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„Ontogeny of stimulus enhancement in juvenile common ravens and carrion crows“

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1. Introduction

1.1. Cognition and learning

Studying animal cognition means to look for the “mechanisms by which animals acquire, process, store and act on information from the environment” (Shettleworth 2010, p. 4). This includes the pathway of perceiving information through the senses and processing this information in terms of memory and learning, amongst other things (Shettleworth 2010, p. 4). Such processes have direct impact on the behavior of an animal. Moreover, complex cognition requires some kind of mental representation of the world and intentionality in decision making (Dickinson 1988). Notably, cognition is a product of evolution. Therefore, animal behavior should lead to fitness benefits. Following Tinbergen (1963), in ethological investigations, it is important to consider the four dimensions of a behavioral trait to answer the question: “Why does the animal do that?”. On the one hand, there are proximate causes, such as the mechanisms an animal uses and the ontogeny of an individual during lifespan. On the other hand, there are the ultimate causes, namely the phylogenetic history and the adaptive value of a trait. Thus, cognition is one of the proximate causes of animal behavior, though cognitive science may also look for ultimate causes (Shettleworth 2010, pp. 11 – 12).

Learning is broadly defined as a change in state of an animal that is caused by experience (Shettleworth 2010, p. 98). Different processes are known in which animals show individual learning, for example through the mental connection of two stimuli. A basic form of this associative learning is the Pavlovian or classical conditioning. In his famous experiment, Pavlov (1927) trained a dog to connect bell ringing with food and as a result provoked the response of saliva production by presenting the bell ringing stimulus alone. Hence, a former neutral stimulus has turned into a conditioned stimulus evoking a conditioned response. Other examples for associative learning are flavor aversion learning in rats (Garcia & Koelling 1966) or operant conditioning (Skinner 1938) by positive or negative reinforcement. However, animals learn only under the right circumstances and with the right motivation. Furthermore, if learning shall be beneficial for an animal respectively for a species in terms of fitness and evolution, there must be reliable learning conditions and a predisposition of the animal for matching learning mechanisms (Shettleworth 2010, pp. 102 – 103).

1.2. Social learning

Social learning has been defined as “learning that is influenced by observation of, or interaction with, a conspecific, or its products” (Galef 1988; Heyes 1994; topic reviewed in Hoppitt & Laland 2008). Many species of different taxa have been shown to acquire information about relevant environmental features via conspecifics in different contexts. For example, females adjust their mate choice preference and choose males that they have seen in the proximity of other females, as it was found in guppies (*Poecilia reticulata*; Dugatkin 1992) and Japanese quails (*Coturnix japonica*; Galef & White 1998; White 2004). Animals might also gain social information about predators, which is for instance known from blackbirds (*Turdus merula*) that join in mobbing behavior of conspecifics (Curio 1988) or rhesus monkeys (*Macaca mulatta*) that learn the fear of snakes (Cook & Mineka 1990). Amongst others, it was also shown that social learning influences the preference for food sources in rats (*Rattus norvegicus*; Posadas-Andrews & Roper 1983) and domestic dogs (*Canis familiaris*; Lupfer-Johnson & Ross 2007). In these cases, individuals use conspecifics as a source of information. From whom and when an animal shall learn seems to depend on different strategies concerning the relationship between the model and the observer and the efficiency and costs of learning (Laland 2004).

The given examples can follow different underlying social learning mechanisms. The mechanism involved in the mobbing behavior of the blackbirds and in the fear learning of the monkeys is most likely observational conditioning (Curio 1988; Cook & Mineka 1990). This mechanism is a kind of associative learning where, following Heyes (1994), an observer is exposed to a stimulus-stimulus relationship due to the behavior of a demonstrator which affects the observer’s behavior in a positive or negative way. However, sometimes the mere presence of another individual might have an effect on the behavior of an animal, which is called social facilitation (Zajonc 1965). For example, the presence of a calm individual might facilitate social learning through fear reduction (Hoppitt & Laland 2008). More cognitively demanding social learning mechanisms are imitation and emulation. This field is discussed controversially in terms of precise definitions. Basically, imitation means copying the form of a demonstrator’s action (Whiten & Ham 1992). A method commonly used to prove imitation is the two-action test, where two groups of observers watch one of two demonstrators solving the same task in two different ways (Heyes & Dawson 1990). Imitation has been shown for example in rats (*Rattus norvegicus*; Heyes *et al.* 1992), Japanese quails (*Coturnix japonica*; Akins & Zentall 1996), marmosets (*Callithrix jacchus*; Bugnyar & Huber 1997; Voelkl & Huber 2000) and great apes (Whiten 1998; Stoinski *et al.* 2001). In contrast, emulation refers to the process of learning about the results of an action by watching a demonstrator rather than a

specific movement (Tomasello 1998). In keas (*Nestor notabilis*) for instance, observers might not copy the technique of a demonstrator to open an artificial fruit, but have a better success in opening it compared to non-observers (Huber *et al.* 2001). Another simpler and widespread mechanism is local enhancement (Thorpe 1956). In this social learning process, an observer is more likely to visit or to interact with objects at a specific location after or during a demonstrator's presence at this very point (Hoppitt & Laland 2008). This might happen in animals that visit a spot where they saw others feeding (Galef & Giraldeau 2001). However, the attention of animals can also be drawn to much smaller specific locations on settings such as a lever or a lid via local enhancement, as was shown for instance in budgerigars (*Melopsittacus undulatus*; Heyes & Saggerson 2002).

1.3. Stimulus enhancement

The social learning mechanism stimulus enhancement, that was first studied by Spence (1937), happens when the "observation of a demonstrator (or its products) exposes the observer to a single stimulus at time t_1 and single stimulus exposure effects a change in the observer detected, in any behaviour, at t_2" (Heyes 1994). In other words, it is the increased likelihood of contacting a stimulus by virtue of observing others doing so, though the observer's subsequent contact with the stimulus does not have to be during the presence of the demonstrator (Shettleworth 2010, p. 467). This enhancement can also have an effect on the observer's response to other similar stimuli in different locations and can lead to further learning about the enhanced type of stimulus in future contacts (Hoppitt & Laland 2008). Thus, this social learning mechanism is a combination of an initial social information transfer followed by individual learning.

Stimulus enhancement is thought to be a widespread form of socially influenced learning (Whiten & Ham 1992; Zentall 1996). In many cases, animals show social learning after the observation of a demonstrator, which could be explained with stimulus enhancement but possibly even with other mechanisms (Hoppitt & Laland 2008). Hence, stimulus enhancement has been suggested to occur in a variety of species and in different contexts: in mate choice preference of female guppies (*Poecilia reticulata*; Dugatkin 1992) and Japanese quails (*Coturnix japonica*; Galef & White 1998; White 2004), in the acquisition of tool use in long-tailed macaques (*Macaca fascicularis*; Zuberbühler *et al.* 1996), in the preference for food sources of rats (*Rattus norvegicus*; Galef & Beck 1985), juvenile canaries (*Serinus canarius*; Cadieu & Cadieu 1998) and capuchin monkeys (*Cepus apella*; Visalberghi & Addessi 2001) as well as in the accomplishment of tasks and discriminations in rats (*Rattus norvegicus*; Kohn 1976; Heyes *et al.* 2000), pigeons (*Columba livia*; Edwards *et al.*

1976; Vanayan *et al.* 1985), graylag geese (*Anser anser*; Fritz *et al.* 2000), jackdaws (*Corvus monedula*; Schwab *et al.* 2008a) and common ravens (*Corvus corax*; Fritz & Kotrschal 1999; Schwab *et al.* 2008b). Nevertheless, it is important to rule out other potential social learning mechanisms that would explain the findings such as local enhancement, observational conditioning or different types of imitation, which not every study can provide (Hoppitt & Laland 2008).

1.4. Social complexity

Social learning is assumed to occur more likely in species with a complex social system. Complexity, in this context, refers to group size (MacLean *et al.* 2013), fission-fusion dynamics (Amici *et al.* 2008) and type of relations and interactions (Dunbar 1998). The social complexity hypothesis predicts that animals living in complex social groups should show enhanced social abilities, following a convergent evolution with those of primate species including humans (de Waal & Tyack 2003).

Moreover, referring to the social brain hypothesis (Dunbar 1998) which claims that social complexity causes the social intelligence of humans and non-human primates, it has been shown that the size of the neocortex positively correlates with group size in primates (Dunbar 1992) but also in other mammals such as carnivores, some insectivores (Barton & Dunbar 1997; Dunbar & Bever 1998) and dolphins (Tschudin 1998). Notably, birds and especially corvids have evolved an analogous brain area to the mammalian neocortex which qualifies them for complex cognitive abilities (Kirsch *et al.* 2008). Thus, recently the social brain hypothesis has been extended to also include birds (Bond *et al.* 2003; Emery & Clayton 2004).

Social life brings challenging problems for the individual: an animal that lives in a complex society has to deal with other individuals that are difficult to predict (Humphrey 1976). This requires specific adaptations in cooperation, problem-solving and social learning. For instance, in non-primate species, there is evidence by Bond and colleagues (2003) that corvids living in large social groups (Pinyon jays, *Gymnorhinus cyanocephalus*) perform better in cognitive tasks compared to corvids living in less complex groups (Scrub jays, *Aphelocoma californica*). Moreover, a direct benefit of social behavior on the reproductive success was found in a group of wild baboons (*Papio cynocephalus*; Silk *et al.* 2003). Furthermore, from a Machiavellian point of view, using and outwitting others can be beneficial and adaptive (Whiten & Byrne 1988).

1.5. Corvids

Corvids (e.g. ravens, crows, jays and nutcrackers) are renowned for their large brain to body size ratio, their wide geographical distribution and their unique socio-ecology (Emery 2006). Amongst other things, this might be a reason for the high degree of cognitive abilities of these birds and enable them for performing on a comparable level to primates in cognitive tasks (Emery & Clayton 2004).

Within the corvids, common ravens (*Corvus corax*) stand out: they are the largest songbirds, they show the widest distribution of all (over the northern hemisphere) and live in difficult and diverse habitats such as mountains, plains, deserts, coastal areas and forests (Goodwin 1986; Heinrich 1989). Additionally, ravens are food opportunists and feed on grains, fruits, hunted insects, birds and small mammals, as well as carrion (Marquiss & Booth 1986; Engel & Young 1989). As scavengers, they co-occur with large predators and show up at carcasses in large numbers of individuals (Heinrich 1988, 2011). Ravens form territorial pairs after sexual maturity, but beforehand, live as non-breeders in large groups of vagrants that share nocturnal roosts and feeding opportunities (Goodwin 1986; Heinrich 2011). These non-breeder groups form relationship networks (Fraser & Bugnyar 2010) and hierarchical structures with a high degree of fission-fusion (Heinrich 1989). Furthermore, ravens show agonistic support with dominant and affiliated individuals (Fraser & Bugnyar 2012).
A closely related species to the common raven is the carrion crow (*Corvus corone/cornix*). This corvid species shows a similar ecological and social organization to its bigger kinsman (Goodwin 1986), but might be more adapted to urban areas and human proximity. Both species are known for caching and pilfering food (Goodwin 1986; Mikolasch *et al.* 2012).

Especially ravens are known for their remarkable socio-cognitive skills such as perspective taking (Bugnyar *et al.* 2004), knowledge attribution (Bugnyar & Heinrich 2005; Bugnyar 2011) and tactical deception (Bugnyar & Kotrschal 2002; Bugnyar & Heinrich 2006). In addition, they are renowned for using social information of conspecifics and human demonstrators in various forms of object manipulation (Fritz & Kotrschal 1999; Scheid *et al.* 2007; Schloegl *et al.* 2007, 2008). However, ravens seem to prefer affiliated and related individuals as a source of information (Stöwe *et al.* 2006; Schwab *et al.* 2008b). Furthermore, both ravens and carrion crows are able to learn by exclusion (Schloegl *et al.* 2009; Mikolasch *et al.* 2012) and to control their impulsiveness in a delayed gratification paradigm (Dufour *et al.* 2012).

1.6. Ontogeny

The term ontogeny means the individual development during lifespan, starting prenatal as zygote and lasting until the maturity of an organism. In the social domain, especially the juvenile period is of interest. At this age, animals have the opportunity to learn useful knowledge and abilities from their parents and peers, which they might need as adults. For example, the pups of the black rat (*Rattus rattus*) learn an efficient method of feeding pine cones from their mothers (Aisner & Terkel 1992) or young meerkats (*Suricata suricatta*) are taught prey-handling skills by older group members (Thornton & McAuliffe 2006; Thornton & Malapert 2009). Other examples for this are young birds that learn the specific songs of their local conspecifics (Eales 1985; Beecher 2010) or young chimpanzees (*Pan troglodytes*) that learn nut-cracking skills by watching experienced individuals (Inoue-Nakamura & Matsuzawa 1997). Obviously, young individuals that need to learn certain skills socially require special adaptations in for example attention and motivation, especially during this phase of life. Notably, if these behavioral variants that are acquired via social learning are constant over generations, they may have the potential to form traditions (Fragaszy & Perry 2003).

Corvids, as large-brained social birds, pass through an extensive early developmental period in which they depend on their parents and learn intensively (Clayton & Emery 2005). However, despite some studies (e.g. Bugnyar *et al.* 2007b; Schloegl *et al.* 2007; von Bayern *et al.* 2007; Hoffmann *et al.* 2011), not much is known about the ontogeny of cognitive abilities in corvids.

Ravens often start reproducing not before their third to fifth year of life (or even later). But at the age of about six to eight months, they leave their parents and join the non-breeder groups in the wild (Heinrich *et al.* 1994). Bugnyar and colleagues (2007b) found that at two months post-fledging, young ravens show all elements of adult-like caching of items, including the covering of caches and look-ups for potential pilferers. Furthermore, this study shows a development of Piagetian object permanence simultaneous to the development of caching: in the first week post-fledging, ravens could uncover partially hidden items (Stage 3) and in the second week, they could uncover fully hidden items (Stage 4). At the same time the birds showed full caching behavior, they also reached Stage 5 of object permanence and thus the understanding of invisible displacement. Furthermore, ravens start following others' gaze direction soon after fledging, but can only track gazes behind visual barriers for the first time in their first autumn four months later (Schloegl *et al.* 2007). Already four to five months post-fledging, young ravens form stable relationships and support social partners in conflicts (Loretto *et al.* 2012). However, definitely at about six months post-fledging, juvenile ravens are capable of using barriers to go outside of others' view during caching and take into

account another individuals' perspective (Bugnyar & Heinrich 2003, 2005). These findings point to a kind of extensive developmental step in the cognitive abilities of juvenile ravens in their first autumn, after about four months post-fledging, about the time of their dispersal.
Considerably less is known about the ontogeny of cognitive abilities in the carrion crow. These corvids have a shorter hatching-to-fledging time compared to ravens but reach the same level of object permanence at a similar age (Hoffmann *et al.* 2011).

1.7. Questions and predictions

The aim of this study was to look for developmental changes in the response of juvenile common ravens (*Corvus corax*) and carrion crows (*Corvus corone/cornix*) to social learning cues. Therefore, we first investigated the predisposition of fledged ravens and crows to show stimulus enhancement, subjecting individuals to a human experimenter touching everyday objects once a week over five months (experiment 1). The intention was to find out (a) when the subjects would start to show stimulus enhancement, (b) how strong the response to stimulus enhancement was and (c) how this response changed within the first months of life. We predicted that the subjects would show a preference for objects enhanced by the demonstrator. Furthermore, the prediction was that the more affected the subjects were by the enhancement cue, the faster they should approach the object and the longer they should manipulate it on their own. We expected the subjects to show a strong response to stimulus enhancement immediately but to become less affected by enhancement cues over time.

In addition, we were interested if and how fast subjects would recognize that social information is either reliable or not reliable. In an object choice task (experiment 2), young ravens were confronted with two types of experimenters that constantly offered either reliable or unreliable information about a food location. We wanted to see if the birds could distinguish between the two persons. Beyond that, we were interested whether the birds would show intention control and would be able to choose against the non-reliable demonstrations. The prediction was that the birds would choose the enhanced cup more often soon after fledging in both conditions and would not be able to choose against the cue of the unreliable demonstrator. But when we confronted the subjects with the same situation a few months later, we expected them to perform differently in the conditions. We predicted that young ravens in their first autumn would be able to overcome their preference for enhanced items and would choose against the non-reliable demonstrations, since other studies indicated an extensive developmental step in the cognitive abilities of juvenile ravens at this age (Bugnyar *et al.* 2007b; Schloegl *et al.* 2007; Loretto *et al.* 2012).

To check for the birds' general ability to discriminate human experimenters, we confronted them with a food providing and a non-food providing experimenter simultaneously (experiment 3A). We expected the subjects to be able to differentiate between the two very fast by choosing the food providing experimenter when given the choice. Additionally, we confronted the ravens with both the reliable and the unreliable experimenter of the object choice task (of experiment 2) offering food simultaneously (experiment 3B). We predicted that if they would have learned about their reliability, they would choose to get the food from the reliable experimenter, respectively to avoid the unreliable experimenter.

2. Material and methods

2.1. Subjects and housing

We used eight hand-raised common ravens (*Corvus corax*), three females and five males, and eight hand-raised carrion crows (*Corvus corone/cornix*), five females and three males. At the end of April 2012, the ravens were taken from three different nests (all from zoos) at the age of three to five weeks. The crows were also taken from three different nests but at the age of about two weeks at the beginning of May 2012. The crows came from the wild, from a park area in Vienna with permission of the 'Magistrat der Stadt Wien MA 22 – Umweltschutz' (MA 22 – 355/2012/4), Vienna, Austria. The ravens fledged at the age of six to eight weeks in mid May 2012 and the crows fledged at the age of five weeks at the end of May 2012. The total number of individuals in the social group of ravens was ten and in the social group of crows it was twelve during the time of this study, but testing was only possible with the tamest individuals. Ravens participated in all experiments of this study. All crows participated in experiment 1 and due to a time limitation only six crows in experiment 3A. We did not test the crows in experiment 2.

Ravens and crows were held and hand-raised under similar conditions and diet. During hand-raising in the nest boxes and after fledging the birds had daily contact to different humans and also got used to video equipment. The diet consisted of meat, bread, eggs, fruit and milk products. All birds were marked with colored rings for individual identification. The subjects were held together in an outdoor aviary complex at the Haidlhof Research Station (University of Vienna and University of Veterinary Medicine, Vienna) in Bad Vöslau, Austria. The aviary complex (see figure 1) was divided in a raven and a crow section, each had different compartments. The section the ravens normally had access to was approximately 80 m^2 large (compartments R1 and E1). Crows normally also had access to a section of 80 m^2 (compartments C1, RC, E2 and E3). Ravens and crows were always spatially separated, but could have contact through the wire mesh. Subjects temporarily had more limited access to the compartments or access to other compartments due to testing. The aviary compartments had a floor substrate of gravel and stones. They were provided with branches of different sizes, some natural plants, weather sheltered places, different platforms, toys and water bowls.

The experimental compartments (4 m x 3 m) had a translucent roof and wooden walls on three sides, which allowed individual testing without recognition of other birds and with less

distraction. Testing took place mostly in the experimental compartment E2 and due to coordination with other experiments sometimes in the compartments E1 or E3. During each experiment, a video camera was installed in the corridor outside of the experimental compartment recording the experiment for a later video analysis.

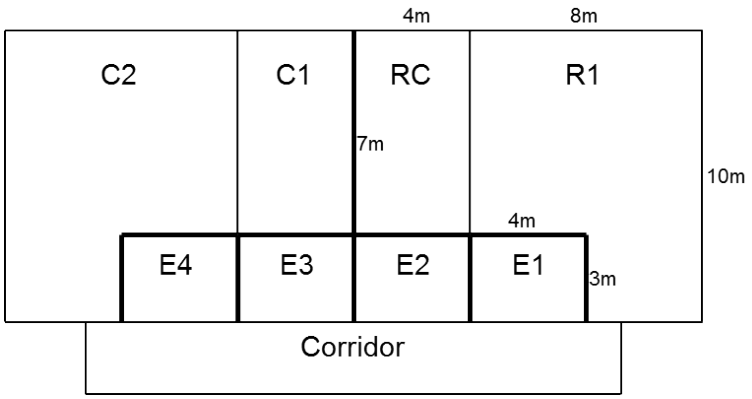

Figure 1. Sketch of aviary complex for ravens and crows (Haidlhof Research Station, Bad Vöslau, Austria). Bold lines represent wooden walls. R1 = main raven compartment, RC = temporary raven or crow compartment, C1 = main crow compartment, C2 = temporary crow compartment, E1 – 4 = experimental compartments.

2.2. Experiment 1: development of stimulus enhancement

We started this experiment two weeks after fledging. Hence, we started with the crows two weeks later as they fledged later. The experiment was conducted once a week for a time period of twenty weeks. Thus, we conducted twenty sessions and tested for the first five months after fledging. We always organized the experiment on the same day of the week, with one day of variation before or after the usual experimental day.

Each time, five similar objects were placed on a wooden board (75 cm x 75 cm) in a pentagonal order 30 cm distant to each other (see figure 2 a). We chose everyday objects which were known to the birds from their aviary and thus wouldn't mean something special to them. The objects changed on a weekly basis. Order and type of objects were the same for ravens and crows (see figure 2 b): (1) small grey stones, (2) wooden sticks, (3) pieces of tree bark, (4) dark blue bottle tops, (5) pieces of fir-tree green, (6) green clothespins, (7) smooth white stones, (8) pieces of bamboo stick, (9) red bottle tops, (10) small smooth grey stones, (11) corks, (12) small pieces of wooden board, (13) big grey stones, (14) purple bottle tops, (15) slim translucent cable ties, (16) light blue bottle tops, (17) pieces of branch, (18) flat white bottle tops, (19) wood chips, (20) blue big Lego® bricks.

Subjects were tested separately. Soon after a bird entered the experimental compartment the objects were placed on the board that was already positioned on the floor. A human experimenter sat down next to the board on the floor. The experimenter handled one of the five objects in each trial of a session for five seconds, in which all five object positions were gone through once randomly within a session. The subjects got 25 seconds of time to manipulate the objects. Afterwards, between the trials, all objects were removed for 30 seconds and then rearranged. Note that the subjects were not rewarded with food during the trials.

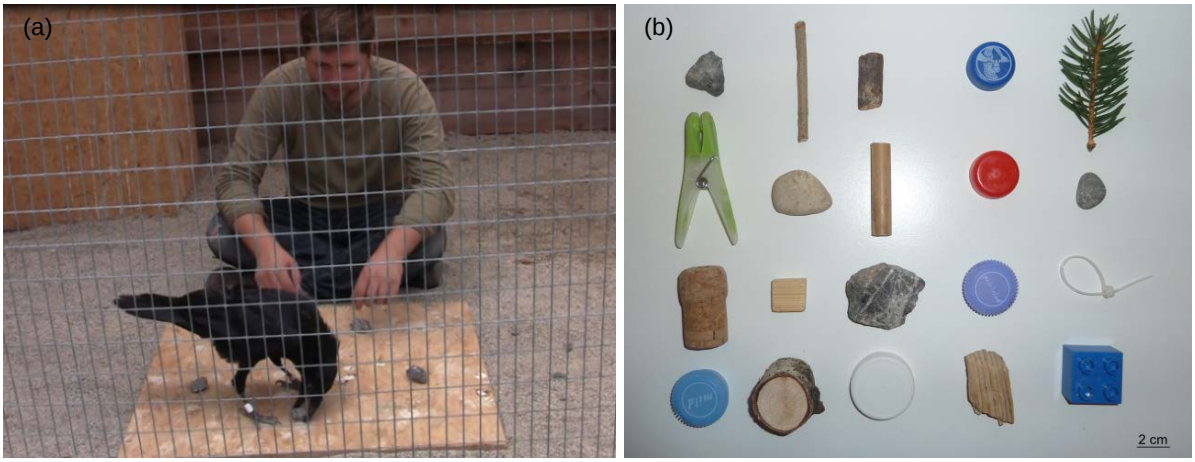

Figure 2. (a) Set-up of experiment 1. Objects are placed on a wooden board in pentagonal order. Subject is manipulating the object that has just been touched by the experimenter. (b) Objects from experiment 1 in chronological order (session 1 – 20) from left to right. In each session five objects of the same type were used.

2.3. Experiment 2: object choice task with reliable and unreliable demonstrator

In this experiment, we placed a small wooden table (60 cm x 25 cm) in front of the wire mesh outside of the experimental compartment (see figure 3). The surface of this table was on the same level with the ground of the experimental compartment. On top of the table lay a slidable wooden board. We used plain white yoghurt cups for hiding the food reward, that were prepared with food before the experiment to avoid olfactory cues. These cups were placed on the slidable board. As food reward we used a small piece of dog food, namely a sixteenth part of a Frolic® pellet. In each round we had two different experimenters, each time one male and one female. They were counterbalanced between the conditions. All four persons were trainees at the Haidlhof Research Station and were of an age between 17 and 30 years. A second person (experimental supervisor) was present during the experiment and coordinated the experimental procedure. It was the same person for each session and both rounds. The side of the food location was chosen semi randomly by throwing a coin, though one side was never chosen more than twice in a row.

Figure 3. Set-up of experiment 2. Experimenter is tipping on a cup. Slidable board with cups lies on a wooden table.

The experimenter sat down in front of the table facing the experimental compartment. At the beginning of a trial, both cups were placed next to each other in the middle of the slidable board with the food reward visible in between. The board was positioned at the middle of the table, so that the bird could not reach the cups. Then the experimental supervisor placed a paperboard (DIN A4), which functioned as occluder, between the set-up and the wire mesh, so that the subject could not see under which cup the reward would be hidden. The experimental supervisor then baited the reward with one of the cups and rotated the two cups. Afterwards, he removed the occluder and pushed the cups in the front corners of the board in the direction of the wire mesh. After doing so, he placed himself behind the experimenter and looked on the ground to avoid visual cues. The experimenter now started tipping on the focal cup (either the baited cup or the empty cup depending on condition) for five seconds. Then he pushed the board into reaching distance for the birds, which allowed the birds to choose a cup by pecking at it. After choosing a cup, the board was moved back to the starting position. The experimenter lifted the chosen cup and gave the food reward to the bird if it had chosen the baited cup. Then he also lifted the other cup. The birds were not rewarded when they chose the empty cup.

We carried out two rounds of this experiment: the first round started ten weeks after fledging and the second round three months after the first round had finished. In each round, subjects got a maximum of ten sessions with each twelve trials to reach a criterion of mastery. When a subject reached this criterion, it completed testing in the passed condition. We confronted each bird separately with two conditions. In one condition, a reliable experimenter touched one of two cups under which a food reward was hidden (baited cup). In the other condition, an unreliable experimenter touched one of two cups under which no food was hidden (empty cup). Both conditions were always conducted once at the same day, counterbalanced at

morning or afternoon with at least two hours in between. The ten sessions were organized within three consecutive weeks.
If we detected that a subject showed a side bias, additional correction sessions were conducted, which did not count as testing. That means, the food rewards were always hidden at the opposite side from the preferred side until the subject chose the non-preferred side three times in a row or in four of five trials.

2.4. Experiment 3

2.4.1. Experiment 3A: discriminating human experimenters

In this experiment, we wanted to test for the birds' general ability to discriminate human experimenters. At the beginning of August 2012, after the end of the first round of experiment 2, we started this experiment. Subjects were presented with three training sessions to habituate to the new set-up, because especially the crows at this age reacted neophobically to unknown humans. In this training, two human experimenters sat down next to each other in front of the wire mesh outside of the experimental compartment. They presented each their open right hand simultaneously to the subject within each trial, while both had a food reward (same as in experiment 2) visibly placed in the middle of the palm (see figure 4). Subjects were rewarded from either experimenter they chose by approaching him. We used four different persons as experimenters for the training (two males and two females between 17 and 30 years). In contrast, in the following testing sessions, two unfamiliar experimenters (a male and a female) offered their closed fists (back of the hand up) to the subjects and only one of the two constantly had the food reward covered in his hand. In this respect, experimenters were counterbalanced over the different birds (for some birds experimenter 1 had the food reward, for others experimenter 2). The side, on which each experimenter was sitting, was chosen semi randomly in each trial by throwing a coin but the same side was never chosen more than twice in a row. When a subject chose one of the persons by approaching, both opened their hands and the subject only got rewarded if it chose the food holding experimenter. We here used the same amount of sessions and trials as in experiment 2. In this experiment, a third person was present coordinating the experimental procedure.

Figure 4. Training session of experiment 3A. Two human experimenters offer their open hands simultaneously with a visible food reward to the subject.

2.4.2. Experiment 3B: preference test of persons from experiment 2

We did this experiment to assess if the subjects would show a preference for the reliable or unreliable experimenter from experiment 2. Thus, we confronted the subjects with the two experimenters from the first round of experiment 2, three days after the last session of that experiment. The procedure was the same as in the training sessions of experiment 3A. Both experimenters offered their right open hand simultaneously to the subject, while the food reward was visibly placed in the middle of the palm. Only one session with twelve trials was conducted. Note that subjects would have gotten a reward from both persons.

2.5. Analysis

Variables were measured from video recordings by using frame-by-frame analysis in *Solomon Coder beta 12.09.04* (András Péter, Eötvös Loránd University, Budapest, Hungary). Statistical tests were done in *IBM SPSS Statistics 21*. Alpha was set at 0.05.

2.5.1. Experiment 1

To calculate the probability of manipulating the enhanced object in a session, we counted the number of times a subject took the enhanced object first in a trial and the number of trials it took any object. For example, if a subject manipulated an object only in four out of five trials, of which in two trails the enhanced object was picked first, then this bird had a probability of taking the enhanced object of 50 % for this session.

Furthermore, the object manipulation time of a subject and the latency to object manipulation were measured. Object manipulation time was defined as the time period starting from the subject's approach to the enhanced object, until the moment the subject left the object on the ground. We started counting the latency to manipulation when the experimenter's hand left the object after the enhancement cue and stopped when the subject started to approach the focal object. We included data also in case the subject touched at most two objects before the enhanced object.

Chi-square tests were performed (Software by Kristopher J. Preacher, http://quantpsy.org) to test the probability of the subjects to take the enhanced object, in order to find out if they showed stimulus enhancement. We tested the average performance of each individual and the average performance over all individuals. The chance level of taking one object out of five objects is 20 %. A chi-square test in this case shows a significant result starting from 32 %. To compare ravens and crows, we did a *t* test with the individual means, as data was normally distributed.

Additionally, we used general linear mixed models (GLMM) in order to detect changes in the development of the response to enhancement and to compare the two species. We performed models for the three variables: probability of manipulating the enhanced object, object manipulation time and latency to object manipulation. We fitted the models with session and species as fixed factors, with subject as random factor and with the interaction between session and species. To look for habituation within the sessions, we fitted the GLMMs for the three variables with trial and species as fixed factors, with subject as random factor and with the interaction between trial and species.

2.5.2. Experiment 2

We counted the number of correct trials each individual had in a session. If a subject attended in less than twelve trials, we corrected the number of correct trials for the analysis percentaged to twelve. In the reliable experimenter condition a trial counted as correct when the bird chose the enhanced cup. In the unreliable experimenter condition, on the other hand, a trial counted as correct when the bird chose the non-enhanced cup. The criterion of mastery was to achieve three consecutive significant sessions or four of five significant sessions. A significant session was defined as having at least nine of twelve trials correct.

Additionally, a GLMM was performed to analyze the subjects' performance of correct trials between the conditions and rounds. We fitted the GLMM with round, condition and session

as fixed factors, with subject and experimenter as random factors and with the interaction between round, condition and session and the interaction between condition and session. We tested a priori for differences in the birds' performance caused by the four different experimenters with a Kruskal-Wallis test. We did this, since it was not possible to enter experimenter as a fixed factor in the GLMM because we used two different experimenter pairs in the two different rounds.

2.5.3. Experiment 3

In experiment 3A, we used the same criterion of mastery and the same analysis as in experiment 2. But the model was fitted with experimenter, species and session as fixed factors, with subject as random factor and with the interaction between species and session.

In experiment 3B, we performed a paired *t* test since data was normally distributed. We compared how often subjects either chose to get the food reward from the experimenter they experienced as reliable or the experimenter they experienced as unreliable in experiment 2.

3. Results

3.1. Experiment 1

In this experiment, a human demonstrator handled everyday objects in front of young ravens and crows on a weekly basis, over five month. On average, each bird showed a significant preference for manipulating the object which had been touched by a human experimenter as the first object of a trial (see table 1). Overall, ravens had a mean probability of manipulating the enhanced object of 74 % (Chi-square test: χ^2 = 58.531, *df* = 1, *P* = 0.00) and crows had a mean probability of 69 % (Chi-square test: χ^2 = 48.608, *df* = 1, *P* = 0.00). However, no significant difference was found between ravens and crows in this trait (*t* test: t_{14} = 0.918, *P* = 0.374, two-tailed).

Table 1. Chi-square statistics of each individual for the percentage probability of manipulating the enhanced object as the first object of a trial (mean over all sessions).

Species	Subject	%	χ^2	*df*	*P*
Ravens	1	63.8	39.403	1	0.00
	2	76.0	62.821	1	0.00
	3	69.3	49.173	1	0.00
	4	84.0	82.051	1	0.00
	5	76.8	64.591	1	0.00
	6	73.8	58.112	1	0.00
	7	61.0	34.879	1	0.00
	8	85.8	86.885	1	0.00
Crows	1	77.3	65.714	1	0.00
	2	74.7	60.010	1	0.00
	3	65.4	42.121	1	0.00
	4	65.8	42.816	1	0.00
	5	79.6	71.044	1	0.00
	6	49.0	18.608	1	0.00
	7	57.0	28.909	1	0.00
	8	83.3	80.225	1	0.00

Subjects showed a constant response to enhancement cues of a human experimenter over all sessions. No significant difference was found between the sessions for the birds' probability to manipulate the enhanced object (GLMM: *F* = 0.255, *df* = 271, *P* = 0.614, figure 5 a), for the time they manipulated the enhanced object after the enhancement cue (GLMM: *F* = 0.050, *df* = 256, *P* = 0.824, figure 5 b) and for the latency to the manipulation of the enhanced object (GLMM: *F* = 1.938, *df* = 256, *P* = 0.165, figure 5 c). Altogether, ravens manipulated the enhanced object for a mean of 9.7 seconds, whereas crows did that for 10.6

seconds. In each session, the probability to manipulate the enhanced object was far above the significance threshold of the chi-square test of 32 % for both ravens and crows (figure 5 a). No significant species difference was found for the object manipulation time and the probability to manipulate the enhanced object between the sessions (see table 2). The species differed significantly in the latency to manipulate the enhanced object (GLMM: F = 7.985, df = 256, P = 0.005, figure 5 c), in which the crows showed a longer latency. On average, the ravens took the enhanced object 1.0 seconds after the experimenter touched it and the crows after 1.9 seconds. The interactions between session and species were not significant (see table 2).

No habituation was found within the sessions, since there was no effect of trial number (continuous) on either of the variables (see table 2). Also the species did not differ within the sessions. The GLMM showed a tendency of a difference for the interaction between trial and species in the latency to object manipulation (GLMM: F = 3.084, df = 76, P = 0.083, figure 5 f). Again, crows showed a longer latency. No difference was found in the interaction between trial and species for object manipulation time and the probability to manipulate the enhanced object within the sessions (see table 2 and also figure 5 d and e).

Table 2. GLMMs for: % = the percentage probability of manipulating the enhanced object as the first object of a trial, manipulation time = the time of manipulating the enhanced object, latency = the latency to the manipulation of the enhanced object. Compared between sessions (above bold line) and within sessions (below bold line).

Variable	Factor	*F*	*df*	*P*
%	Session	0.255	1,271	0.614
	Species	1.851	1,271	0.175
	Session*Species	0.693	1,271	0.406
Manipulation time	Session	0.050	1,256	0.824
	Species	0.015	1,256	0.903
	Session*Species	0.567	1,256	0.452
Latency	Session	1.938	1,256	0.165
	Species	7.985	1,256	**0.005**
	Session*Species	1.665	1,256	0.198
%	Trial	2.840	1,76	0.096
	Species	0.026	1,76	0.872
	Trial*Species	0.374	1,76	0.543
Manipulation time	Trial	0.843	1,76	0.361
	Species	0.494	1,76	0.484
	Trial*Species	1.921	1,76	0.170
Latency	Trial	0.143	1,76	0.706
	Species	0.001	1,76	0.975
	Trial*Species	3.084	1,76	0.083

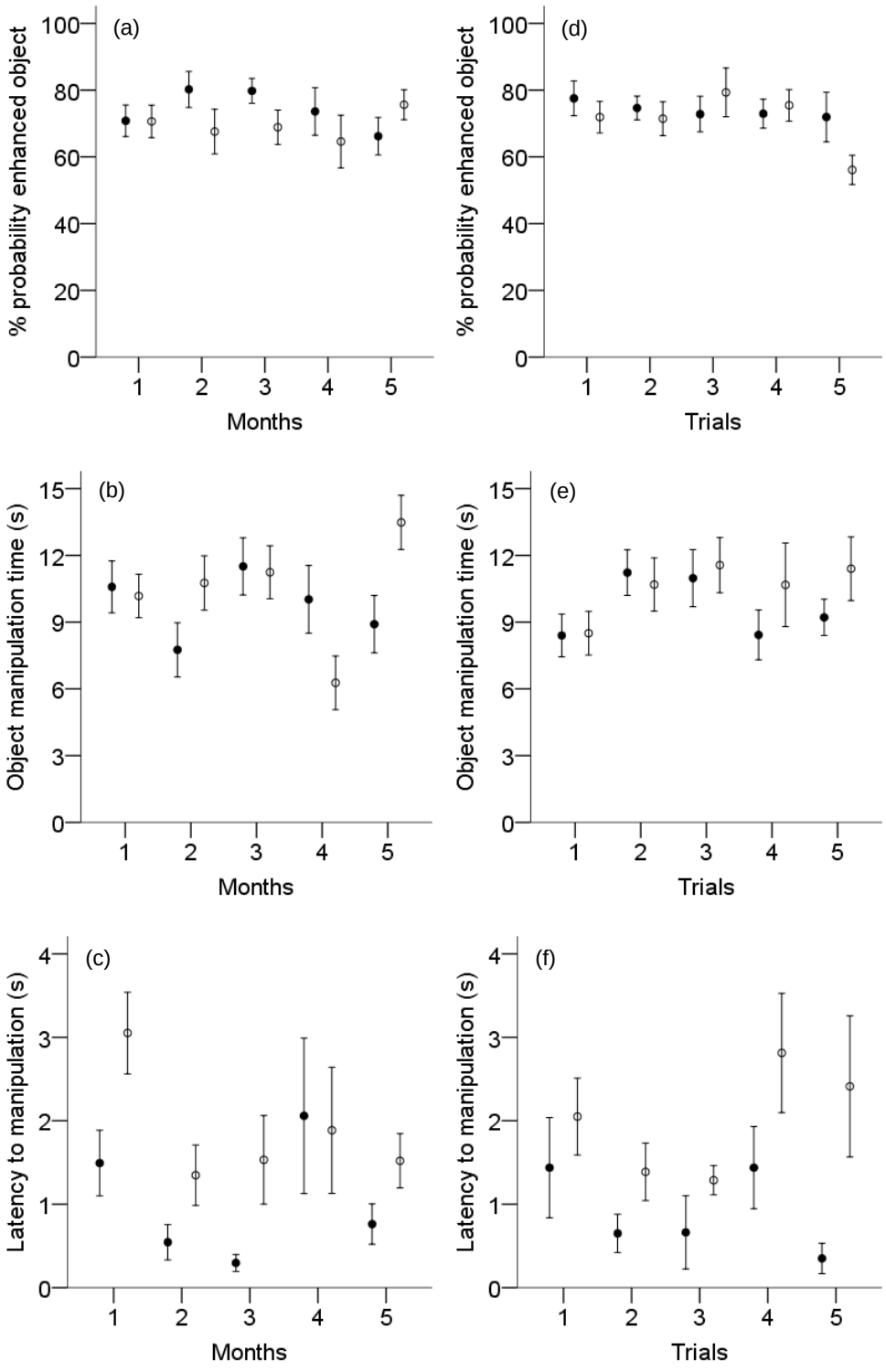

Figure 5. Response to enhancement cues by a human experimenter (mean ± s.e.m.) of ravens (filled circles) and crows (open circles). Shown are the percentage probability of manipulating the enhanced object as the first object of a trial for (a) between and (d) within sessions, the time of manipulating the enhanced object for (b) between and (e) within sessions and the latency to the manipulation of the enhanced object for (c) between and (f) within sessions. Each month (a, b and c) represents four sessions with each five trials.

3.2. Experiment 2

In experiment 2, ravens were confronted with a reliable and an unreliable experimenter in an object choice task. Almost all birds reached the criterion of mastery with the reliable experimenter in round 1 of this experiment (see table 3 for this paragraph). Only half of the birds showed this behavior with the reliable experimenter in the second round. Overall, in both rounds subjects had nearly the same number of correct trials (mean 8.6 correct trials in round 1 and 8.3 in round 2), so they chose the enhanced cup on average in a similar amount of cases. No bird reached the criterion of mastery in neither round with an unreliable experimenter in the course of 120 trials. In addition, the number of trials in which the subjects chose the non-enhanced cup in both rounds of the unreliable condition was below chance level (also see figure 6).

Table 3. Performance of ravens in an object choice task with either a reliable or an unreliable experimenter. Shown are the (a) the number of subjects that reached the criterion of mastery, (b) the sessions the subjects needed to reach this criterion and (c) the number of trials in which the birds chose the baited cup.

		Round 1	Round 2
Reliable	Criterion reached[a]	7/8	4/8
	Sessions needed[b]	4.7 ± 0.7	3.5 ± 0.4
	Correct trials[c]	8.6 ± 0.2	8.3 ± 0.4
Unreliable	Criterion reached[a]	0/8	0/8
	Sessions needed[b]	-	-
	Correct trials[c]	4.8 ± 0.3	4.0 ± 0.2

[b, c] mean ± s.e.m.

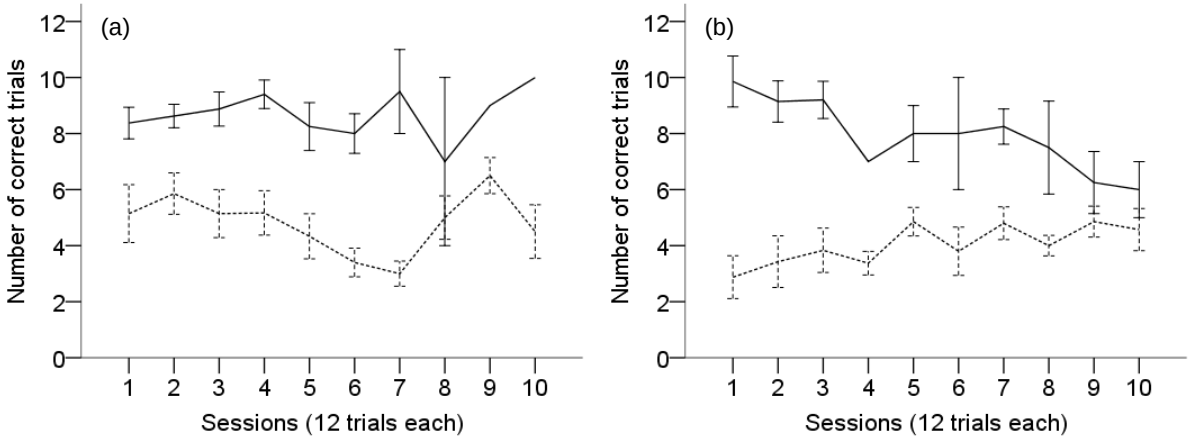

Figure 6. Learning curves (mean ± s.e.m.) of ravens in an object choice task with a reliable experimenter (continuous line) and an unreliable experimenter (broken line) in (a) round 1 and (b) round 2 of this experiment. Correct trials are trials in which the birds chose the baited cup.

The model (see table 4) showed a significant difference between the conditions (GLMM: F = 105.159, df = 197, P = 0.000) and a significant interaction between condition and session

(GLMM: F = 8.087, df = 197, P = 0.005, figure 6). In all sessions of both rounds, the number of correct trials was much lower in the unreliable condition compared to the reliable condition. Furthermore, there is a decrease in the birds' performance of correct trials in the reliable condition of round 2, starting from session 4 until session 10 (figure 6 b), after the four birds that reached the criterion completed testing. From then on, the mean number of correct trials of the birds stayed shortly under the significance threshold of nine correct trials. There was no significant difference between the two rounds and no significant interaction between round, condition and session (see table 4).

Table 4. GLMM for correct trials of ravens in two rounds of an object choice task with a reliable and an unreliable experimenter (conditions).

Factor	*F*	*df*	*P*
Round	0.681	1,197	0.410
Condition	105.159	1,197	**0.000**
Session	1.578	1,197	0.211
Round*Condition*Session	0.126	2,197	0.881
Condition*Session	8.087	1,197	**0.005**

A significant difference between the four human demonstrators of this experiment was found (see figure 7). The birds showed a higher amount of correct trials (mean 1 or 2 correct trials more) with one experimenter (experimenter 1) of the first round compared to all other experimenters (Kruskal-Wallis test: H = 15.311, df = 3, P = 0.002). Between the other three experimenters the birds' performance of correct trials did not differ significantly (post-hoc test, P > 0.1).

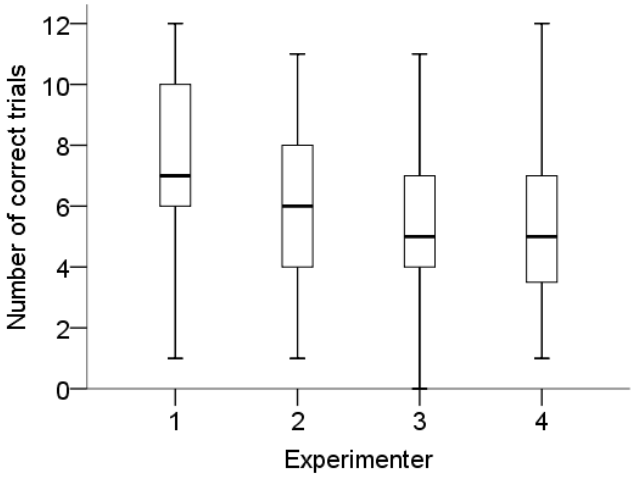

Figure 7. Comparison of the birds' performance of correct trials (both conditions) between the four experimenters of experiment 2. Experimenters 1 and 2 participated in round 1, while experimenters 3 and 4 participated in round 2. Boxplot shows minimum, first quartile, median, third quartile and maximum.

3.3. Experiment 3

3.3.1. Experiment 3A

When ravens and crows were confronted simultaneously with a food holding and a non-food holding experimenter, all birds of both species reached the criterion of mastery. On average, ravens needed two sessions less to figure out the food holding experimenter compared to crows (see table 5). Though, no difference between the two species was found in the performance of correct trials over the sessions (GLMM: $F = 1.399$, $df = 82$, $P = 0.240$, figure 8) and in the interaction between session and species (GLMM: $F = 0.207$, $df = 82$, $P = 0.650$). Also no effect of the two different experimenters was found (GLMM: $F = 1.618$, $df = 82$, $P = 0.207$). Only session number (continuous) had a significant effect on the model (GLMM: $F = 28.820$, $df = 82$, $P = 0.000$). The performance of both species in this experiment showed a constant increase in the number of correct trials over the sessions (see figure 8).

Table 5. Performance of ravens and crows in discriminating two experimenters while only one experimenter held food covered in his hand. Shown are (a) the number of subjects that reached the criterion of mastery, (b) the sessions the subjects needed to reach this criterion and (c) the number of trials in which the subjects chose the food holding experimenter.

	Ravens	Crows
Criterion reached[a]	8/8	6/6
Sessions needed[b]	5.4 ± 0.6	7.3 ± 0.8
Correct trials[c]	8.8 ± 0.3	8.4 ± 0.3

[b, c] mean ± s.e.m.

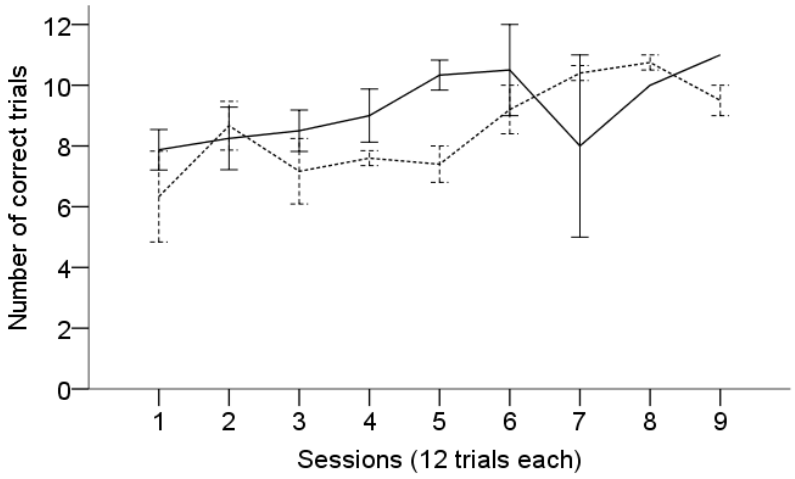

Figure 8. Learning curves (mean ± s.e.m.) of ravens (continuous line) and crows (broken line) for discriminating two human experimenters while only one experimenter held food covered in his hand. A correct trial means choosing the food holding experimenter.

3.3.2. Experiment 3B

When the ravens were confronted simultaneously with the two experimenters from the first round of experiment 2 both offering food visibly on their palm, there was a significant difference in the choice response. The birds chose the food reward more often from the experimenter they experienced as reliable compared to the experimenter they experienced as unreliable beforehand (*t* test: $t_7 = 2.393$, $P = 0.048$, two-tailed, figure 9).

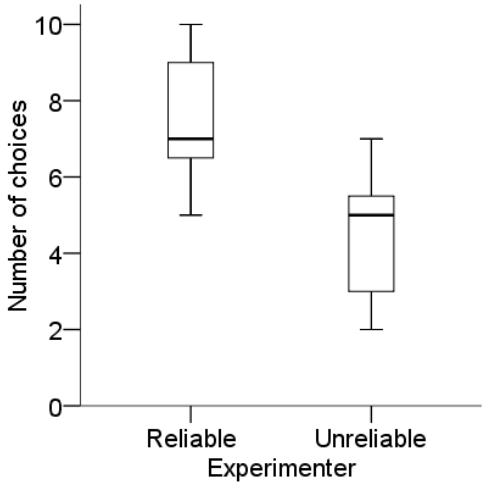

Figure 9. Choice response of ravens being confronted with the reliable and unreliable experimenters from experiment 2 offering food simultaneously on their palm. Boxplot shows minimum, first quartile, median, third quartile and maximum.

4. Discussion

4.1. Predisposition for stimulus enhancement

In experiment 1, we examined the responses of juvenile corvids to enhancement cues during an early developmental phase. As expected, young common ravens and carrion crows immediately showed a high preference for objects that had been touched by a human experimenter. The birds approached the enhanced object directly after the demonstrator's touching and handled the object for a fair amount of time. We found this behavior in each individual of both species. Moreover, this preference stayed constant over all sessions and unexpectedly we found no decrease in the response to enhancement cues over the five months of testing. In addition, there was no habituation within sessions over the whole study period. From trial 1 to trial 5, the birds reacted almost similar to enhancement cues.
These findings indicate a very strong predisposition for stimulus enhancement in ravens and carrion crows in the first five months after fledging. Our results match with the findings of others that young ravens are receptive for social cues (Stöwe *et al.* 2006; Scheid *et al.* 2007; Schloegl *et al.* 2007) and particularly use stimulus enhancement as a social learning mechanism (Fritz & Kotrschal 1999; Schwab *et al.* 2008b).

At the age of our birds during the time of our testing, young ravens in the wild would still be dependent on their parents. After that time, in their first autumn, they would disperse and integrate to socially complex non-breeder groups (Heinrich *et al.* 1994). Thus, for young ravens of this age it might be of high value to learn important skills before their dispersal, using parents and siblings as potential peers (Schwab *et al.* 2008b). In our opinion, such a strong predisposition for social learning in terms of high motivation and attention to social cues facilitates the process of learning in these juveniles. This does also apply for other young animals such as meerkats (Thornton & Malapert 2009) and chimpanzees (Inoue-Nakamura & Matsuzawa 1997) that need to learn more difficult skills, or juvenile canaries that learn preferential food sources via stimulus enhancement (Cadieu & Cadieu 1998). But especially for food caching species like ravens and crows, which are known to show high interest to novel objects as juveniles (Heinrich 1995; Stöwe *et al.* 2006) and to compete over caches (Bugnyar & Heinrich 2005, 2006), it seems necessary to be attentive to others' object manipulations to gain information about items and to improve own caching skills.

However, in the context of play caching also the value of learning about the qualities of other individuals is of importance for ravens (Bugnyar *et al.* 2007a). During the life in the non-

breeder flocks, until the achievement of adulthood, being attentive to others and playing with low-value items could be important for the formation of relationships and coalitions (Fraser & Bugnyar 2010; Loretto *et al.* 2012). This may be a reason why we did not find a decrease in the predisposition of the birds towards the end of the study time. Furthermore, this predisposition for high attention to others' activities might also be important to young corvids in non-breeder groups in food contexts, as they are renowned for visiting for example carcasses where other conspecifics feed on (Heinrich 1988).

No difference was found between juvenile ravens and crows in the predisposition for stimulus enhancement over time. These two closely related species not only seem to be comparable in their socio-ecology (Goodwin 1986) and general cognitive skills (Hoffmann *et al.* 2011; Dufour *et al.* 2012; Mikolasch *et al.* 2012), but also share social learning abilities. The only difference was that the ravens approached the enhanced object faster than the crows. This could be due to differences in attention of ravens and crows but also an effect of the corvid-typical neophobia (Heinrich 1988, 2011), which might vary between the species. Another explanation could be a difference in the agonistic behavior of ravens and crows, as crows for example are known to avoid the competition over food sources more (M.J. Sima, T. Matzinger, T. Bugnyar & S. Pika, unpublished data). Therefore, crows might also be more careful to rush for desirable items compared to ravens. Since we found only a difference of one second and crows reacted similar as ravens to enhancement cues with object manipulation and the probability to manipulate the enhanced object, it is only a marginal effect.

For completeness, we definitely can rule out observational conditioning as a mechanism explaining the response of the birds, because no food reward was provided during testing (Hoppitt & Laland 2008). One possible explanation would be local enhancement. Observations showed that already when the experimenter manipulated the object in his hand, the subjects reacted heavily and tried to fetch it. Furthermore, the birds picked the object directly after replacing it on the board and showed no searching behavior at its location, which might argue for stimulus enhancement as the main mechanism here.

4.2. Control of intentions

In the second experiment, juvenile ravens showed a high preference for the cup that was enhanced by a reliable human demonstrator and most of the ravens succeeded in this condition. However, with an unreliable experimenter, the birds stuck to that pattern and were

not able to choose against the non-reliable demonstrations. This confirms our findings of the previous experiment, that young ravens are strongly predisposed for social cues.

When young ravens are confronted with a reliable demonstrator, they seem to use the experimenter given cues as a steady source of information. This is a reasonable behavior and would be beneficial for a young individual in the wild that depends on learning about novel food sources or caching skills. However, when these juveniles are confronted with unreliable social cues, one would expect that after a while they would avoid the interactions. Our findings show that juvenile ravens irrespectively of success follow unreliable demonstrations, indeed not as consistently as they perform with reliable social cues. It is possible that ravens are not able to control their predisposition for enhancement at the age of our birds, but will be able to choose against non-reliable demonstration when they get older. However, although initially the birds' behavior in the unreliable condition seems to be inefficient, because they do not get the offered food reward, the benefit of learning in a broader context might be given according to the principle: "take all information you can". For a naïve young raven it might be advantageous to react to every social cue that potentially offers some kind of useful knowledge about an item or even about the demonstrator. This might especially be beneficial with regard to the complex social system that the birds expect after dispersal and that requires a high amount of socio-cognitive skills (Heinrich 1989, 2011). Additionally, in such a neophobic species like ravens (Heinrich 1988, 2011), the social facilitation and enhancement of another individual might be particularly important for learning.

Contrary to our expectations, young ravens were still not able to choose against the non-reliable demonstrations in the second round of this experiment in their first autumn. Other studies indicate a large step in the cognitive development of ravens at this time (Bugnyar *et al.* 2007b; Schloegl *et al.* 2007; Loretto *et al.* 2012). Moreover, ravens are known to inhibit and to wait up to five minutes for a delayed gratification (Dufour *et al.* 2012). We expected them to show this behavior also in our context. However, this phenomenon is not only due to a problem in discriminating the experimenters. Ravens as well as crows were able to distinguish very fast which of two experimenters provided food in our experiment 3A. In addition and even more relevant here, the birds showed a significant preference for the reliable experimenter when the two experimenters of experiment 2 simultaneously offered food (experiment 3B). This emphasizes that they noticed the difference in reliability and that they have learned about the cooperativeness of the persons. Thus, our study shows that juvenile ravens at about five months post-fledging are not able to control their predisposition and to inhibit the power of enhancement when they are confronted with non-reliable social cues.

A reason for the lack of intention control might be that a strong predisposition for enhancement retains beneficial after the dispersal to the non-breeder groups. Additionally, it could be possible that the birds generally expected positive consequences by the behavior of humans due to the experience of hand-raising. Furthermore, stimulus enhancement is often referred to as a simple form of socially influenced learning (Whiten & Ham 1992; Zentall 1996). It could be assumed that in general it is strongly enrooted in these birds and that there is no necessity to be very selective with those learning cues as failures might not bring disadvantages. Especially in an object choice set-up where the subjects have a fifty-fifty chance to get the food reward, there might be no need for complex strategies. However, for common ravens that are known for fake-caching and misleading of others while caching (Heinrich & Pepper 1998; Bugnyar & Kotrschal 2004), it should be useful to learn about the reliability of conspecifics. Hence, it is possible that the ability to control intentions develops at a later stage, which is a reason for further investigations.

Against all expectations, we found a difference in the response of the ravens between one experimenter of the first round of experiment 2 compared to the other three experimenters. At this point, we do not know why this happened and if it was caused by differences in the demonstration behavior of the experimenters. However, it might help explaining the seemingly worse performance of the ravens in the second round of this experiment. The birds' performance of correct trials in the reliable condition did not differ significantly between the two rounds, but fewer subjects reached the criterion of mastery in the second round. Instead, the number of correct trials of the birds stayed shortly under the significance threshold. This might be caused by attention problems of the birds or distractions or be due to a confusion by the two conditions. Further video analysis and additional experiments may help answering the questions.

4.3. Conclusion

Young common ravens and carrion crows showed a significant preference for handling everyday items that had been touched by a human demonstrator. This preference retained constantly over the whole testing period of five months post-fledging. Furthermore, in an object choice task with a reliable and an unreliable experimenter, ravens chose the enhanced cup more often irrespectively of the reliability of the experimenter and even without getting the food reward. This phenomenon cannot be explained by a problem in discriminating the experimenters, since in a following test, were the same persons simultaneously offered food, birds showed a significant preference for the reliable experimenter. Thus, they have learned about the cooperativeness of the persons. To sum

up, young ravens have a very strong predisposition for stimulus enhancement which might facilitate learning. Yet, at this age they seem to have problems to control this predisposition, even in their first autumn. Further investigation will show how strongly predisposed older individuals are for such enhancement and if they will be able to choose consistently against non-reliable demonstrations.

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Appendix

Zusammenfassung

Soziales Lernen ist ein einfacher Weg, um relevante Informationen über die Umwelt zu erhalten. Doch diese Informationen von Artgenossen sind nicht immer zuverlässig und es ist nicht klar, ob und wann Tiere zwischen zuverlässigen und unzuverlässigen Sozialpartnern unterscheiden. Wir haben zunächst die Prädisposition für „stimulus enhancement“ von jungen Kolkraben und Aaskrähen getestet, die bekannt für ihre Fähigkeiten im Bereich des sozialen Lernens sind. Dazu berührte ein menschlicher Experimentator einmal wöchentlich alltäglich Objekte vor den Vögeln. Wie erwartet zeigten Raben und Krähen von Anfang an eine starke Präferenz für jene Objekte, die manipuliert wurden. In einem weiteren Experiment konfrontierten wir die Raben je mit einem zuverlässigen Experimentator, der immer auf einen von zwei Bechern tippte, unter dem sich Futter befand und einem unzuverlässigen Experimentator, der auf den Becher tippte, unter dem sich kein Futter befand. Die meisten Raben waren erfolgreich mit dem verlässlichen Experimentator, jedoch schaffte es kein Individuum sich gegen die unzuverlässigen Demonstrationen zu entscheiden. Junge Corviden weisen eine sehr starke Prädisposition für „stimulus enhancement“ auf, scheinen jedoch Probleme zu haben diese Prädisposition zu kontrollieren.

Abstract

Social learning is considered a cheap way of obtaining information about relevant features in the environment. However, information provided by others may not always be reliable, raising the questions if and when animals can come to tell apart reliable from unreliable demonstrations. We here tested this idea in young common ravens and carrion crows, as they are renowned for using social information in various forms of object manipulation. We first investigated the predisposition of fledged ravens and crows to show stimulus enhancement, subjecting individuals to a human experimenter touching specific objects once a week. As expected, birds readily showed a significant preference for handling those items that had been touched. Next, we subjected ravens to two types of human experimenters, one who provided reliable information about cached food by touching the object under which food was hidden, whereas the other one always touched the object under which no food was hidden. Most ravens quickly succeeded in the reliable condition but none of them reached significance in choosing against the non-reliable demonstrations in the course of 120 trials.

Young corvids seem to have a very strong predisposition for stimulus enhancement. Yet, at least as juveniles they seem to have problems to control this predisposition.

Curriculum Vitae

Personal Information

Name	Sebastian Dörrenberg
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Education

2006	Abitur (Diploma from German secondary school) at Sophie-Scholl-Gesamtschule, Remscheid, Germany
2006 – 2013	Studies of Biology at the University of Vienna, Austria, Focus: Zoology, Animal behavior

Work Experience

2001	Three weeks work experience in a pharmacy
2003 – 2004	Holiday jobs in different factories
2005	One week work experience in a bank
2005 – 2008	Waiter in different restaurants
2008 – 2011	Child care at several events of the association “Take Part”, Vienna, Austria
2008 – present	Shop assistant in the pet shop “Megazoo”, Vienna, Austria, Focus: Aquaristics

Personal Skills & Additional Qualifications

2005	Driving license
2011	Diving license (CMAS* Germany)
2012	Help in hand-raising of ravens and crows at the Haidlhof Research Station (University of Vienna & University of Veterinary Medicine, Vienna)
Mother tongue	German
Other languages	English (fluent, written and spoken), Qualification in Latin, French and Spanish (very basic knowledge)
Interests	Keeping and breeding of fish, reptiles and birds Reading, Basketball and Guitar playing

Research Experience

2009	Project: Investigation of changes in social behavior of orangutans (*Pongo pygmaeus*) after the removal to a new enclosure in the Zoo Vienna. *Tiergarten Schönbrunn & University of Vienna, Supervisor: Prof. Helmut Kratochvil*
2009	Project: Benefit of neighbors in terms of mobbing behavior in a colonially breeding cichlid (*Neolamprologus caudopunctatus*). *Department of Behavioral Biology,*

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2011 Project: Influence of different habitats on the growth of *Salamandra salamandra* larvae. *University of Vienna, Supervisor: Prof. Günter Gollmann*

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Publications & Presentations

Müller C. A., Dörrenberg S., Mayer C., Riemer S., Huber L., Range F. (2010) Understanding of size constancy in dogs: A new approach to account for novelty effects. Poster presented at the 2nd Canine Science Forum, 25. – 28. July, Vienna, Austria.

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