The ability of ravens (Corvus corax Linnaeus, 1758) to evaluate human behavior from a bystander perspective

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Gavrani (*Corvus corax*) imaju složenu socijalnu strukturu u kojoj su jedinke izložene različitim situacijama u interakciji s drugim jedinkama. Stoga, predviđanje ponašanja drugih, pomoću informacija dobivenih opažanjem, može biti korisno u budućim interakcijama. Kako su u prijašnjim studijama gavrani razlikovali ljude nakon direktne interakcije s njima, zanimalo me mogu li razlikovati ljude i iz pozicije promatrača. U ovom eksperimentu, svaki je gavran promatrao dva izvođača pokusa koji su ili uzeli hranu koju su sami prethodno sakrili ili su ukrali hranu iz skrovišta drugog izvođača pokusa. Naknadno, dva izvođača pokusa (kradljivac ili osoba koja je uzela svoju hranu natrag i neutralna osoba) ponudili su hranu gavranu, koji je potom odabrao od koga uzeti hranu. Suprotno predviđanjima, gavrani nisu odabrali niti jednog izvođača pokusa značajno više od drugih. Ipak, analiza njihovih odabira prije i nakon promatranja pokazuje da imaju sklonost razlikovanju osoba. Također, gavrani su promijenili svoje ponašanje (okretaji glavom) kroz pojedine faze pokusa, ali ne i kroz tip pokusa. U konačnici, ovo istraživanje je dalo dvosmislene rezultate, vjerojatno zbog male veličine uzorka. Potrebna su dodatna istraživanje kako bi se potvrdilo jesu li gavrani sposobni razumjeti prikazanu ljudsku interakciju i na koje njene elemente obraćaju pozornost.

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Ravens (*Corvus corax*) have a complex social structure with various interaction between individuals. Predicting the behavior of others based on observation would be advantageous for future interactions. While previous studies showed that ravens can discriminate between human experimenters after direct interaction, I was interested to see if they would be able to do so when put in a bystander position. In this study, individual ravens could observe two experimenters engaging in the retrieval of their food previously cached or in the pilfering of the other's cache. Two experimenters (pilferer or retriever versus a neutral person) offered food and each raven had the choice to take the food from one of them. Contrary to expectation, the ravens did not choose one experimenter significantly over the other. Yet, when comparing their choices made before and after the observation, I found a tendency to discriminate. Furthermore, the ravens changed their visual behavior (head turns) across the phase types of a trial, but not between the conditions. This study produced equivocal results, which might be caused by small sample size. Further investigation is needed to confirm whether ravens are capable to understand displayed human interaction and what behavioral actions ravens are paying attention to.

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Contents

1. Introduction

1.1 Cognitive biology

Cognitive biology is relatively young science field developed in 1970's. Animal cognition, in a broad sense, includes all ways in which animals receive inputs to their brain through the senses, process, retain and decide to act on (Shettleworth, 2000). The field originates from comparative psychology, including the study of animal conditioning and learning (Shettleworth, 2000). At the beginnings, through the 20th century ethology and animal psychology developed independently (Richards, 1987). Ethology was developed by zoologists in Europe, whereas animal psychology was developed mostly in North America. Because of big spatial distance, it is not surprising there was little communication between the two fields and consequently different approaches to the field. Ethologists focused more on innate animal behavior in the field, whereas psychologists examined learned behaviors of a few species in the laboratory (Shettleworth, 2001).

Modern days, this is strikingly interdisciplinary field, integrating traditional comparative psychology and ethology, as well as comparative neuroscience and behavioral ecology (Osiurak et al., 2020). Nowadays, areas of research overlap from human cognitive sciences (Baumeister et al., 2001; Hamlin et al., 2010), studies of concept learning (Wright et al., 2017), spatial learning and memory (Biegler et al., 2001; Daneri et al., 2015) to attention (Scheid et al., 2007), imitation (Kis et al., 2015), cooperation (Bshary & Grutter, 2006; Seed et al., 2008), problem solving (Benson-Amram & Holekamp, 2012), decision making (Kotrschal & Bugnyar, 2002; Zentall et al., 2017) and information spread (Kulahci et al., 2016; Whiten & van de Waal, 2016).

Together with the increasing interest and research of the cognitive abilities of animals in the wild, we are also discovering how human activity impact those abilities: e.g. neonicotinoids impair spatial memory in bumblebees (Samuelson et al., 2016), odor coding in honeybees (Andrione et al., 2016), and sex allocation decision-making in parasitic wasps (Whitehorn et al., 2015).

1.2 Third-party evaluation

It is known that humans regularly evaluate others, based both on direct interactions with them and on others' interaction with third parties (Anderson et al., 2013). Evolutionary biologists are using the term 'indirect reciprocity' to describe how individual subjects gain different information based on others' helpful or hindering acts towards third parties, as well as to describe how they use the acquired knowledge in future interactions with these parties (Alexander, 1987).

There are two types of 'indirect reciprocity': upstream and downstream (Nowak & Sigmund, 2005) and I will concentrate on the latter. Downstream reciprocity is based on reputation and the easiest way to explain it is by giving an example: individual C will help individual A, because individual A has helped individual B. This is also supported by mathematical methods which show that natural selection can favor strategies that help others based on their reputation (Nowak & Sigmund, 2005).

However, there are problems with indirect reciprocity, especially when the individual is defecting or cheating (Nowak & Sigmund, 2005). This problem is tackled in direct reciprocity with the help of the Prisoner's dilemma (Axelrod & Hamilton, 1981). That is a cooperation game where, evolutionary speaking, costs and benefits are represented by fitness (the relative reproductive success of a genotype). If both subjects decide to cooperate, then their net yield will be higher than mutual defection. However, if only one defects then that player yields a higher payoff. One theory says indirect reciprocity derives from direct reciprocity when an interested bystander is present (Alexander, 1987). Observer Tit-for-Tat strategy in the prisoner's dilemma has been proposed as an effective strategy to evaluate someone's reputation (Nowak & Sigmund, 1998; Pollock & Dugatkin, 1992), relying on eavesdropping on the others' choice in the first round and on direct experience in all subsequent rounds, against the same co-player (Nowak & Sigmund, 2005). Thus, in relatively stable populations, where the likelihood of individuals' subsequent meetings with the same individuals is high, both direct experience and eavesdropping on reputation (i.e. observing interactions between other individuals to differentiate cooperators from noncooperators) could be used (Akçay et al., 2010).

From a cognitive point of view, indirect reciprocity has been considered challenging as individuals have to keep track of others' interactions and their valence from a bystander perspective (Brosnan et al., 2010). A basic building block could be seen in the ability to comprehend third-party relationships, which has been demonstrated in a handful of species, mainly primates (Bergman et al., 2003), and has been suggested to be a core feature of social intelligence (Massen et al., 2014)

1.3 Common raven

The common raven (*Corvus corax* Linnaeus, 1758) (Figure 1), represents a good model organism because it is relatively easy to maintain and breed in captivity which allows for a more controlled research environment. They have been highly studied in the field of social learning and cognitive biology, from investigating vocalization, foraging, social learning, and group dynamics to information spread (Enggist-Dueblin & Pfister, 2002; Kulahci et al., 2016; Loretto et al., 2015; Luef et al., 2017; Marzlufi & Heinrich, 1991). Ravens represent a good model species for cognitive biology research, especially because of highly complex social life and comparison to, often more popular, primate abilities, which was discussed in many research papers (Boucherie et al., 2019; Bugnyar et al., 2004; Fraser & Bugnyar, 2010b; Pika et al., 2020; Schwab et al., 2008; Stöwe et al., 2006)

Common ravens, members of class Aves, order Passeriformes, family Corvidae, are black, large-brained passerine birds broadly distributed throughout the Northern Hemisphere (Haring et al., 2007). They are mainly scavengers, but can eat vegetables, grains, acorns, fruits, and buds (Marquiss & Booth, 1986; Nelson, 1934). They often cache their food in various places. It has also been noticed that young ravens begin to experiment with caching edible and non-edible objects soon after leaving the nest (Boarman & Heinrich, 1999) and that older ravens may still use play caching with objects to learn about others, like unfamiliar human experimenters (Bugnyar et al., 2007)

Figure 1: Common raven (*Corvus corax*). (Photo: https://www.pinterest.com/pin/684758318325004017/)

Adults form long term monogamous bonds with their mates (Boarman & Heinrich, 1999). Breeding and egg laying occurs between mid-February and late May. Usually a female lays 3 to 7 eggs per nest and the eggs incubate for 20 to 25 days. Already, five to seven weeks after hatching the young fledge, however, they become sexually mature between 3 to 5 years of age (Berg, 1999) and in some cases it can take up to 10 years or more (Boucherie et al., 2019). Since the survival age is around 15 years in the wild (Fransson et al., 2010) it is clear that ravens spend most of their lives as non-breeders and have one of the longest periods of socio-cognitive development of any avian species (Fraser & Bugnyar, 2010b).

The non-breeders usually form a temporary flock consisting of young, immature birds, adults without a pair and/or a territory (Braun & Bugnyar, 2012; Heinrich, 1989). Non-breeder aggregations are characterized with high fusion- fission dynamics, meaning that these social groups are frequently changing in respect to group size and composition (Aureli et al., 2008). Although being in a group is advantageous in finding and accessing unpredictable food sources which are often monopolized by the predators (Heinrich & Marzluff, 1991; Kotrschal & Bugnyar, 2002), it often results in high food competition.

Nevertheless, juveniles try to assemble affiliate bonds with other ravens, firstly regardless of sex, but then more and more with a single opposite sex partner which ultimately results in a pair bond (de Kort et al., 2006; Loretto et al., 2015; Von Bayern et al., 2007). Affiliative bonds with other conspecifics are important for survival and reproductive success (Braun & Bugnyar, 2012) in raven social life. Bonded ravens tend to resolve conflicts between each other (Fraser

& Bugnyar, 2011), support each other in conflicts with conspecifics (Fraser & Bugnyar, 2012), and console each other after severe conflicts with other group members (Fraser & Bugnyar, 2010a). Affiliative bonds are also important in spreading information between ravens. Ravens observe more frequently individuals with whom have more affiliative interactions, and the ones who frequently both received and began affiliative interactions were quicker in solving the task (Kulahci et al., 2016).

The emerging picture of a relatively complex social life in ravens fits well to other studies in Corvids (Logan et al., 2013; Seed et al., 2008) Accordingly, it has been suggested that the evolution of high social intelligence in corvids is a result of cognitive skills required to deal with the complexity of their relationships, rather than the number of social interaction partners (Emery et al., 2007). Similarly, papers from Freeberg et al. (2012) and Bergman & Beehner (2015) propose that the number of differentiated relationships that individuals have in a group are a better proxy to quantify social complexity than just mere group size.

1.4 Third-party evaluation in common raven

Cooperative behavior through indirect reciprocity has been well researched in primates and gained considerable attention from the scientific community (Anderson et al., 2013; Borgeaud et al., 2013; Cheney, 2011; Seed et al., 2008), especially the timeframe of reciprocation and its cognitive implication. However, there are only a few studies regarding reciprocity in birds (Fraser & Bugnyar, 2012), which is surprising since corvids and parrots show impressive cognitive abilities both in the physical and social domain (Emery, 2006).

One of the studies showed that wild ravens regularly interrupt others´ affiliative interactions even though these are potentially risky (Massen et al., 2014). Ravens with strong bonds initiated most interventions, which mainly affected loosely bonded individuals. Thus, selective intervening by a third-party toward a particular dyad may prevent the formation of these bonds and the subsequent rise in rank. These results suggest that, similar to baboons (Bergman et al., 2003), ravens may use their third-party knowledge flexibly for rank and social relations (Massen et al., 2014).

In a study by Sima et al. (2016) captive ravens were presented with food that varied in the number of pieces. Agonistic behavior was observed during feeding, while affiliative behavior was observed afterwards. They found that ravens use their social bonds to avoid conflicts by choosing with whom to feed, and to mitigate effects of conflicts by engaging in third-party affiliation as post-conflict behavior. A similar result on post-conflict management was reported by Fraser & Bugnyar (2010).

Loretto et al. (2015) showed that, in their first few months, ravens often intervene in others' conflicts but mainly support the aggressor; later on, they supported more selectively towards kin and affiliative partners, possibly due to a progress in understanding relationships as well as their ability to apply this knowledge strategically. These findings indicate that ravens engage in sophisticated social behaviors and form stable relationships as early as in their first year of life.

The only experimental study which incorporated playbacks has shown that ravens react differently to recordings of expected and unexpected dominance interactions of conspecifics. Therefore, ravens seem to understand third-party rank relations which are entirely based on the observation of other's interactions (Massen et al., 2014). These findings confirm that ravens, just like primates (Bergman et al., 2003; Borgeaud et al., 2013; Slocombe & Zuberbühler, 2007), are able to discriminate between different types of simulated encounters based on their knowledge about those played back individuals.

In an experiment by Müller et al. (2017) ravens' were given an option to exchange a piece of low-quality food for a high-quality piece with a 'fair' or an 'unfair' experimenter; while the former would readily trade its food item with the raven, the latter would eat its after receiving the item form a raven. Additionally, they have tested bystander ravens that had observed the experiment for the preference for a 'fair' or an 'unfair' experimenter. The results showed that ravens with direct experience were more likely to interact with 'fair' experimenters. Observers did not discriminate between the experimenters when interacting with them. However, ravens that could experience a direct interaction before being tested as observers tended to perform better from a bystander perspective, but this trend was not significantly above chance.

2. Aims and predictions of the study

The objective of this master's thesis was to assess ravens' capability to evaluate intrahuman interactions, between pilferer or retriever and neutral person, as bystanders.

I predicted that ravens would show a positive bias towards the retriever, in contrast to a negative bias towards the pilferer. Thus, I posed the following hypotheses: i) ravens pay attention while human experimenters are caching, ii) they can discriminate between experimenters and their roles, and consequently make decisions based on whether the two experimenters acted on their own or the other's caches, or did not act on a cache at all and iii) the neutral person would be always a safe bet when choosing from whom to take food.

For the hypothesis i) to be true, I expected the ravens' attention levels, measured by the rate of head turns per second and distance from the wire-mesh, would differ between observing pilferer and retriever. Specifically, I expected increased attention measured by fewer head turns and more time spent near the wire-mesh, during pilfering compared with retrieving. This was expected because pilfering features a violation on the other's cache, but also because of the violation of the raven's expectation on the apparent ignorance of the pilferer about the location of the cache from the other person. Next, I expected an increase of the left eye use, measured by a higher frequency of head turns to the right per second, during pilfering compared retrieval, as some studies suggest that animals' right-hemisphere is dominant when faced with fear and aggression and left-hemisphere when presented with rewards (Leliveld et al., 2013). Additionally, I anticipated increased attention, measured in fewer head turns, during the caching, retrieving/pilfering compered when experimenters were coming and leaving from their positions (in other words – when experimenters were not present), as caching is a highly salient behavior for ravens in their everyday life. For the hypothesis ii), I expected that the ravens would rather choose to take food from the neutral person than the pilferer/retriever, and rather from neutral experimenter than the pilferer. I expected no preference towards the specific experimenter prior the observation. Furthermore, I expected that they would make significantly different choices after the observation of the experiment compared to the decisions made prior to the experiment. In that way, even if they collectively do not show a preference toward the specific experimenters' role, their individual choices would indicate their cognitive ability to differentiate between these roles. Lastly, for the hypothesis iii) I anticipated that their latency to decision will be the shortest when choosing neutral person, due to their nonspecific role.

3. Materials and methods

3.1 Study objects

For this study, I tested hand-raised adult non-breeder and breeder ravens at the Haidlhof Research Station, which is part of the Department of Cognitive Biology, University of Vienna, Austria. The non-breeders are held in a big outdoor aviary (Ludus, 15x18x5m) enclosed with mesh wire, while paired breeders are kept in separate aviaries (Domus and Castrum, 4 units, each 8x10x5m). All aviaries are equipped with wooden braches, trees and enrichment objects such as boots, bottles, caps etc.

The birds are being fed twice a day, at 8:00 and 16:00, with the meals containing various types of food such as: meat, vegetables, fruit, diary, and cereals. Water is provided *ad libitum* in all the aviaries.

3.2 Experimental set-up of caching experiment

The testing phase lasted from the middle of June until the end of September 2020. Parts of the experiments were conducted before noon and parts in the afternoon. Each bird participated in only one trial per day. In all cases, the experiment was conducted after the morning feeding, but prior to the afternoon feeding.

During the experiment the tested bird was in the part of the enclosure which can be spatially separated from the rest of the aviary by closing the wooden doors (in Domus and Castrum) or by closing sliding wire mesh doors (in Ludus). As it is a part of the birds' enclosure and daily routine, the habituation phase for the separation procedure was not necessary.

The plan was to test 18 ravens (10 non-breeders and 8 breeders) in total, but at the end only 10 ravens (5 breeders and 5 non breeders) successfully completed the testing. All breeders were older than 6 years and non-breeders were 4 years old. In total, 4 males and 6 females were tested. Such a big drop in experimental subjects was due to ravens' neophobic behavior (which is more prevalent in adults than in juveniles (Heinrich, 1995), to the new, unknown human experimenters. Neophobic behavior is an extreme or irrational dislike of anything new or unfamiliar. I tried to familiarize these individual ravens to the test procedure by bringing in unknown people, who would give them some treats, multiple times. Unfortunately, 8 ravens still remained skeptical towards new persons and simply would not approach unknown experimenters in the set-up; hence they were excluded from the study.

I conducted 2 sessions (one with pilferer and neutral person, and one with retriever and neutral person), each consisting of 2 trials. Specifically, 6 birds completed 3 trials, and 4 birds completed 4 trials. New experimenters were used for each bird's trial, so the raven would not develop any bias based on previous experience with a person.

Trials, as well as roles and sides of the experimenters within the trials were randomized. I was present in all the trials as a familiar person to the ravens, so I was always standing in the middle, between the pilferer/retriever and the neutral person. Regarding the gender of the experimenters, in most of the trials both experimenters were either male or female, except in 4 trials (where I had male and female combinations). Both, the experimenters and I were outside the aviary for the whole duration of the experiment.

Positions of the experimenters were marked by one cache on the far left and one on the far right outer side of the experimental part of the aviary (Figure 2). Caches were placed 2 m apart, next to the wire mesh, on the ground level. They were represented by plain wooden boards, measuring approximately 20x20 cm. Additionally, a third board was placed approximately 1m from each cache and was used as food plate. From this middle board the experimenters would take the piece of food and either offered it to the raven or cache it. This board marked my position.

Regarding the reward, experimenters offered a piece of familiar and highly liked dog food (brand of Frolic) to each raven which they put through the wire mesh at the same time. The same type and amount of food was used for caching purposes.

The sessions were recorded by a camera fixed on the top of the aviaries for the purpose of further behavioral analysis (rate of head turns per second, the position in the aviary, decisions made, latency to the decision and proximity to the wire mesh)

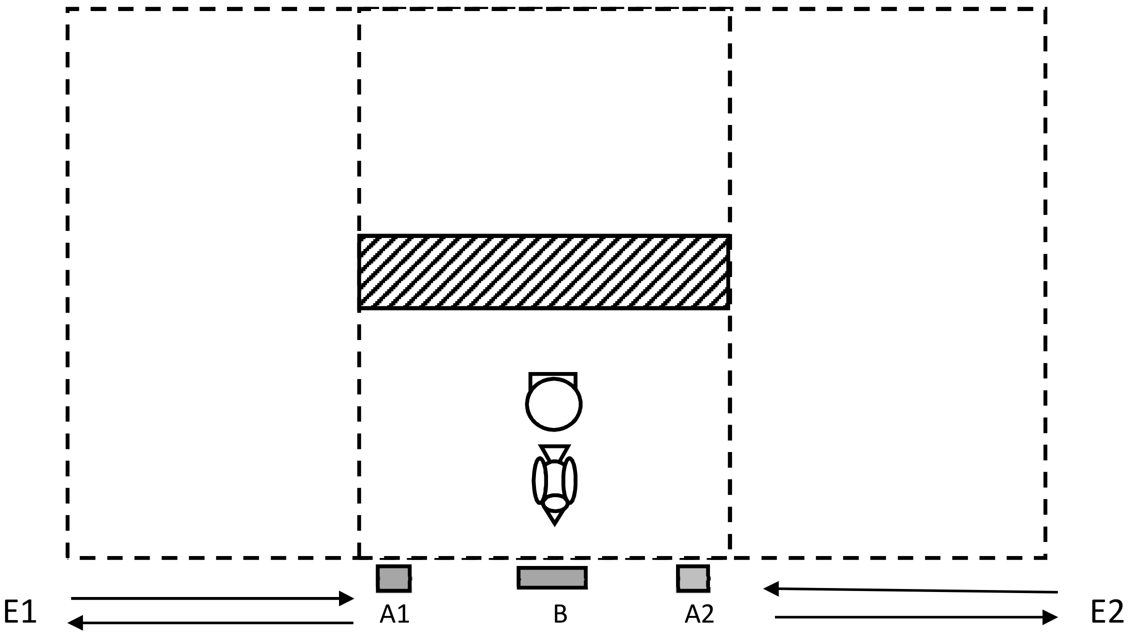

Figure 2: Schematic display of the experimental setup. It consisted of two caching sites (A1 and A2) for two experimenters, the experimenters' hiding spots (E1 and E2), the middle board (B), the raven and one camera.

The whole experiment consisted of four phases: the first decision phase, the caching phase, the pilfering/retrieving phase, and the final decision phase.

1. First decision phase

I put two pieces of food on the middle wooden board, after which both experimenters would emerge from their hiding sites (a few meters from their positions, where ravens could really see them). They would simultaneously pick the food up, position themselves in front of their cache and put the food through the wire mesh at the same time. The raven could then choose from whom it took the food first. Right afterwards, both experimenters left and went back to their hiding spots.

This first decision (from whom to take the food first) served as a control, because at that point the raven had no relevant information about the experimenters.

2. Caching phase

   Again, I would put two pieces of food on the middle wooden board. One by one, experimenters would come, taking the one piece of food closer to their side, showing it to the raven, placing it under the wooden board – caching and leaving. Which experimenter would cache first as well as on which side was randomized at the beginning of the experiment.

3. Pilfering/retrieving phase

   In this phase, same as in the last one, experimenters were coming and leaving one by one. In the trial with the pilferer, the experimenter would steal the food out of the cache of the other experimenter. In the trial with the retriever, the experimenter would retrieve his/her own food. The neutral experimenter, in contrast, would not manipulate any cache but would just stay a few seconds in front of his/her cache in both trials.

   Prior to the final decision phase, there was a one minute waiting time, to make sure that the tested raven would have time to consolidate the observed actions.

4. Final decision phase

   I would open both caches by flipping the wooden boards and I would take the food left in one cache. That way the raven could see that both caches were, at the time, empty to avoid bias towards the side where a cache was not pilfered/retrieved. Again, I would put two pieces of food on the middle board followed by the same steps as in the first decision phase, i.e. the experimenters would simultaneously pick the food up, position themselves in front of their cache and put the food through the wire mesh at the same time and the raven could then choose from whom it took the food first.

Note that in this second decision phase, the raven could choose based on experimenters' previous actions. Hence, I could not only compare which person they prefer to take the food from, but also if their choice differs from their choice in phase one, when they were naive about the experimenters.

3.3 Behavioral coding

For behavioral coding, I used the Solomon coder software (Péter, 2019). First I had to make a configuration sheet with the categories of all behavioral events and durations. After that, I uploaded a video file to create a configuration sheet and add certain behaviors to specific time stamps. A behavioral event is defined as a behavior taking place immediately and with no duration (e.g. a switch in gaze). A behavioral duration is defined as a behavior which takes place across a duration (e.g. duration of gaze).

Specifically, I coded the following behavior:

- The position (left, middle, right; duration) of the raven was defined as the position compared to the location of the middle board. The position compared to the middle board was established from the raven's perspective. Thus, the middle position was defined as the position in front and within the width of the middle board, the left one as position on the left side of the compartment from the middle board, and the right one as a position on the right from the middle board.
- Head turn (right, left; event) of the raven was defined as raven turning its head to the right or left side by approximately 90° angel. Raven's beak was used for the easier head orientation tracking and angel estimation. The turn side was established from the raven's perspective.
- Close distance observation (duration) was defined as raven being distanced less than 1 m from the wire mesh, with its body positioned towards the caches.
- Latency to the decision (duration) was defined as the time it took for the raven to take the food from the one of the experimenters from the point both experimenters threw their food through the wire mesh.

- Decision (event) was defined as the first experimenter from whom the raven took the food. There were two decisions recorded: one in first decision phase, and another one in the second decision phase.

The coding of the behavioral parameters per trial was further divided into phase types (experimenter phase and interphase) to facilitate statistical analysis. Experimenter phase refers to the total duration when experimenters were present in front of the raven, while interphase includes all the time when experimenters were absent from their positions in front of the raven.

3.4 Statistical analysis

I used a binomial test to analyze if the ravens had any preference regarding the experimenter's role, for the first and final choice in each session. I also used a binomial test to analyze the distribution of choices for the left and the right position side of the chosen experimenter for both choice opportunities in a trial. The test was conducted due to a suspicion of a bias towards one side of the experimenter's standing position for the retrieval and pilfering conditions, as well as for the combined sum of the two conditions. I used a Wilcoxon signed test to compare the choices made in the first and final decision phase for the pilfering and retrieval conditions. I also used a Wilcoxon rank sum test to compare the rate of head turns to the right and left in the third phase between the pilfering and the retrieval session. I used an independent samples T test to compare the rate of head turns in total time between pilfering and retrieval conditions as well as specifically during the time experimenters were present between the two sessions. I also used the T test to compare the difference in rate of head turns during the time experimenters were absent between pilfering and retrieval, and to compare the difference in time spent within 1 m distance from the wire-mesh between pilfering and retrieval condition.

Finally, I used a linear mixed model to analyze the attentiveness of the ravens, which was measured by the number of head turns per second the ravens have done in the experimenter phase and interphase. The following model was done: head turns ~ phase + session + raven. With phase and session modelled as fixed factor, and raven as a random factor. As there were four experimenter phases and three interphases in each trial, the rate of head turns was calculated from the sum of head turns and durations of all experimenter phases and interphases combined.

To analyze is there a difference in a latency duration during the final choice phase regarding the chosen experimenter between pilfering and retrieval condition, I used a Wilcoxon rank sum test.

All data was tested for normality, which was done by using Shapiro-Wilk tests (Shapiro & Wilk, 1965) and diagnostics plots. All statistics were done using the statistical program SPSS (IBM Corp., 2021)

4. Results

When the ravens were naive about experimenters (first decision phase), the binomial test revealed that they had no significant preference for one of the experimenters (pilferer-neutral: Binomial test, *p* = 0.30; retriever-neutral: Binomial test, *p* = 1), which was in line with the prediction (Figure 3). Contrary to the prediction that the ravens will choose the neutral person more often compared to the pilferer and/or the retriever in the final decision phase (Figure 4), the binomial test showed there was no significant difference from 50/50 split for the pilfering session (Binomial test, *p* = 1) nor for the retrieval session (Binomial test, *p* = 0.24). Additionally, the binomial test showed no significant difference in choosing neutral experimenter over pilferer/retriever combined from random distribution in first decision phase (Binomial test, *p* = 0.377) and in the final decision phase (Binomial test, *p* = 0.392). This indicates that the ravens did not show differentiation between experimenters and their cache manipulation (pilfering and retrieving).

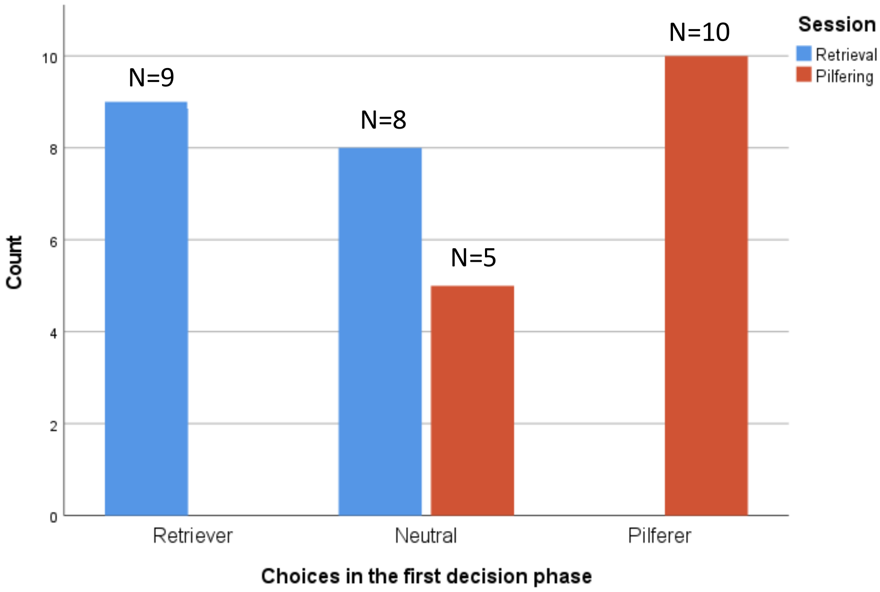

Figure 3: Bar chart representing the number of ravens who chose Retriever and Neutral experimenter in the retrieval session and number of ravens who chose Pilferer and Neutral experimenter in the pilfering session, during the first decision phase.

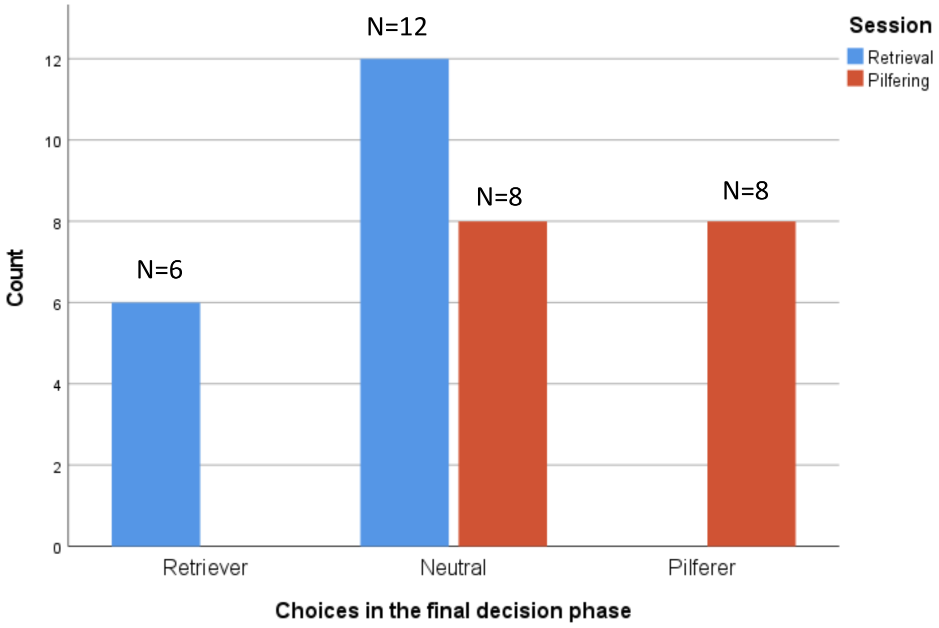

Figure 4: Bar chart representing the number of ravens who chose Retriever and Neutral experimenter in the retrieval session and number of ravens who chose Pilferer and Neutral experimenter in the pilfering session, during the final decision phase.

The binomial test showed a significant deviation from 50/50 split for the left side (Figure 5) of the experimenter when analyzing combined conditions in the first decision phase (Binomial test, p = 0.05), indicating that the ravens showed a bias towards specific cache/experimenter side when they had no information about the experimenter. However, the binomial test showed no significant deviation from the equal distribution for side preference when analyzing combined conditions in the final decision phase (Binomial test, p = 0.60). The Binomial test was also not significant for side preference when analyzing each session individually for the choices made in the first decision phase: in pilfering condition (Binomial test, p = 0.30), in retrieval condition (Binomial test, p = 0.14) and for final decision phase: in pilfering condition (Binomial test, p = 0.80), and in retrieval condition (Binomial test, p = 0.80).

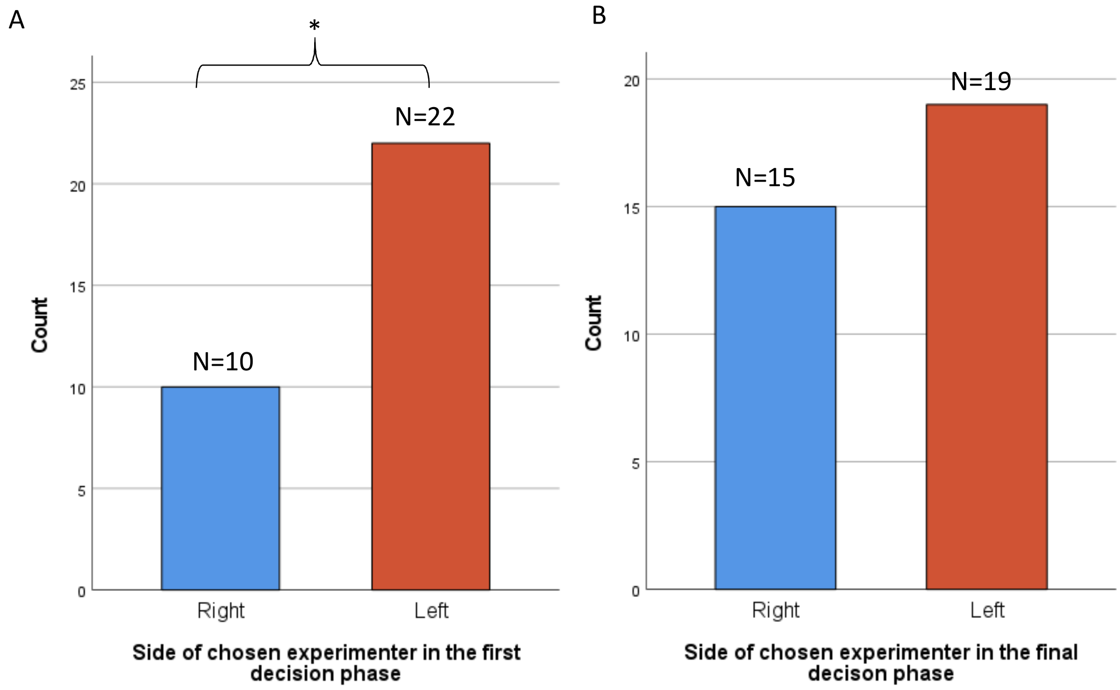

Figure 5: Number of ravens who chose the experimenter who stand on the Right and Left side in A: first decision phase and in B: final decision phase. *=p<0.5

Because I noticed a bias to the left side, I checked whether the tested birds spent generally more time on the side of the chosen experimenter. The independent samples t-test showed such a tendency for the right side (Independent sample t-test, t=-1.994, df= 32, $p = 0.055$), but not for the left (Independent sample t-test, t=0.967, df= 32, $p = 0.341$).

When comparing the first and the final choice for each session, a Wilcoxon signed test showed trends but no statistical significances for both, the pilfering session (Wilcoxon signed test, Z=-1.342, $p = 0.108$) and the retrieval session (Wilcoxon signed test, Z=-1.480, $p = 0.139$; Figure 6). These tendencies were in line with what was predicted in hypothesis ii).

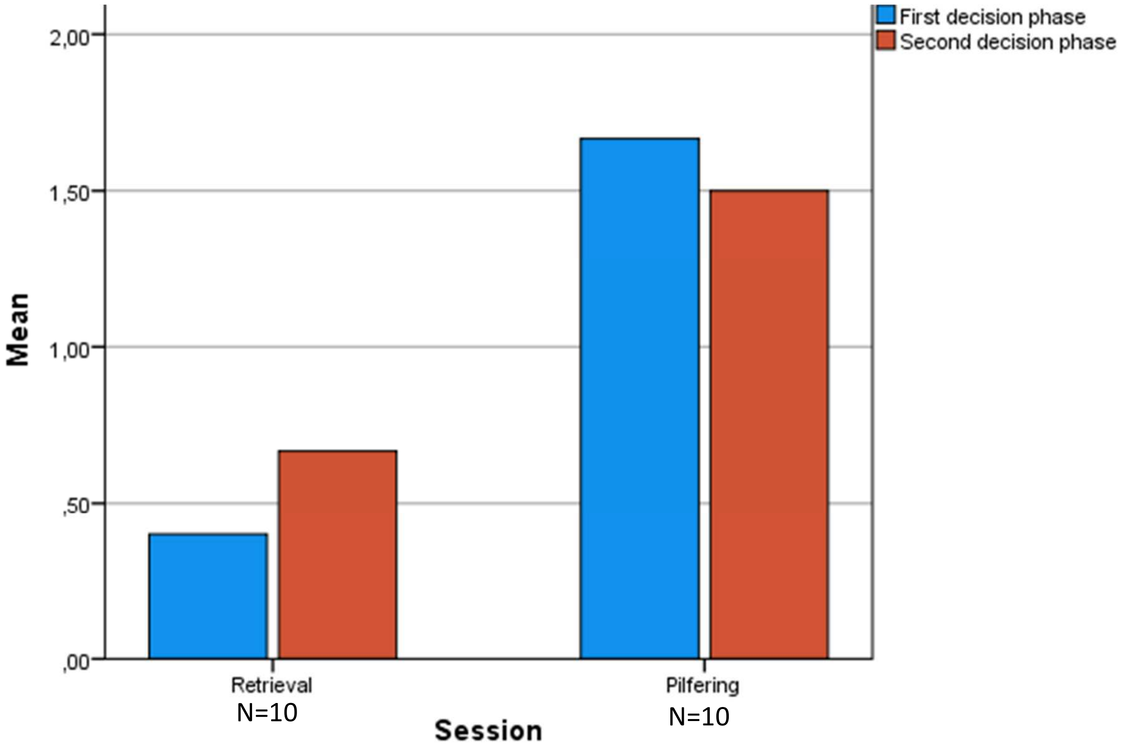

Figure 6: Bar chart showing difference in the mean of choices made in the first and final decision phase by a session type. Statistical analysis showed a trend but no difference in retrieval and pilfering condition.

In contrast to the prediction of hypothesis iii), there was no significant difference in the latency duration in which neutral experimenter or retriever were picked first in the final choice (Wilcoxon rank sum test, W=99.5, *p* = 0.172), and no significant difference in the latency duration in which neutral experimenter or pilferer were picked first in the final choice (Wilcoxon rank sum test, W=64.5, *p* = 0.713).

Focusing on head turns as a proxy for attention, there was no significant difference in frequency of head turns per second in total time (Independent samples t – test, t= -0.296, df=18, *p* = 0.770), as well as during the experimenter phase (Independent samples t – test, t= 0.077, df=18, *p* = 0.939) and during the interphase between pilfering and retrieval condition (Independent samples t – test, t= -0.654, df=18, *p* = 0.521).

Furthermore, frequency of head turns per second in the pilfering/retrieval phase between the two sessions was not statistically significantly different neither for the turn to the right side (Wilcoxon rank sum test, W=93.5, *p* = 0.381; Figure 7), nor for the turn to the left side (Wilcoxon rank sum test, W=97.5, *p* = 0.381). Comparing the time the raven spent in proximity of 1 meter to the wire-mesh between the session, the results revealed no statistical significance either (Independent samples t –Test, t= -0.081, df=18, *p* = 0.937)

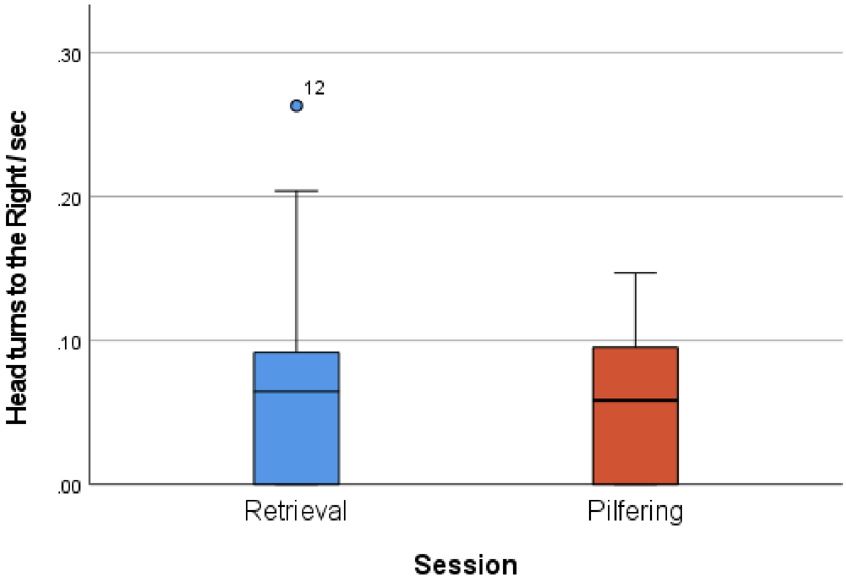

Figure 7: Boxplot showing number of head turns to the right per second during pilfering and retrieving the cached food. Contrary to the prediction, ravens did not show any difference in the number of head turns by session. The middle line of the box represents the median or middle number and the whiskers (vertical lines) extend from the ends of the box to the minimum value and maximum value.

The linear mixed model showed a significant difference in the rate of head turns between the experimenter phases and interphases (Figure 8) in combined conditions (LMM, denDF=36, F=7.758, *p* = 0.008), but no significant difference regarding the session type: pilfering and retrieval (LMM, denDF=36, F=0.284, *p* = 0.598), and no significant difference for rate of head turns between the experimenter phases and interphases together with the session type (LMM, denDF=36, F= 0.370, *p* = 0.547).

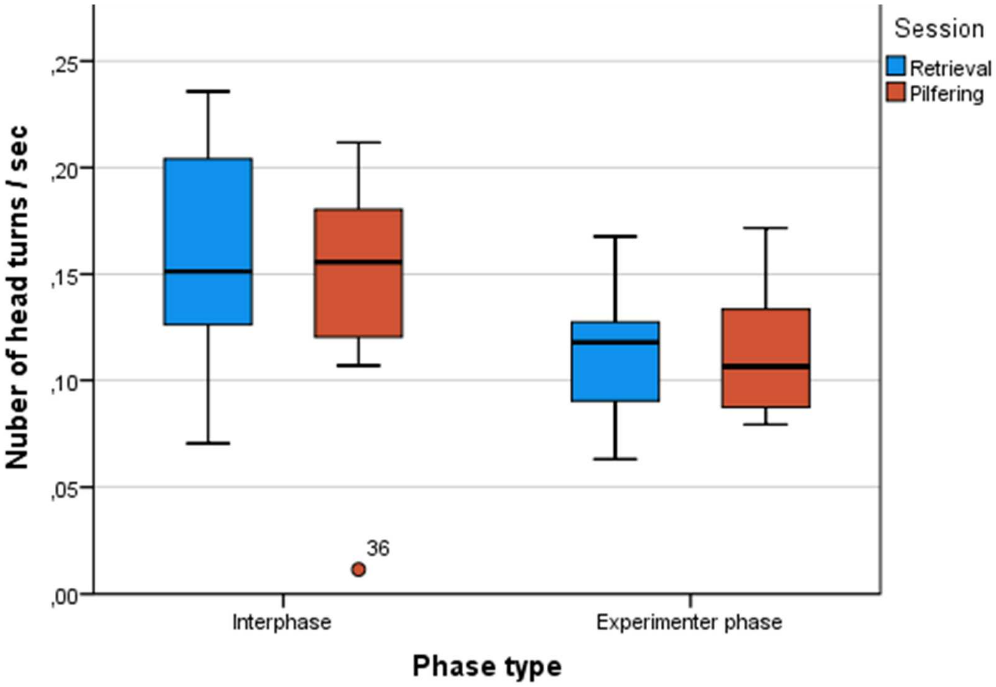

Figure 8: Boxplot of the number of head turs per sec. by phase type. A linear mixed model confirms that there is a difference between the rate of head turns between experimenter phase and interphase, but not between session types. The middle line of the box represents the median or middle number and the whiskers (vertical lines) extend from the ends of the box to the minimum value and maximum value.

5. Discussion

In this experiment, I examined the behavior of ravens towards human experimenters before and after they have experienced those humans caching food, and pilfering or retrieving the food caches, respectively. I was interested if the observer ravens pay attention to the humans' behavior at the caches and subsequently discriminate between the roles of the experimenters, i.e. whether they preferred a pilferer or a retriever over a neutral person (that was present but did not act on any cache). Contrary to my expectation, the ravens did not differ in their choices between the pilferer and neutral experimenter, nor the retriever and the neutral experimenter. The fact that there is also no significant difference between choosing the neutral experimenter and the pilferer/retriever together indicates that they did not take into account whether or not the experimenter manipulated the cache in the pilfering/retrieval phase. This is corroborated by the 50/50 distribution between retriever/neutral experimenter, pilferer/neutral experimenter and neutral experimenter/pilferer/retriever. These results speak against the second hypothesis that ravens differentiate between humans based on bystander information.

Since this study is among the first studies on third party social evaluation of humans by ravens it is hard to make a comparison with other papers. Most third party studies involving ravens (Bourdiol & Massen, 2016; Fraser & Bugnyar, 2010a; Massen et al., 2014) were done between conspecifics (while this experiment involved observation between heterospecifics). Likewise, most of the studies involving human experimenters (Blum et al., 2020; Bugnyar et al., 2007) aimed to answer the question whether ravens can discriminate between the actions of experimenters, which were directly oriented towards the raven; hence, these studies did not investigate the birds' ability to discriminate based on indirect reciprocity. The exception is one study, which examined the ravens' ability to discriminate between a ‘fair’ and an ‘unfair’ experimenter with the information gained both in a direct and an indirect manner. According to the results, ravens that had directly interacted with the experimenters were more likely to exchange tokens with the fair experimenter than with the unfair experimenter afterwards. However, there was no firm evidence that ravens who had previously only observed interactions between experimenters and other ravens were able to discriminate between the 'fair' and the 'unfair' experimenter once given the opportunity directly interact with them (Müller et al., 2017). Similar conclusions were reached in an unpublished study received by personal exchange involving a caching experiment on juvenile ravens involving human experimenters by Rejsenhus Jensen (2019). These results stand in contrast to studies which revealed positive results regarding the ravens' third-party understanding and experimenter differentiation abilities. The study by Massen et al. (2014), for instance, shows the ravens' ability to understand third-party rank relations, as the birds showed different reactions to playbacks of expected and unexpected dominance interactions of other ravens. The ability to remember the behavior of the experimenters and discriminate between a pilferer and a non-pilferer has been shown in a study by Bugnyar et al. (2007) in which the ravens made their caches more quickly, and hid them more often behind visual obstacles when confronted with the pilferer. Possibly, the ravens in the current study had problems in remembering and telling apart the faces of human experimenters. However, in the study by Müller et al. (2017), they chose the 'fair' experimenter over the 'unfair' up to a month after the original experiment was done and in a study by Blum et al. (2020) the ravens differentiated between dangerous and neutral humans for up to four years.

A more plausible possibility for the current results could be that ravens have difficulties to interpret human interactions. Although statistical tests showed no significance, there is a slight indication that individual ravens could differentiate between pilferers and retrievers, as they tended to choose differently in the first and the final decision phase. This (marginally significant) difference in choice behavior could be explained by the small sample size (only 10 birds) and might indicate that the ravens were attentive to the behavioral characteristics of the experimenters. Support for this interpretation comes from the analysis of side bias: in the first decision phase, the ravens chose significantly more experimenters positioned on the left side. This bias to the left is also found in another caching experiments by Rejsenhus Jensen (2019). The interesting part is that the bias is gone in the final decision phase which supports the prediction that the ravens do pay attention to what experimenters are doing. Taken together, these findings are in favor of the first hypothesis (that ravens pay attention to humans) and tentatively supports the second hypothesis (that ravens discriminate between experimenters).

Contrary to the study in which ravens used their left eye significantly more when presented with the unsatisfying food, suggesting negative emotional lateralization of the right-hemisphere (Adriaense et al., 2019), in this study the used ravens did not exhibit a statistically different rate of head turns to the right, nor to the left, in the phase when the experimenter was retrieving or pilfering the cache. Maybe in my experiment the ravens have not perceived any difference in valence of the actions, or they perceived them differently because they were observing an interaction between human experimenters. Furthermore, in this study they were bystanders, so the positive and negative valence was not directed towards themselves, as it was in the study mentioned above. Similarly, the lack of any statistical difference in the rate of head turns per second between the pilfering and the retrieval condition for: i) the whole trial, ii) the phases when experimenters were present and iii) the interphases suggests that the ravens were equally attentive in both the pilfering and the retrieval condition. A comparable result was found in an study involving a pilferer and a retriever as experimenters, in which there was also no difference in the number of head turns per second during pilfering and retrieval (Rejsenhus Jensen, 2019).

Furthermore, the linear mixed model has not found a significant difference in the rate of head turns between phase type combined with the session type; but it has found a significant difference in the rate of head turns between the experimenter phases and interphases in the combined condition, which suggests that the ravens were equally attentive throughout the sessions but not throughout the phase types. This indicates that the ravens paid longer attention to those phases when experimenters were present, represented by lower frequency in the rate of head turn per second in these phases compared to the rate of head turns in the interphases. These findings confirm predictions based on the first hypothesis that ravens pay attention to human experimenters.

Third hypothesis predicting a quicker response rate when choosing a neutral experimenter compared to a retriever/pilferer was not supported by the statistical analysis. This could mean that the ravens simply need an equal amount of time to process the information and make a decision, no matter of the experimenters' role.

6. Conclusion

Overall, the results of our study do not confirm that ravens can use bystander information to discriminate between different human experimenters, although there is a slight indication that they might have the ability to do so, based on the comparison between the first and final choice. Likewise, not all predictions regarding the hypothesis that they pay attention during the experiment were met. The ravens showed less head turns, indicating a longer attention span, when experimenters were caching, pilfering/retrieving and when they had the opportunity to choose one of them. However, they appeared to be equally attentive in both conditions, pilfering and retrieving. Also, they did not differ in response time, irrespective of the experimenter, when given a food choice.

Although studies on third-party evaluation are scarce, this findings are in line with their preliminary results that ravens have problems to discriminate between human interactions as bystanders. Why exactly they have difficulties with, the differentiation of the experimenters via observation but not when confronted with them directly remains unclear. Follow-up experiments with a bigger sample size might give us firmer results and hopefully shed some light on cognitive abilities of ravens during the observation of humans caching and pilfering.

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