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ORIGINAL PAPER

Ravens (*Corvus corax*) are indifferent to the gains of conspecific recipients or human partners in experimental tasks

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Abstract Although cooperative behaviours are common in animals, the cognitive processes underpinning such behaviours are very likely to differ between species. In humans, other-regarding preferences have been proposed to sustain long-term cooperation between individuals. The extent to which such psychological capacities exist in other animals is still under investigation. Five hand-reared ravens were first tested in an experiment where they could provide food to a conspecific at no cost to themselves. We offered them two behavioural options that provided identical amounts of food to the actor and where one of the two options additionally delivered a reward to a recipient. Subsequently, we made the ravens play a no-cost cooperation game with an experimenter. The experimenter had the same options as the animals and matched the ravens' choices, making the prosocial choice the more profitable option. In both conditions, ravens were indifferent to the effects of their choices and hence failed to help conspecifics and to cooperate with the experimenter. While our negative results should be interpreted with care, overall, our findings suggest that the ravens had no understanding of the consequences of their actions for a potential recipient. This study adds to several others that have used a

similar set-up and have reported negative results on other-regarding preferences in animals.

Keywords Ravens · *Corvus corax* · Other-regarding preferences · No-cost cooperation

Introduction

Cooperation, functionally defined as interactions that increase on average the direct fitness of all participants (Bshary and Bergmueller 2008), is widespread in nature, both within and between species (Bronstein 2001; Bshary and Bronstein 2004; Sachs et al. 2004; Noë 2006; Leimar and Hammerstein 2010). Nevertheless, the underlying cognitive mechanisms may differ greatly between species (Noë 2006, Brosnan et al. 2010). Some authors propose that an understanding of working together should be part of the definition (Noë 2006) but we use the purely functional definition given above. It has been argued that human cooperation differs from cooperation in other species because it is often based on psychological mechanisms like a sense of fairness, the willingness to punish cheaters and to reward co-operators at one's own expenses (Fehr and Gächter 2002; Fehr and Fischbacher 2003). Primatologists have challenged this notion, initially based on detailed field and laboratory observations (Boesch and Boesch 1989; de Waal 1982; Aureli and de Waal 2000) that documented food sharing, complex forms of alliances like collaborative hunting and conflict resolution, while genetic analyses demonstrated that these interaction often take place between unrelated individuals (Langergraber et al. 2007). It was argued that emotions and in particular concerns for others might maintain these strong and long-lasting forms of cooperation.

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More recently, experimental paradigms have been developed to explicitly test the psychological mechanisms underlying cooperation in primates (Brosnan and de Waal 2003, Silk et al. 2005). To test for other-regarding preferences, the standard experimental protocol has been to offer a focal individual two behavioural options that provided identical amounts of food to the actor and where one of the two options delivered additionally a reward to a recipient (Silk et al. 2005 based on: Colman et al. 1969). This paradigm has produced largely negative results (review by Jaeggi et al. 2010).

As the first positive evidence was on cooperatively breeding marmosets (Burkart et al. 2007), it was hypothesised that prosocial behaviours, like other-regarding preferences, evolved in social systems with strong interdependency between individuals, notably in cooperatively breeding species (Burkart et al. 2009). However, more recent evidence on cooperatively breeding species has provided mixed evidence (Cronin et al. 2009, 2010; Stevens 2010; Skerry et al. 2011). In addition, tufted capuchins exhibited prosocial sharing behaviour, though they are not cooperative breeders (de Waal et al. 2008; Lakshminarayanan and Santos 2008; See also Fletcher 2008 and Takimoto et al. 2010 for conflicting results). Finally, new experimental designs have provided evidence that both chimpanzees and bonobos show prosocial helping (Greenberg et al. 2010; Hare and Kwetuenda 2010; Horner et al. 2011; Melis et al. 2011). Thus, there is evidence for other-regarding preferences in human primates (de Waal and Suchak 2010), though it remains unclear what conditions favour its expression and what factors may explain differences between species (Jaeggi et al. 2010).

Until now, research on prosocial behaviour has largely focussed on primates. This is probably because primatologists are generally interested in the phylogenetic roots of human psychology and cognition. In this context, the mechanisms underlying human cooperative behaviour like concerns for others are assumed to be cognitively demanding (Baumard et al. 2012; de Waal 2008). However, in order to test how the social system, cognitive abilities and experimental set-ups affect the evolution, respectively, the occurrence of prosocial behaviour, data on other taxa should be helpful. Members of the corvid family appear to be good candidates for comparisons because we know much about their cognitive abilities, which appear to rival those of primates (Dally et al. 2006; Emery 2006; Emery et al. 2007). Here, we tested whether hand-raised captive ravens show other-regarding preferences in the standard experimental design (Silk et al. 2005). Ravens exhibit high levels of food competition (Bugnyar and Kortschal 2002; Heinrich et al. 1993) and some forms of cooperation (Heinrich and Marzluff 1991; Marzluff et al. 1996). Some of our five subjects were related, and others

were mated pairs (for more details, please see the Methods section), allowing us to get some first ideas about the potential effects of these factors on the subjects' prosocial behaviour.

In the final phase of the experiment, we introduce a new condition that we suggest is a good control for the subjects' ability to relate their choices to the consequences for a recipient. We let the ravens interact with the experimenter as recipient. The experimenter's behavioural options were identical to those of the ravens, and he matched their behaviour. Thus, if the ravens chose the option that made food available to the experimenter, they would receive food in return and otherwise not. The payoffs were thus such that cooperation was possible at no cost apart from the need to assess the options in order to make the appropriate choice. Given that the literature on primates provides variable results, predictions seemed to be difficult to make. Nevertheless, we assumed that if strong food competition typically hinders helping in the standard paradigm, then ravens should not show other-regarding preferences in the first part of our experiment. For the final phase, we predicted that if ravens fully understand the consequences of their actions on a receiver and that the receiver matches their action, then they should quickly start to cooperate. At the very least, they should cooperate eventually as the task seems to be soluble through learning via instrumental conditioning.

Methods

Animals and housing

The experiments were carried out between February and August 2007 in Grünau, Almtal, Austria. A total of five adult hand-reared ravens (two females and three males) were used, all of whom had participated in previous studies. Four birds, the sisters Columbo and Nemo and the brothers Gwaihir and Ilias, were four years old. They had been kept in one social group for three years, during which they showed strong affiliate relationships (Fraser and Bugnyar 2010); at the end of the third year, they formed two mated pairs.

The fifth bird (Hugin) was thirteen years old, unrelated to the other subjects and paired with another female. All ravens were kept in outdoor aviaries. The aviaries comprised several compartments. Each pair had its own compartment. During the experiments, the subjects that were not currently being tested were isolated in the compartments provided. The ravens were fed in the morning and in the evening. The amount of food the ravens received was adjusted according to their motivation to take part in the experiments, that is, daily rations were restricted whenever

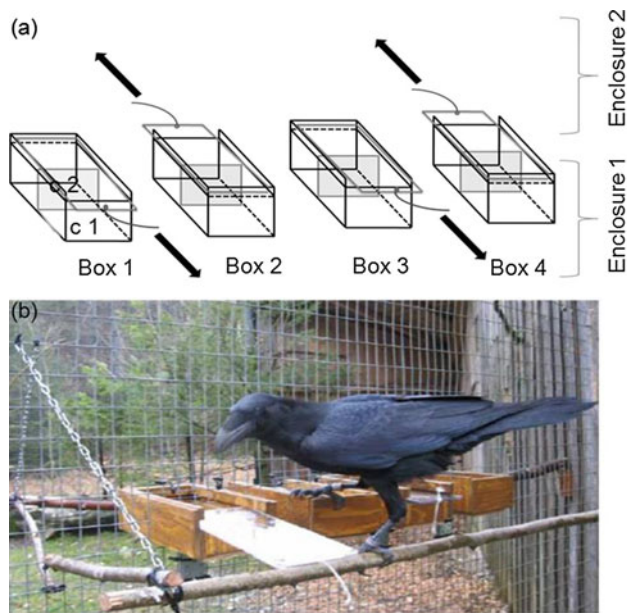


Fig. 1 Experimental set-up. **a** Sketch of the set of four boxes. C1 and C2 denote compartments one and two. *Black arrows* show the pull directions by which the *boxes* can be opened. For the sake of clarity, the wire mesh is not shown in the sketch. **b** Picture of the apparatus with the raven Ilias opening the first box

the ravens showed a decrease in their willingness to participate in the experiments. During the experiments, they could collect small pieces of cheese, a highly preferred food to which they rarely had access. The ravens had unrestricted access to water.

Apparatus

We used a set of four wooden boxes. Each box was divided into halves by a Plexiglas plate inserted in the middle of the each box. Boxes were closed by a removable Plexiglas lid with a string attached. The ravens opened the box by pulling on the string and in this way removed the lid. The set of boxes was integrated into the fence between two adjacent enclosures so that one half of each box was accessible from enclosure 1 and the second half from enclosure 2. When a subject removed a lid, both halves of the box and their food content became accessible (Fig. 1). It was impossible for a bird to access a food item situated in the partner's side of the box.

Experimental procedure

During the experimental phase, data were collected almost daily between 8:00 am and 11:00 am and between 13:00 pm and 16:00 pm by two different observers: François Nyffeler (FN) and Felice Di Lascio (FD). The experiment was divided into five phases. Since the observers were novel to the ravens, FN and FD spent 10 consecutive days

in the aviary prior to commencing the experiments. Each individual was tested in one session a day. Sessions lasted for a maximum of ten trials, but typically lasted for about five. The exact number of trials depended on the ravens' motivation to participate in the experiments. For all five phases, the positions of the rewards were counterbalanced across boxes. The experimenter first baited the boxes, as described below for each phase, closed them with the Plexiglas lids and finally left the enclosure. In phase five, the experimenter entered the adjacent enclosure, faced the boxes from the opposite side and assumed the role of a reciprocating partner. The subjects were then allowed to open one of the two baited boxes and to recover the food items. FN collected the data for the first four phases and FD collected the data for the fifth phase. The first three phases were control phases and were successfully completed by the ravens. Phases four and five are the experimental phases strictly so called, and like the control phases are briefly described below (Fig. 2a–e).

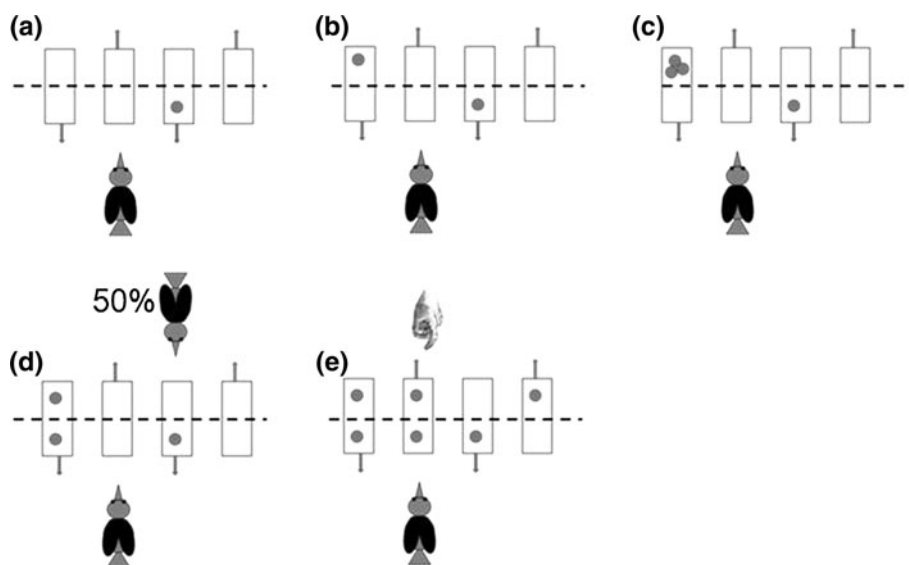
Phase 1: Empty versus baited

The aim of this first phase was to see whether the ravens were able to distinguish between an empty and a baited box. It was also essential for the ravens to learn to open the boxes properly. The subjects were confronted with two options: (1) an empty box (referred in the Results section as the “0/0 option”) and (2) a box baited with one food item (referred in the Results section as the “1/0 option”) on their side. All five ravens participated in this first phase and successfully completed it (individuals: Columbo, Ilias, Gwaihir, Nemo and Hugin). We considered a subject as successful when their choices became significantly different from a 50:50 distribution. The deviation was calculated on data pooled over two to three sessions. This flexibility in our calculations is due to the fact that the ravens did not always complete the session, with the number of trials within a session varying between three and ten. In every case, the minimum number of trials over which an individual performed significantly above chance was 15. The same passing criterion was used for phases two and three.

Phase 2: Accessible versus inaccessible

Our second aim was to test whether the individuals were able to learn that the food items placed on the other side of the fence (named recipient's side below) were not accessible to them. The ravens had two options: (1) a box baited on the actor's side (referred in the Results section as the “1/0 option”) and (2) a box baited on the recipient's side (referred in the Results section as the “0/1 option”). As in the previous phase, all five subjects participated in this second phase (individuals: Columbo, Ilias, Gwaihir, Nemo

Fig. 2 Summary of the experimental phases. Phase 1 (a), phase 2 (b), phase 3 (c), phase 4 (d), phase 5 (e). In phase 4 (d), the 50 % indicates that the recipient was present in half of the trials. The horizontal dashed lines show the position of the wire. The picture of the hand indicates human presence. Circles indicate the food items



and Hugin). Unfortunately, one raven (Columbo) did not reach the significance level because she was stopped prematurely after 21 trials due to a calculation error. We decided to test her also in the subsequent phase, which she solved successfully.

Phase 3: Much versus less

The aim of this last control phase was to rule out the possibility that the ravens simply preferred to open the box that contained more food items. The ravens had two options: (1) one box baited on the actor's side with one food item (referred in the Results section as the "1/0 option") and (2) a second box baited with three food items on the recipient side (referred in the Results section as the "0/3 option"). As in the previous two control phases, all five subjects took part in this last control phase and solved it successfully.

Phase 4: Other-regarding preferences

In this first experimental phase, we tested the ravens under two different conditions: (a) with another raven present in the adjacent enclosure, where the actor had the opportunity to give the recipient access to a food item and (b) with no raven present in the adjacent enclosure. Half the trials were conducted under condition (a) and the rest under condition (b). Each individual was tested as many times as possible until the first experimenter (FN) left the study site, with the total number of trials per individual varying between 136 and 214. In both conditions, the subjects were confronted with two options: (1) a box baited on the actor side and on the recipient side (referred in the Results section as the "1/1 option") and (2) a box baited only on the actor side (referred in the Results section as the "1/0 option"). In

order to avoid a potential reciprocation, birds within each dyad did not exchange the role as actor and recipient. The individuals within each dyad are given below. The individual cited first is the actor, and the second individual is the recipient.

Columbo with Nemo (sisters),
 Ilias with Columbo (former affiliates, now a mated pair),
 Gwaihir with Columbo (former affiliates),
 Nemo with Gwaihir (former affiliates, now a mated pair),
 and Nemo with Ilias (former affiliates).

Nemo was tested with two different individuals to see whether the ravens could adjust their cooperativeness according to the identity of the individual they were interacting with. Hugin, the fifth individual, did not take part in this fourth phase because his motivation to do so suddenly decreased for no known reason. The experimental situation was interspersed with attention trials, that is, trials in which the options were the same ones as in phase 2 (1/0–0/1). These trials allowed us to check whether the ravens were still attentive to what was happening and whether their choices could be due to an inattentive state. Each test session included up to two attention trials. In each session, the first attention trial was carried out after two test trials and provided that the ravens completed the test session (ten trials), the test session ended with a second attention trial.

Phase 5: No-cost cooperation with a human

In this last phase, the raven had the same options as in phase four except that the boxes accessible from the recipient's side were also baited and the recipient had the same two options as the actor. The recipient was a human who matched the moves of the raven. In this last phase, only

three individuals were tested (individuals: Ilias, Gwaihir and Hugin) and each individual was tested for 50 trials. All the subjects were males because they were less fearful than the females that refused to approach the experimenter and were thus excluded from this last phase. As in phase 4, we interspersed attention trials among test trials to verify that the ravens paid attention to the distribution of food items.

Data collection and analysis

The experiments were video-taped and the data coded from the movies. The ravens' choice could be determined unequivocally by noting the lid they removed, which led to the experimenter manually blocking the alternative option. Data were analysed with the statistical program SPSS 16.00. All tests were nonparametric and two-tailed.

Results

Phases 1–3: Control phases

In phase 1, all five ravens passed our criterion of choosing the 1/0 option significantly more often than the empty 0/0 option. They required a median of 18 trials to do so. (range, 16–67; binomial tests, all individuals $P < 0.05$; Fig. 3a). In phase 2, one bird (Columbo) failed to reach significance while trials were stopped prematurely due to a calculation error. All other birds chose the 1/0 option significantly more frequently than the 0/1 option. They required a median of 22.5 trials to do so (range, 15–31; binomial tests, Columbo *NS*, all other individuals $P < 0.05$; Fig. 3b). In phase 3, all five birds chose the 1/0 option significantly more often than the 0/3 option. They required a median of 29 trials to do so (range, 17–53 trials; binomial tests, all individuals $P < 0.05$; Fig. 3c).

Phase 4: Other-regarding preferences

None of the four ravens tested showed a shift in their choices in the presence of a potential recipient. Consequently, none of the four actors chose the 1/1 option significantly more often when the recipient was present than when they were alone (chi-square test: Columbo: $n = 159$, $\chi^2 = 0.0005$, $df = 1$, $P > 0.1$; Ilias: $n = 187$, $\chi^2 = 0.007$, $df = 1$, $P > 0.1$; Gwaihir: $n = 136$, $\chi^2 = 0.64$, $df = 1$, $P > 0.1$; Nemo: $n = 214$, $\chi^2 = 0.21$, $df = 1$, $P > 0.1$; Fig. 4a). Nemo, which was tested with 2 different recipients, did not chose 1/1 option significantly more often when his partner (Gwaihir) was present than when the individual she was unrelated to (Ilias) was present (chi-square test: $n = 117$, $\chi^2 = 1.19$; $df = 1$, $P > 0.1$). Also,

none of the birds chose the 1/1 option significantly different from a 50 % expectation (Fig. 4a).

A power analysis indicated that for three of our subjects, our sample sizes were large enough to detect a difference of only 15 % with a likelihood of missing such a difference that was in all cases smaller than 5 % (Columbo: $n = 159$, $\beta = 0.02$; Ilias: $n = 185$, $\beta = 3.22$; Nemo: $n = 214$, $\beta = 1.12$). Regarding our last subject, the same analysis indicated that we should have been able to detect a difference of 18 % (Gwaihir: $n = 136$, $\beta = 2.95$). Three out of four individuals developed a significant side bias (chi-square test: Nemo: $n = 214$, $\chi^2 = 3.41$, $df = 1$, $P > 0.05$; Ilias: $n = 187$, $\chi^2 = 11.31$, $df = 1$, $P < 0.01$; Gwaihir: $n = 136$, $\chi^2 = 17.65$, $df = 1$, $P < 0.01$; Columbo: $n = 159$, $\chi^2 = 25.76$, $df = 1$, $P < 0.01$). The side bias of our study subjects varied between 56 % and 70 % (individuals: Nemo, 56 %; Ilias, 62 %; Gwaihir, 68 %; Columbo, 70 %).

Phase 5: No-cost cooperation

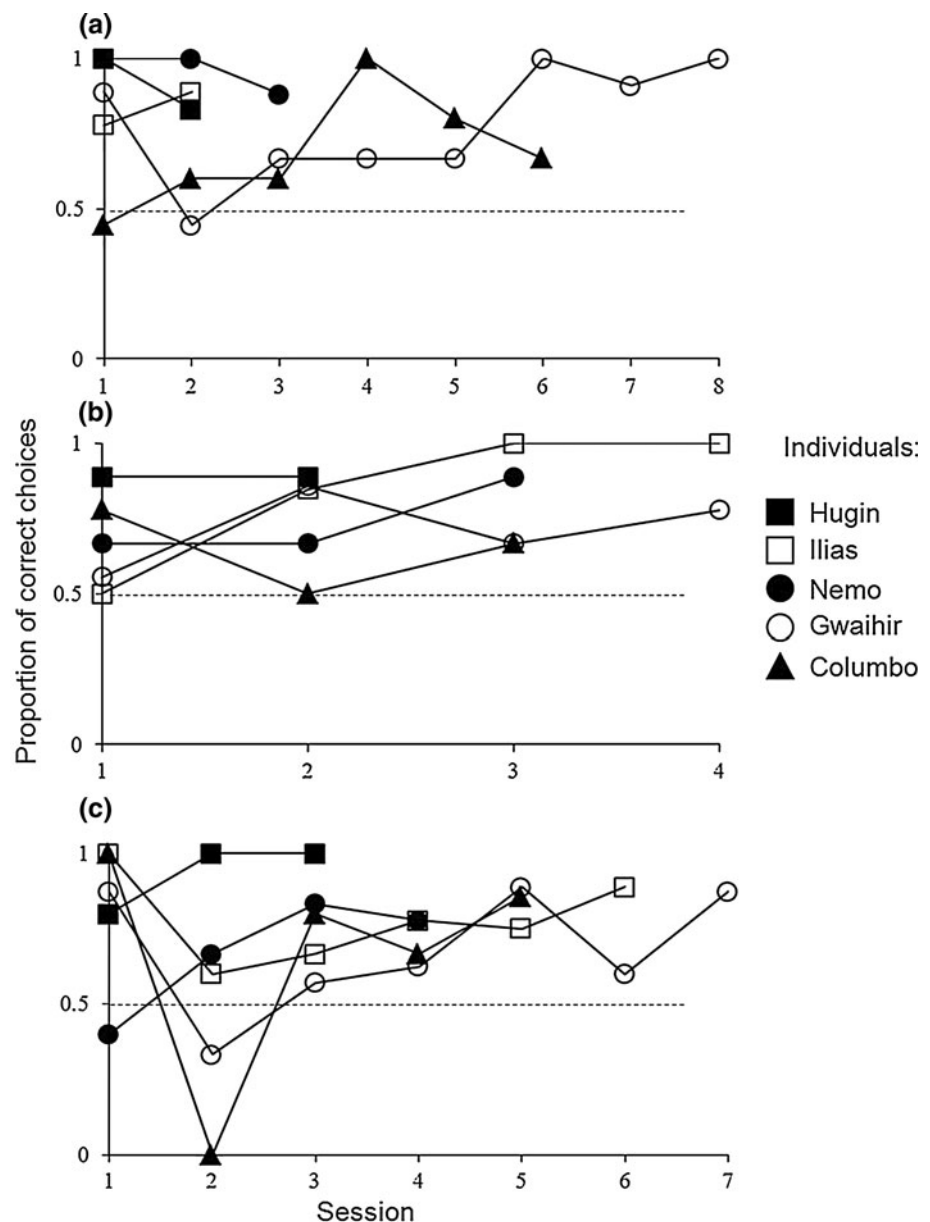
In this last phase, the ravens showed no significant preference for either of the two options (1/1 or 1/0). On average, they chose the (1/1) option 51 % of the time, yielding results not significantly different from a random choice (chi-square test: Ilias: $n = 50$, $\chi^2 = 0.01$; $df = 1$; $P > 0.1$; Gwaihir: $n = 50$, $\chi^2 = 0.01$; $df = 1$; $P > 0.1$; Hugin: $n = 50$, $\chi^2 = 0.01$; $df = 1$; $P > 0.1$; Fig. 4b).

A power analysis indicates that given our sample size, we should have been able to detect a switch in the behaviour of our subjects of 20 % ($n = 50$; $\beta = 0.032$). Two out of the three tested subjects developed a significant preference for one of the two sides (chi-square test: Ilias: $n = 50$, $\chi^2 = 0.50$, $df = 1$, $P > 0.1$; Hugin: $n = 50$, $\chi^2 = 5.78$, $P < 0.05$; Gwaihir: $n = 50$, $\chi^2 = 8.82$, $P < 0.01$). Their side bias varied between 56 and 72 % (individuals: Ilias, 56 %; Hugin, 68 %; Gwaihir, 72 %).

Attention trials

The percentage of the correct responses made by the ravens during the attention trials, which were interspersed throughout phases four and five, varied between 69 and 86 % for phase four and between 67 and 71 % for phase 5. In phase four, all the subjects chose the 1/0 options significantly more often than the 0/1 option (chi-square test: Columbo: $n = 40$, $\chi^2 = 7.22$, $df = 1$, $P < 0.01$; Ilias: $n = 57$, $\chi^2 = 28.07$, $df = 1$, $P < 0.01$; Gwaihir: $n = 34$, $\chi^2 = 12.97$, $df = 1$, $P < 0.01$; Nemo: $n = 56$, $\chi^2 = 7.87$, $df = 1$, $P < 0.01$). While the percentage of correct choices was quite similar in phase 5, the results were not significantly different from a random choice (chi-square test: Ilias: $n = 6$, $\chi^2 = 0.17$, $df = 1$, $P > 0.1$; Gwaihir: $n = 6$,

Fig. 3 Proportion of correct choices made by the ravens in each session for 5 different individuals in phase 1 (a), phase 2 (b) and phase 3 (c). The dashed line indicates the 0.5 proportion (random choices)



$\chi^2 = 0.17$, $df = 1$, $P > 0.1$; Hugin: $n = 7$, $\chi^2 = 0.57$, $df = 1$, $P > 0.1$).

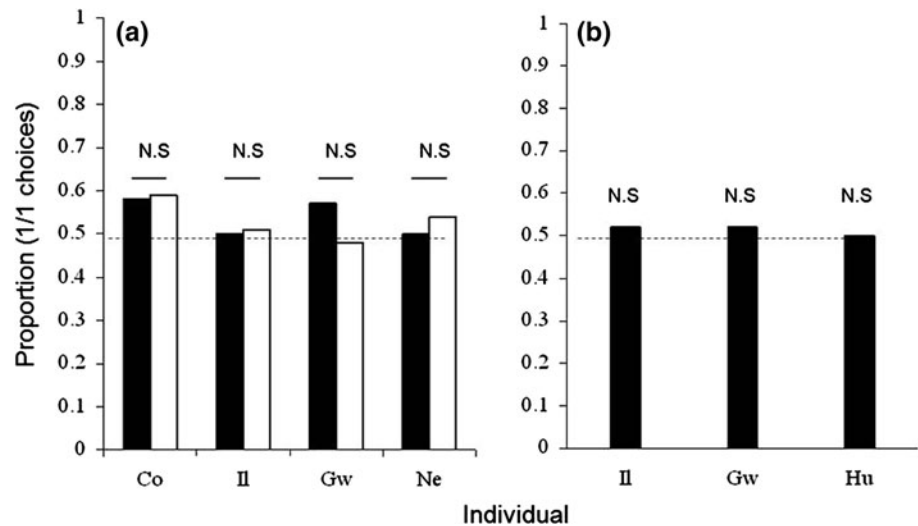
Discussion

Do ravens show other-regarding preferences?

The ravens were apparently indifferent to other-regarding preferences in the classic paradigm. As the result matches those obtained on chimpanzees (Silk et al. 2005; Jensen et al. 2006, 2007) and both species show typically strong competition over food, the current results are in line with the idea that such competition leads to the suppression of

prosocial behaviour in a foraging context (Hare 2001; Hare and Tomasello 2004). In line with this argument, the positive evidence for other-regarding behaviour in chimpanzees was obtained in an experimental set-up where tokens were used instead of food (de Waal et al. 2008, Horner et al. 2011). However, in other experiments where food was involved, it has been shown that brown capuchins, chimpanzees and bonobos were willing to help their conspecifics and that their prosocial behaviour was quite robust (Lakshminarayanan and Santos 2008; Hare and Kwetuenda 2010; Greenberg et al. 2010). Hence, the recent developments of this research field suggest that it is probably slight variations in the experimental set-ups rather than the food per se that explains the contrasting results

Fig. 4 Proportion of 1/1 choices made by the ravens in phase 4 (a) and phase 5 (b). In phase 4 (a), *black columns* represent sessions in which a potential recipient was present in the adjacent enclosure. *White columns* represent the sessions in which the raven was alone. In phase 5, the experimenter was always present and matched the move of the raven (*black bars*). *Individuals Co, Columbo; II, Ilias; Gw, Gwaihir; Ne, Nemo; Hu, Hugin. N.S.* no significant difference. The *dashed line* indicates the 0.5 proportion (random choices)



obtained within the same species or between different species. Thus, it would be interesting to test ravens on these other paradigms in the future.

A slightly modified set-up used in a recent study on jackdaws, *Corvus monedula*, revealed clear but context-dependent asocial and prosocial preferences (Schwab et al. 2012). Notably, the recipients' position and behaviour, aside of their identity, affected the decision of the focal subjects: when the recipient was at the apparatus first and tried to access food by manipulating the baited box, jackdaws behaved more cooperatively than when the recipient stayed away. That recipients can positively influence the choices of the acting subject has also been found in chimpanzees (Melis et al. 2011). Whether they do so intentionally is another question. In our current experiment, recipients never approached the apparatus together with, or even before, the acting subject.

Do ravens face cognitive constraints in the standard paradigm?

An important question in any experiment on other-regarding preferences is whether subjects actually understood the apparatus and the consequences of their actions for a potential recipient. Silk et al. (2005) put forward a series of logical arguments why they thought that the chimpanzees understood the task. Cronin et al. (2010) let their tamarins first learn that some choices make food available in the neighbouring compartment by allowing them to access the food in the absence of a conspecific. Similar pretests were conducted in a study on reciprocity in chimpanzees (Yamamoto and Tanaka 2009). We think that our no-cost reciprocity game provides a perfect experiment to test whether subjects properly understand the experimental apparatus. As it turned out, we have no indication that the ravens understood the consequences of their

actions for a potential recipient and that this recipient might respond in a conditional way. This differs from results in other species where individuals cooperated successfully by pulling levers (rats: Rutte and Taborsky 2008; Viana et al. 2010). A difference between these studies and the current one was that the actor could only provide food to a recipient but not to itself, which may be important for successful cooperation. Reciprocal cooperation in blue jays (Stephens et al. 2002) was established only after many more rounds, and the birds were not even aware that they were playing with a partner. Thus, it is possible that the number of trials was too low to enable our study subjects to learn the contingencies by operant conditioning. In chimpanzees, mutual helping has been observed in a laboratory experiment but there was no evidence for helping being contingent on receiving help in return (Brosnan et al. 2009).

Recent studies on reciprocal cooperation based on ecologically relevant situations have yielded spontaneous conditional cooperation during predator mobbing in pied flycatchers (Krams et al. 2008) and in cleaner wrasse pairs (Bshary et al. 2008; Raihani et al. 2010). Consequently, the ecological validity of a study appears to be a key point that should be taken into account in experimental designs that test for other-regarding preferences and reciprocal cooperation (Raihani and Bshary 2011). For our cooperation experiment, we note not only that opening a box in order to make food available might be problematic, but that the interaction with a human experimenter may have failed to trigger important social cues necessary for cooperative behaviour. Many social learning experiments on primates are suspected to have failed because humans were used as demonstrators (Boesch 2007; Call and Tomasello 1996; Kuroshima et al. 2008). Furthermore, a recent experiment of Hattori et al. (2010) has shown, with the help of eye-trackers, that chimps follow the gaze of conspecifics but

not of humans. Nevertheless, in previous experiments conducted with the same ravens, they responded perfectly to the behaviour of the experimenters (Bugnyar et al. 2007; Schloegl et al. 2007, 2008). Moreover, as scavengers, ravens have a strong tendency to pay attention to hetero-specifics (Stahler et al. 2002).

In conclusion, our study joins several other laboratory studies that provided negative results for other-regarding preferences and reciprocity. The final phase of our experiment strongly suggests that a lack of understanding caused the apparent ‘indifference’ of our subjects in the current set-up. We hypothesise that social animals should rarely be neutral about the success of their partners and that a 50:50 distribution warrants control experiments like our fifth phase to establish whether subjects understood the consequences of their actions. Finally, we advocate the development of experimental designs that are less technical and closer to natural conditions to facilitate interpretation of results.

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Conflict of interest The authors declare that they have no conflict of interest.

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