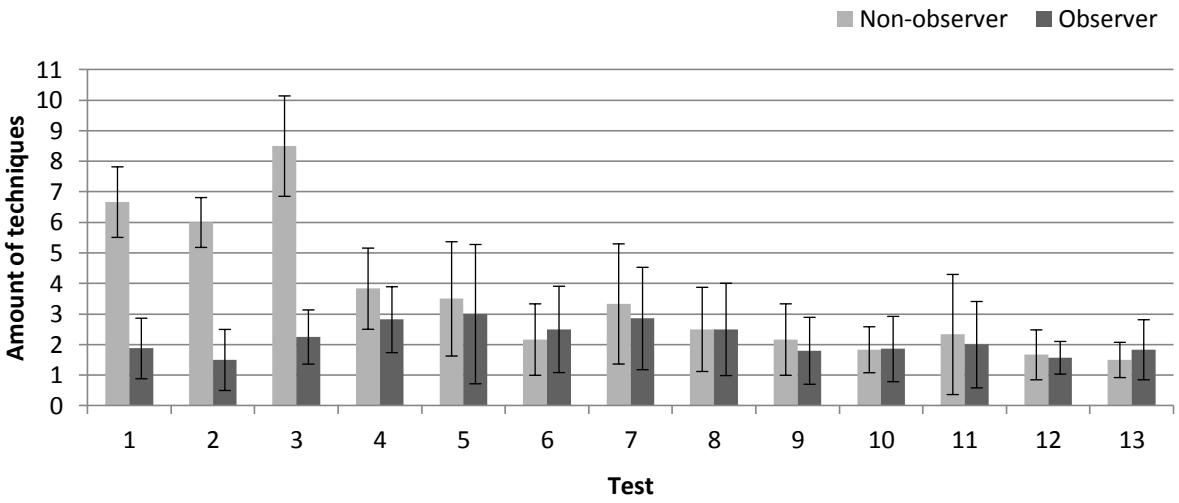


Fig. 3.4.1. Mean individual total amount of techniques used by non-observer and observer piglets.

There was a slight increase of the mean individual amount of techniques used by the observers during tests 2 to 5 (1h1 – 1h4), which decreased again for the next four tests (6/1m1 – 9/1m4) and reached a level of around two techniques (Fig.3.4.2). Non-observers started with a slightly higher amount of techniques than observers, but lowered it down to almost one technique per trial and individual from the fourth test on. Non-observers used more techniques to figure out how to open the door in the most preferred way, which was accomplished by the fourth test. Observers on the other hand tried fewer techniques in the beginning, but increased their repertoire over the next tests.

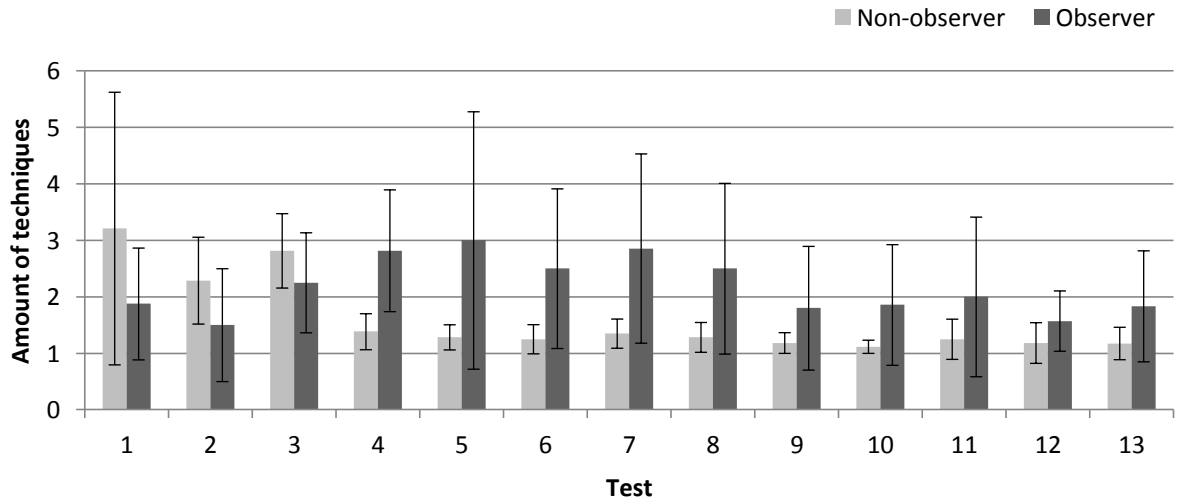


Fig. 3.4.2. Mean individual amount of techniques per trial used by non-observer and observer piglets.

4. Discussion

This study investigated the ability of six month old Kune Kune piglets to (a) learn an extractive foraging technique by observing their mother or aunt and (b) remember this technique over different retention intervals. The previous study by Burin (2015) on domestic pigs, using the same apparatus, suggested that pigs are able to learn socially by local or stimulus enhancement. The first touch of the observer pigs happened significantly more often at the demonstrated bar. The Kune Kune pigs, investigated in this study, were also expected to use the demonstrated bar first. Additionally they were expected to memorise the observed behaviour of either the demonstrator or the door, for up to 24 hours until it had to be reproduced.

Social learning mechanism & memory

Observers showed a preference for the demonstrator matching technique in their first interaction with the apparatus during the 1 day delay test, both in the "fixed door" and "movable door" condition. However, these results do not confirm the ability of imitative learning by vertical transmission in pigs, since it cannot be excluded that, instead of copying the behaviour of the demonstrator, the observer subjects only memorised the movement of the sliding door. Indeed, the results of the following tests in the "fixed door" condition seem to support this notion. The behaviour of the observer piglets during the 1 day delay test still provides evidence for the ability of pigs to (a) learn and memorise an observed extractive foraging technique or the movement of the object manipulated by the demonstrator, and to (b) recreate it after a 24 hours delay. A previous study by Kornum and colleagues (2007) found that pigs are not able to memorise objects for more than one hour. The results of the present study are however in accordance with a study on object recognition where pigs were able to choose the object which they were exposed to five days before testing (Gifford et al., 2007). This has already been interpreted as evidence for the capacity of long-term memory (Marino & Colvin, 2015). The findings of the present study also point towards the ability of pigs to build a long-term or reference memory of the observed behaviour of either the conspecific or the object. However, definitions on long-term (reference) and short-term (working) memory overlap in regard to exact durations and should be distinguished rather on the performance of the subjects (Kornum & Knudsen, 2011). Working memory typically uses stimuli to form behaviour within a specific task. This type of memory is delay sensitive, and normally does not occur between test sessions (Dudchenko, 2004). Long-term memory on the other hand forms rules of a given task, and is mainly acquired with repeated training. It can persist from days to months, and up to a lifetime (Kornum & Knudsen, 2011). Therefore, in order to safely conclude the type of memory, which was used to enable the observer pigs to perform the matching technique, more tests are needed. This study however did find evidence for the long-term memory in pigs, when non-observer piglets recreated their self-acquired opening technique after a 5 months period.

In the “fixed door” condition the usage of the demonstrator matching technique (DMT) decreased with each condition. In the 1 hour delay condition, only a trend to open the door using the DMT was observed. Subjects thereby preferred to use the matching bar, but only tended to push towards the matching direction. This points towards local or stimulus enhanced behaviour, which was still elicited after a retention interval of 1 hour. In the 1 minute delay condition subjects did not prefer the matching bar but mainly used the matching side of any bar to push the door in the matching direction, showing flexibility in their behaviour in order to get to the reward. This indicates an understanding of the task even though no experience was gained during previous tests since the sliding door was immobile. Given that observers switched from matching the area of the door (1 hour delay) to pushing into the matching direction (1 minute delay), object movement re-enactment might have been another mechanism used, in order to solve the task. In the majority of the tests of condition 1h and 1m subjects recreated the movement of the door, without matching the exact behaviour of the demonstrator. If the subjects were aware of the reward behind the door, which may safely be assumed since they experienced open box sessions, even goal-emulation is a possible mechanism used by the piglets. It can be argued that the piglets rather focussed on the matching bar in the 1 hour delay tests, whereas in the 1 minute delay tests subjects seemed to have broadened their techniques in order to open the door in the observed direction by using the matching side of any bar. However, to investigate the assumption, that pigs are able to emulate, more controls would be needed. The switched bars condition of the observer testing was intended to investigate, whether the subjects based their choice of the bar on local or stimulus enhancement. When confronted with the switched bars, subjects chose the matching area of the door rather than the demonstrator-used coloured bar. This indicates the effect of local enhancement over stimulus enhancement. Additionally, there was no difference between the usage of the possible techniques (DMT, matching bar only, matching direction only, non-matching technique). It is likely that subjects acted differently in the switched bars condition due to the change of the bar colour, and possibly used techniques rather erratically.

In the “movable door” condition half of the piglets used the DMT to open the door in the 1 day delay test. Considering the probability of using this technique, it again can be assumed that pigs are able to learn and recreate the observed action of either the model or the object, even over a 24 hour retention interval. Two piglets changed their opening technique to the DMT when the delay was lowered to one hour. This is insofar surprising as three others did not change their technique and rather stayed with the non-matching technique. Additionally, five out of the six non-observers chose their previously preferred technique when being retested 5 months later, which indicates a strong bias towards techniques being used and established before, a kind of habit formation which has been described before in marmosets (Pesendorfer et al., 2009). However, non-observers altered their opening techniques during the first and second openings, which could contradict with the assumption, that the first opening push of the observers in the “movable door” condition would have been repeated. On the

other hand, we do assume an observation effect, where non-observers acted differently during their first tests, than non-observers did.

Observation effect

As suggested by Heyes and colleagues (1992), non-observers should take longer to interact with the apparatus than observers. First, in the present study none of the non-observers interacted with the sliding door, if they were not additionally motivated. In contrast, more than two thirds of the observers participated in the first test, which in turn suggests that observer piglets were more motivated to interact with the apparatus than non-observers. Secondly, non-observer piglets used more techniques during the first three test sessions than observers used in their first three tests. This indicates an observation effect, where observers had a more precise notion or representation of how the door could be opened. However, this effect was only apparent up until the third test. Since the observers were not able to open the door in the "fixed door" condition, the amount of techniques used per individual increased up to around five, whereas non-observers used up to two techniques during each of the following test sessions. This increase might have been due to a frustration effect.

Frustration effect

Frustration has been defined as the impediment of goal-directed behaviour (Berkowitz, 1989) and can lead to increased activity levels (Lewis, 1999), suggesting problem solving behaviour, which when not successful can induce repetitive behaviour like stereotypes (Terlouw et al., 1991.), and even aggression (Duncan & Wood-Gush, 1971; Arnone & Dantzer, 1980). It was assumed that due to the "fixed door" condition observers would not learn the affordances of the task by one trial learning. The data analysis was therefore based on the fact that no experience of previous tests would interfere with behaviours in the following tests in lower delay conditions. The impediment of the movability of the door, however, might have resulted in alternating techniques due to frustration. An increase of different techniques used per test was apparent, however, it cannot be concluded that observer piglets used different techniques for their first interaction with the door in their consecutive tests, due to frustration about the immobile door. The fact that there was a high reoccurrence of matching the demonstrated direction of the door opening since test 1h2 until condition Sw started, leads to the conclusion that the first push was in most cases meant to open the door and was not affected by frustration. Another indication for this conclusion was the fact that of the techniques seen in the "movable door" condition, 90 % of the first push directions were according to the following opening direction, regardless whether the direction was matching the demonstration or not. It can hereby be concluded, that subjects were not very likely to change their initial push direction in the "fixed door" condition either. The increased pushes in the matching direction over the first three conditions might however indicate a delay-dependent performance.

Effect of the demonstrators

Demonstrators are usually chosen dependent on their rank in hierarchy, when looking at horizontal transmission. Domestic fowl (*Gallus gallus*) pay more attention to high-status than to low-status individuals (Nicol & Pope, 1999). This strategy of copying the successful individual in terms of high social status (Galef & Laland, 2005) was used in the previous studies on social learning in commercial farm pigs by Ricke (2013) and Burin (2015). Ricke (2013) could not show the pigs' ability to imitate the behaviour of their demonstrators, both of which were chosen because of their highest rank within the group. High ranks are due to high levels of agonistic behaviour. Choosing these more aggressive individuals might have had an inhibitory effect on the observers' performance on the apparatus. Comparing the results of both observer groups in this study, it becomes apparent that there is a difference in both the observation quality and the pushing activity over all tests. The piglets observing Zora, who was the most dominant pig in the group at the time, showed lower attention during observation sessions and participated significantly less in all tests. This in turn can be due to a strong influence of Zora biting at the observers during observation sessions, thereby impairing observation quality or later motivation to interact with the apparatus. On the other hand, no difference between success ratios of observer groups was detected for either matching the bar or the direction.

Observation quality effect

Contradictory to this study's predictions, individual success ratios in terms of choosing the matching bar or pushing to the matching direction were not influenced by the individual observation ratio. However, there was a tendency towards matching the bar choice more often when observation quality was higher. Thereby, the influence of observation quality on choosing the matching bar should not be ruled out. Burin (2015), for example, found that pigs with higher observation scores were more likely to interact with the apparatus, but she did not report an effect of the observation quality on the success of the performance.

Side bias

The side bias of the non-observers towards the technique of pushing the right bar into the left direction might partly explain why Beauty observers were participating more. However, since there was no difference in the performance of both observer groups in terms of matching the technique of the demonstrator, the side bias effect is not plausible. The side bias possibly occurred due to the position of E2 on the right fence of the testing compartment. This fact also makes it more plausible to reject the influence of the side bias effect. In order to avoid this side bias we could have started the procedure with E2 in the back of the testing compartment. However, the pigs would have likely been distracted by her presence. In turn, only one trial test, comparable to the observer tests, would have been favourable.

Conclusion

The tested pigs were able to recreate the movement of the door by using the matching bar after a 24 hours delay. The influence of local rather than stimulus enhancement was concluded from comparing the results of the 1 hour delay and the switched bars condition. Object movement re-enactment probably occurred due to the ability of the pigs to use references in the experimental compartment in order to determine the direction towards which the door has to be moved. Without a 'ghost control' it is not possible to determine with certainty whether the pigs learned by observing the behaviour of the demonstrator or the movement of the door. One could argue that the most striking and interesting object of the observation sessions was the moving door, since the demonstrators were part of the observers' daily lives. Similarly, Japanese macaques learned to wash potatoes by observing the new behaviour of one group member (Kawai, 1965). The identity of the demonstrator and the object was not particularly interesting, since both were known to the other individuals. However, the behaviour of washing the sweet potato itself was new and interesting enough to be observed. Like the washing behaviour, in this study the movement of the door might have been the most salient and was therefore recreated. However, observers did learn more than the direction of the door movement, because they also used the demonstrator matching area of the door. Additionally, it was not possible to prevent the observers from watching the closing of the door by sliding it into the opposite direction. This in turn makes it possible that the pigs learned about the movability of the door by indeed observing the demonstrators' behaviour. The conclusion of an observation effect is supported by the fact that observers used fewer techniques than non-observer piglets during the first three tests. The effect of the identity of the demonstrator was apparent when looking at both the observation quality and the participation of the individuals per test, but did not influence the overall performance. The "fixed door" condition might have interfered with the amount of techniques used per test, but the results of the "movable door" condition in turn indicate no change between first and opening push, at least in terms of push direction. Therefore it is justified to use the first push as the basis for the analysis. Further it can be assumed that the first push of each test was not influenced by own behaviour, due to the "fixed door" condition, thereby supporting the pooled data analysis per condition. However, even for the 1 day delay test, for which it was not possible to pool data, the demonstrator matching technique was found to be used significantly more often than any other possible technique. This might be the most impressive result of the study, especially because the subjects memorised not their own behaviour, but another individuals' or the objects' 'behaviour' for a whole day. This in turn could provide evidence for long-term memory of observed, instead of experienced behaviour in pigs.

Altogether this study uncovered the ability of pigs to learn from their mother or aunt how to solve a manipulative foraging problem, most probably by acquiring essential information about locality and moving direction of an object through observation and then storing it in memory for at least a day.

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6. Appendix

Tab. 7.1. Timetable of observer tests in the fixed door condtion. Prior to every test, one observation session (OS) was conducted. Some tests involved open box session (OB) as motivation enhancement. Testing of B piglets started one month later than testing of R & Z piglets.

R & Z piglets (7 subjects)	B piglets (5 subjects)
20 Observation sessions	
1 day delay	
1 day delay test (1d)	
7 days break	3 days break
OS	1 hour delay test 1 (1h1)
5 days break	4 days break
OB OS	1 hour delay test 2 (1h2)
3 days break	2 days break
OB OS	1 hour delay test 3 (1h3)
4 days break	1 day break
OB OS	1 hour delay test 4 (1h4)
2 days break	10 days break
OB OS	1 minute delay test 1 (1m1)
1 day break	1 day break
OS	1 minute delay test 2 (1m2)
4 days break	1 day break
OB OS	1 minute delay test 3 (1m3)
2 days break	1 day break
OS	1 minute delay test 4 (1m4)
1 day break	1 day break
OS	Switched bars test 1 (Sw1)
10 days break	3 days break
OS	Switched bars test 2 (Sw2)
1 day break	1 day break
OS	Switched bars test 3 (Sw3)
7 days break	1 day break
OS	Switched bars test 4 (Sw4)

Tab. 7.1. First push techniques of observer piglets in fixed door paradigm. Dark green marks DMTs, light green marks matching direction techniques, light blue marks matching bar techniques and red marks non-matching techniques. Empty cells depict tests where individuals did not push at the door.

	1d	1h 1	1h 2	1h 3	1h 4	1m 1	1m 2	1m 3	1m 4	Sw 1	Sw 2	Sw 3	Sw 4
BI					RM*R			MR*R			ML*L		ML*L
BJ	ML*R	L*R	L*R	LM*R	ML*L			MR*R					
RO	L*R		R*L	M*R	M*R	MR*R	MR*R						RM*R
ZE	ML*R									R*L			
ZP			R*R	L*R	L*R	RM*R	L*R	L*R		L*R		MR*R	M*R
ZW				RM*L	M*L								
BA	R*L		M*L	R*L	M*L	R*L						M*L	
BE	LM*L	ML*R	MR*R	MR*L	RM*R	MR*R	ML*L	ML*L	ML*L	ML*L	MR*L	ML*L	
BS	LM*R	MR*R	ML*L	ML*L	R*L	RM*L	R*L		ML*L	R*L	R*L	R*L	MR*R
RP			RM*R	M*R	ML*L	M*L	L*R	ML*L	L*R	L*R	M*R	RM*R	MR*R
ZC	LM*R			R*L	RM*R	MR*R	L*R	ML*L	R*L	RM*R		RM*L	
ZU	LM*R	MR*R	R*L	ML*L	M*L	RM*L	M*L	ML*L	M*L	MR*R	M*R		

Abstract

Being able to learn via observation from others is especially beneficial for young and naïve individuals. The relationship towards the social partner is thereby important. While peers are often used as demonstrators in order to test for the ability of social learning in a species, thereby studying horizontal transmission of information, this study focuses on the vertical transmission of information, i.e. learning across generations. Half-a-year-old piglets of the Kune Kune breed were first exposed to their mother or aunt pushing one of two differently coloured bars on a sliding door to either the left or right side respectively, and were then tested after one day, one hour and one minute retention intervals. Results indicate the ability of pigs to use the demonstrated opening technique and even remember it over a delay of 24 hours. Further tests using lower delays suggest that piglets operated on the basis of object movement re-enactment in order to try to open the sliding door. Additionally subjects based their choice of the bar rather on local than stimulus enhancement. Altogether this study uncovered an impressive ability of piglets to learn from their mother or aunt how to solve a manipulative foraging problem, most likely by acquiring some essential information through observation and then memorising it for at least a whole day.

Zusammenfassung

Die Fähigkeit durch Beobachtung anderer zu lernen ist besonders für junge und unerfahrene Tiere vorteilhaft. Dabei ist die Beziehung zum beobachteten Sozialpartner besonders wichtig. Häufig werden Gleichaltrige als Demonstratoren herangezogen um die Fähigkeit von sozialem Lernen einer Art zu testen, wobei horizontale Übertragung von Information untersucht wird. Diese Studie hingegen untersucht die vertikale Übertragung von Information über Generationen hinweg. Sechs Monate alte Ferkel hatten zunächst die Möglichkeit ihrer Mutter oder Tante dabei zuzuschauen, wie diese mit Hilfe einer spezifisch gefärbten Leiste eine Schiebetür nach links oder rechts aufschob. Nach einer Verzögerung von einem Tag, einer Stunde und einer Minute wurden die Beobachtertiere getestet. Die Ergebnisse ergaben, dass Schweine dazu in der Lage sind die demonstrierte Technik zu nutzen und sich diese sogar über ein Verzögerungsintervall von 24 Stunden hinweg zu merken. Weitere Tests mit einem geringeren Verzögerungsintervallen lassen darauf schließen, dass die Ferkel „Objekt movement re-enactment“ nutzen, um zu versuchen die unbewegliche Tür zu öffnen. Außerdem trafen die Ferkel ihre Entscheidung welche Leiste sie benutzen eher auf Grund der Lokalität, anstatt mit Hilfe des Farbreizes. Diese Studie enthüllt die beeindruckende Fähigkeit von Schweinen, von der Mutter oder Tante zu Lernen ein manipulatives Futtersuchproblem zu lösen. Wahrscheinlich erlangten die Ferkel diese essentielle Information über Beobachtung und behielten diese über mindestens einen Tag im Gedächtnis.