ORIGINAL PAPER

The performance of ravens on simple discrimination tasks: a preliminary study

Friederike Range · Thomas Bugnyar · Kurt Kotrschal

Abstract Recent studies suggest the existence of primate-like cognitive abilities in corvids. Although the learning abilities of corvids in comparison to other species have been investigated before, little is known on how corvids perform on simple discrimination tasks if tested in experimental settings comparable to those that have been used for studying complex cognitive abilities. In this study, we tested a captive group of 12 ravens (*Corvus corax*) on four discrimination problems and their reversals. In contrast to other studies investigating learning abilities, our ravens were not food deprived and participation in experiments was voluntary. This preliminary study showed that all ravens successfully solved feature and position discriminations and several of the ravens could solve new tasks in a few trials, making very few mistakes.

Keywords Raven · Corvids · Discrimination learning

Introduction

Recently, scientific interest in the cognitive abilities of corvids has gained momentum. Several research groups working on different species of corvids have provided

Communicated by J. C. Senar

F. Range · T. Bugnyar · K. Kotrschal
Konrad Lorenz Research Station,
4645 Gruenau 11, Austria

F. Range (✉)
Department of Neurobiology and Cognition Research,
Universität Wien,
Althanstrasse 14,
1091 Vienna, Austria
e-mail: friederike.range@univie.ac.at

evidence that corvids show sophisticated skills in physical (e.g. Chappell and Kacelnik 2002, 2004; Kenward et al. 2005; Weir et al. 2002; Heinrich 1995) and social tasks (e.g. Bugnyar and Kotrschal 2002b; Heinrich 1999a; Bond et al. 2003). Moreover, several studies have investigated corvids' speed and flexibility of learning novel tasks and compared their abilities with those of other species. These studies have revealed substantial and significant transfer of relational rules by corvids but not pigeons (Mackintosh et al. 1985; Wilson et al. 1985), the application of the matching (and oddity) concept to stimuli of numerical category (Smirnova et al. 2000) and excellent spatial learning and memory (Lipp et al. 2001). Furthermore, studies on learning set formation showed that blue jays *Cynaocitta cristata* (Hunter and Kamil 1971) and greater hill myna (*Gracula Regiliosa*) (Kamil and Hunter 1970), like primates (Drea and Wallen 1995; Harlow 1949; Warren 1966), could extract a general rule when presented with a series of different discrimination tasks, such that new problems could be solved after only one trial.

Although many studies have investigated learning abilities of corvids, speed and flexibility in discrimination tasks have not been studied in ravens. Ravens are scavengers that feed mainly on ephemeral carcasses or kills, but may also exploit regular food resources at garbage dumps or in game parks (Drack and Kotrschal 1995; Hauri 1956; Ratcliffe 1997). Carcass availability fluctuates both in space and time. As such, one would expect rapid learning as an adaptation to ensure effective exploitation. Moreover, ravens use a variety of strategies to cope with the high competition over food (e.g. scrounging: Bugnyar and Kotrschal 2002a; caching food: Heinrich and Pepper 1998; Heinrich 1999b; pilfering caches: Bugnyar and Kotrschal 2002b; Heinrich and Pepper 1998). Some of these strategies may require cognitively demanding skills

(Bugnyar et al. 2004) and may partially be learned by experience, as has been shown for Western scrub jays (*Aphelocoma californica*) (Emery and Clayton 2001; Emery et al. 2004). Based on these ecological indicators, one would expect that ravens are relatively fast learners.

More importantly, we were interested in whether the results of previous studies concerning corvids' learning abilities would still hold true if the animals were tested in our standard and semi-natural (non-behaviorist) test situation. In this situation, participation in experiments is voluntary, animals are not food deprived and the animals live in social groups. This is of interest because most recent studies that revealed sophisticated cognitive skills of corvids were carried out under semi-natural test situations (e.g. Bugnyar and Kotrschal 2004; Clayton and Dickinson 1999; Heinrich 1995; Weir et al. 2002) or directly in the field (Hunt 1996, 2000; Hunt and Gray 2003, 2004. However, we have no knowledge of how fast corvids learn and improve in a limited set of discrimination problems under such relaxed semi-free conditions.

To test ravens' learning abilities and behavioral flexibility in a preliminary study, we conducted four operant discrimination tasks, which were novel to them. In such discrimination tasks, the subject is presented with two stimuli at the same time and has to select the item that is consistently reinforced (Pavlov 1927). To test how rigid those learned associations are in ravens, we reversed the reinforcement contingencies when the subjects had reached a certain criterion such that the previously reinforced stimulus was now not-reinforced and the previously not-reinforced stimulus was reinforced.

Materials and methods

Subjects and setting

Subjects were eight zoo-bred (four males, four females) and four wild-caught (three males, one female) raven nestlings that were hand-reared from 12 to 40 days after hatching. In addition, we tested a zoo-bred male that was 9 years old and also had been hand-raised. All other birds were juveniles in their first year (8 months at the beginning of the study). Unfortunately, two juvenile males were lost during the study due to predation by a martin. Ravens were marked with colored rings for individual identification. Except for the adult male, none of the juveniles had any prior experience with discrimination tasks. The birds had ad libitum access to water and were fed once or twice a day depending on ambient temperature. The diet consisted of various kinds of meat, milk products and fruit.

The ravens were housed together in a large outdoor aviary. The aviary was divided into three outside compart-

ments (2×10 m, 1×6.5 m in diameter) and experimental rooms in the back. The experimental rooms were arranged into two side rooms and a central room connected through two pathways. While the main compartments were equipped with tree trunks, rocks and natural vegetation, the experimental rooms had only fine-grained sand on the floor and a few perches. Wooden walls between the main and back compartments, and between each of the side rooms and the central experimental room prevented the view into, and between, the experimental rooms. Moreover, the doors between the central room and the pathways were covered with opaque plastic to prevent the animals from watching.

Discrimination tasks

Individual learning was tested using three different feature discrimination tasks (color, form, size) and one right/left discrimination task (position). In the color discrimination test, for example, birds had to choose one of two different colored tubes, of which one was filled with a highly valued food item (cheese). No cue was given in the beginning as to which color would be rewarded. Individuals received 10 trials per session (one session per day), and to reach the first part of the criterion they had to choose the rewarded color five times in a row in the same session. If the first part of the criterion was reached before the 10 trials were over, the session was terminated. In the session after the first part of the criterion was reached, the subjects had to choose the rewarded color again in the first three trials to reach full criterion and continue with the reversal training. When they chose correctly on those first three trials, they received 10 additional trials in that session where the previously unrewarded color was rewarded and the previously rewarded color was unrewarded. The reversal training was terminated when the animals chose the rewarded (previously unrewarded) color five times in a row. If the animals did not choose correctly on the first three trails in the session after the first part of the criterion was reached, they would resume normal testing until they reached the first part again. The second part of the criterion was used to confirm that individuals had learned the discrimination well and remembered it even after a time lag of 24 h.

According to Grant (1946), the probability of a run of 8 correct choices in a series of 13 with a single-trial probability of 0.5 would be 0.014. The probability of reaching the criterion of 8 correct choices in a row remains below 0.05 until 32 trials are completed and below 0.1 until 59 trials are completed. In the reversal, the probability of having 5 correct choices in a series of 10 is 0.11. Because ravens easily loose interest in tasks (personal observation), we chose a relatively easy criterion to ensure their participation.

Color discrimination (CD) We used plastic tubes that were 11 cm long with a diameter of 3 cm. The tubes were red, yellow or blue. Colors were randomly assigned to the birds so that each color combination was present at least twice.

Form discrimination (FD) We used a heart symbol and a square for the form discrimination. Both forms were made out of aluminum. They were 1.5 cm high and 4 cm wide and were covered with a piece of cardboard that was cut according to the respective form. Even though the forms were of the same size, the "heart" had somewhat less volume than the square.

Size discrimination (SD) We used two round aluminum bowls of the same shape with a diameter of 12 and 9 cm, respectively. The smaller bowl was 5 cm in height, while the height of the larger one was 7 cm.

Position discrimination (PosD) We used identical plastic yogurt cups and baited either the right one or the left one. Only two birds had prior side preferences (Schlögl 2005). To one bird (L), the opposite contingency was assigned; the other (Q), however, received the same contingency but without any apparent effect on his performance.

The experimental design was the same for the four tests. The rewarded color, form, size and position (right/left) was randomly assigned and counterbalanced between individuals. All individuals except one (the adult male) were tested in the same sequence (color, form, size and position) to ensure that if task difficulty differed (e.g. colors could be easier for ravens to differentiate than forms), individuals had the same kind of experience in every task, which was important for another study (Range et al. 2006). Because the adult male did not participate well on the first color discrimination task (he would only participate for a few trials and then stop), but improved considerably in taking part on the other tasks, he was retested with the color discrimination again at the end of the experiment (different colors than in the first attempt were assigned).

Procedure

The present study was conducted from November 2004 until February 2005. Typically, each bird was tested once per day receiving 10 consecutive trials, except a 10-day break during Christmas.

Subjects were tested individually in visual isolation from the other birds. All birds participated voluntarily in the experiments and approached the door to be let in as soon as it was opened. If animals did not want to participate on a given day, they were tested the next day. There were only three sessions in which birds refused to participate; refusal to participate occurred after 9, 9 and 8 trials, respectively.

After a subject was isolated from the other birds, it was put into one of the experimental rooms and the door between the birds and the experimenter was closed so that the bird could not view the experimenter's actions. The two objects were placed on the ground approximately 40 cm apart. In the feature discrimination tasks, the position of the positive and negative stimuli was changed randomly, so that each stimulus appeared five times on each side in each 10-trial session and no stimulus appeared on the same side more than three times in succession. In the position discrimination task, only the space in the room was varied randomly. After the objects were placed on the ground, the subject was allowed to enter the room and make a choice. After they made the choice, the second object was removed. During the test, the experimenter looked towards the wall. The experimenter noted the choice of the animal and the right/left position of the object chosen.

Data analysis

We used four dependent measures. The number of trials to reach full criterion indicated how quickly the ravens learned the tasks to the set criterion. We also measured the number of errors to reach criterion and the proportion of correct responses. The reversal index (RI) was calculated as the ratio of the number of trials to criterion plus five on the reversal learning to the number of trials to criterion plus five on the original acquisition. Adding five was necessary because some individuals reached criterion in zero trials. Due to the predation events on two juvenile males, sample sizes differ between experiments.

Statistics

Because the sample size was small, all statistics were calculated per hand according to Siegel and Castellan (1988). Alpha was set at 0.05, trends were reported for $0.1 > \alpha > 0.05$. All tests were two-tailed.

Results

Feature discrimination

All ravens were able to solve the acquisition and reversal of the feature discrimination tasks (Fig. 1). Overall, there was no difference in acquisition between the color, form and size discrimination in the number of trials to reach criterion (Friedman: $N=9$, $F_R=0.78$, $df=2$, NS). However, the number of errors made differed significantly over the three feature tasks (Friedman: $N=9$, $F_R=12.06$, $df=2$, $p<0.01$). Pairwise comparison between the three tasks revealed that they made significantly fewer errors in the CD than in the

Fig. 1 **a** Box plots (10th and 90th percentile) of the number of trials to reach criterion for the four discrimination tasks and overall. A lower score suggests quicker learning. **b** Box plots (10th and 90th percentile) of the number of errors out of total trials for the four discriminations and overall. A lower score indicates greater accuracy. *CD* color discrimination, *FD* form discrimination, *SD* size discrimination, *PosD* position discrimination, *all* all tasks taken together
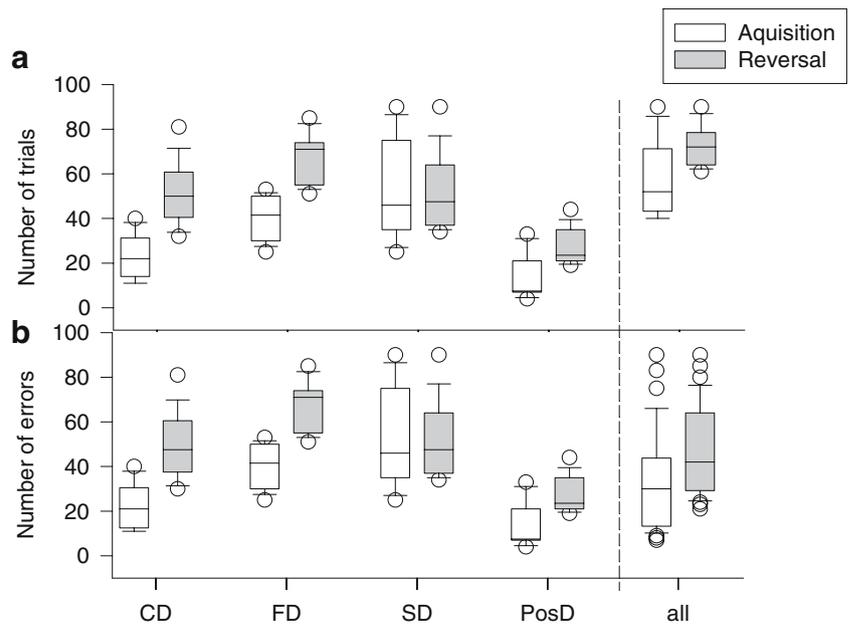
FD (multiple comparisons, $p<0.05$), but no difference was found between CD and SD or between FD and SD.

During reversal trials, we found a trend towards a difference between the color, form and size discrimination in the number of errors made (Friedman: $N=9$, $F_R=6.0$, $df=2$, $p<0.1$) but there was no difference in the number of trials to reach criterion (Friedman: $N=9$, $F_R=-1.6$, $df=2$, NS).

In the CD and in the FD, ravens were significantly worse during the reversal than during the acquisition in the number of trials to reach criterion and in the number of errors they made (Table 1). However, no significant

difference was found in the third feature discrimination task (SD) between acquisition and reversal. To further analyze reversal versus acquisition, we analyzed the reversal index. Ravens reached lower reversal indices on the second and third task than on the first one; however, individual variation was high (Friedman: $N=9$, $F_R=5$, $df=2$, NS) (Fig. 2).
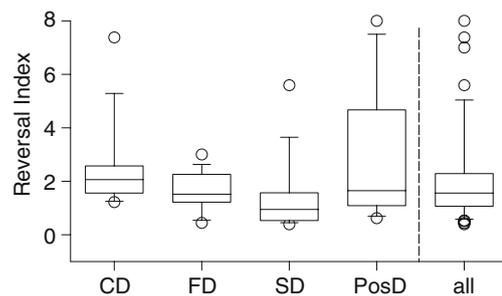
Positional discrimination

In the fourth task, ravens had to distinguish objects based on their position (right or left). All ravens took significantly fewer trials to learn the task to the set criterion in the acquisition and in the reversal than they did during the feature discriminations (Table 2). Ravens were also more accurate in the positional discrimination than in the feature discrimination, making significantly fewer mistakes across sessions (Table 2).

Table 1 Comparisons of the number of trials needed and errors made in the acquisition and reversal phases of the discrimination tasks (Wilcoxon signed-ranks test)

Task	Acquisition, median (range)	Reversal, median (range)	T^+	p Value
CD ($N=11$)				
Trials	22 (3–40)	50 (22–81)	55	0.001
Errors	7.5 (2–14)	27 (10–45)	55	0.001
FD ($N=10$)				
Trials	41.5 (25–52)	71 (15–85)	42	0.01
Errors	16 (12–25)	40.5 (10–55)	44	0.004
SD ($N=10$)				
Trials	46 (12–90)	47.5 (13–90)	20	NS
Errors	17.5 (4–35)	24.5 (7–36)	34.5	0.102
PosD ($N=10$)				
Trials	4.5 (0–33)	22 (2–44)	39	0.027
Errors	1.5 (0–17)	12.5 (2–24)	44	0.004

N: sample size, *CD*: color discrimination, *FD*: form discrimination, *SD*: size discrimination, *PosD*: position discrimination, *NS*: non-significant


Fig. 2 Box plots (10th and 90th percentile) of the reversal index for ravens in the four discrimination tasks and overall. *CD* color discrimination, *FD* form discrimination, *SD* size discrimination, *PosD* position discrimination

Table 2 Comparison between the feature (mean of color, size and form discrimination) and positional discrimination tasks in the number of trials the ravens needed to reach the criterion and in the number of errors they made (Wilcoxon signed-ranks test, $N=9$)

	Acquisition		Reversal		
	No. of trials		No. of errors	No. of trials	No. of errors
T^+	52		45	55	55
p Value	<0.002		0.002	<0.002	<0.002

There was a significant increase in trials to reach criterion from the acquisition to the reversal phase (Table 1) and a significant increase in the errors they made (Table 1). This is not surprising because three animals needed zero trials to reach criterion (they choose the correct side on the first trial and stayed with their choice) and one animal needed only one trial. Thus, they could not have been better in the reversal than in the acquisition phase, even if they had shown one-trial learning in the reversal phase (and the first trial of the reversal phase would have been omitted). However, the adult male needed as few as two trials to reach the criterion in the reversal phase. The reversal index
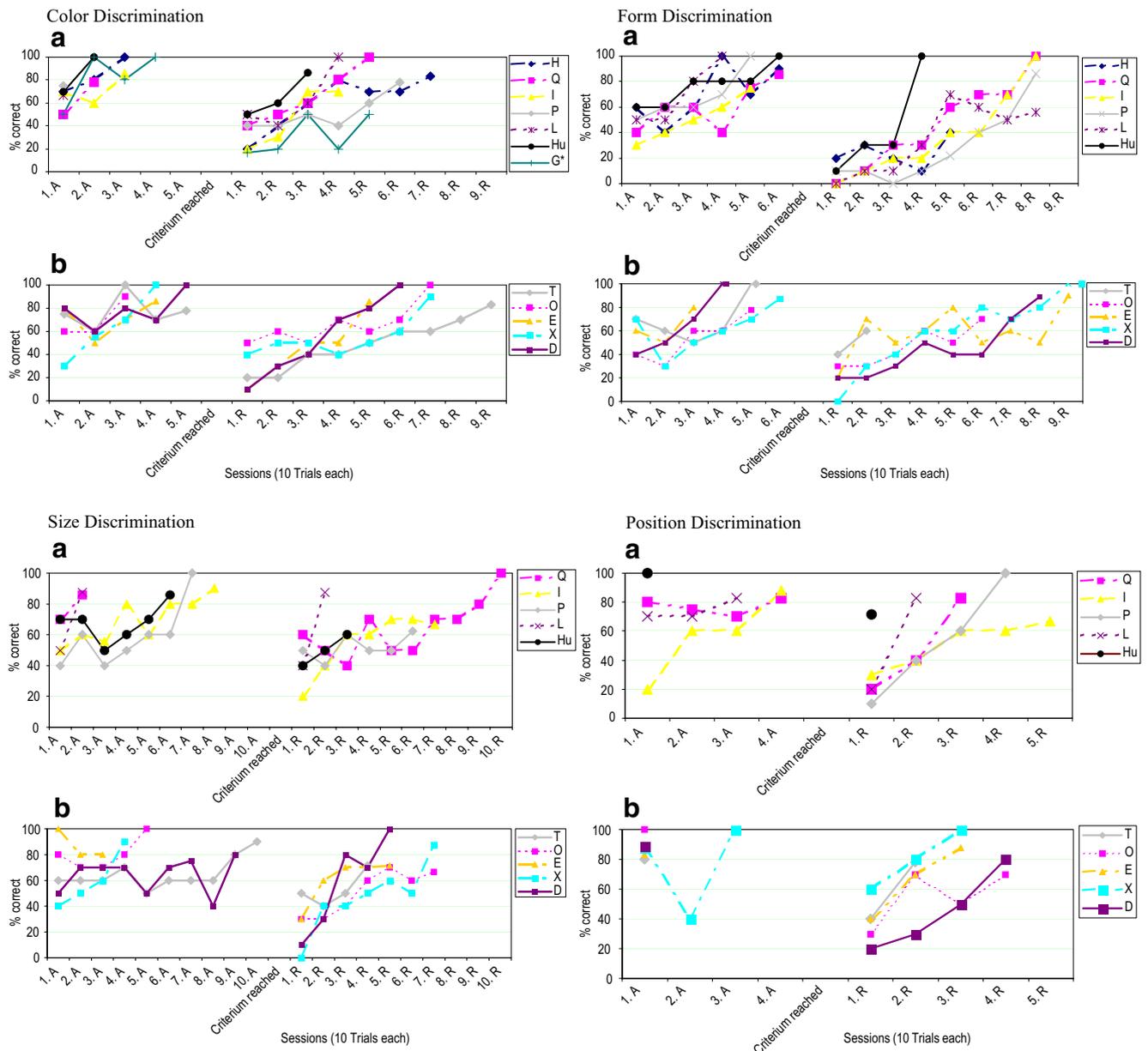
Fig. 3 Individual learning curves for the four discrimination problems. The graphs show the percentage of correct responses in the acquisition and reversal phases for males (**a**) and females (**b**). *A* acquisition sessions, *R* reversal sessions. *Letter codes* denote individuals. *G** died during the reversal discrimination, *Hu* Hugin (the adult male)

was slightly higher (median=1.65) compared to the reversal indices of the form and size discrimination tasks.

Figure 3 depicts the individual learning curves to reach the criterion for the three feature and positional discriminations showing inter- and intra-individual variation in the acquisition phase of tasks. In addition, individuals had a difficult time switching from the previously unrewarded to the rewarded object in the reversal phase as apparent in the low percentage of correct choices in the very first reversal sessions of the discriminations. Note that reversal started within the same session after passing the second part of the criterion.

Discussion

Acquisition phase

Ravens participated equally well in the three feature discrimination tasks. However, they were much better in the acquisition of the color discrimination than in the form and size discriminations. This effect could be due to (1) color discrimination being an easier task for ravens than form or size discrimination as has been shown for other avian species (Brown and Dooling 1992, 1993; Troje et al. 1999) or (2) individuals lost interest in the discrimination problems over time. Males, in particular, grew less attentive to the task at hand and instead investigated the room and started singing, supporting the latter possibility. Remarkably, grey parrots (Psittacus erithacus) also become inattentive when faced with multiple trials on a given task (Pepperberg and Lynn 2000, Pepperberg and Gordon 2005).

All ravens performed much better in the positional task than in the feature discrimination tasks with four birds showing one-trial learning in the acquisition phase. There are two possible explanations for this difference in performance: First, ravens could have learned how to solve the task at hand across the different problems as has been shown for a number of species including corvids (Hunter and Kamil 1971; Kamil and Hunter 1970). Second, the positional discrimination is easier for ravens to solve than the feature discrimination tasks. Ravens cache food (Heinrich and Pepper 1998; Heinrich 1999b) and also pilfer caches of conspecifics (e.g. have to remember where the food was stored) (Bugnyar and Kotrschal 2002b; Heinrich and Pepper 1998), thus it is likely that they have a predisposition to solve spatial problems as has been shown for other caching species (Olson and Kamil 1995; Kamil et al. 1994). Our data are in favor of the latter explanation, or at least of a cumulative effect, because eight of ten individuals dropped substantially in the number of trials/errors to reach the criterion between the last feature

and the position discrimination task (e.g. from 90 to 5 or from 60 to 0), suggesting that learning alone can hardly account for this improvement.

Overall, this preliminary study showed that ravens can learn new tasks in few trials under semi-natural conditions (e.g. two males needed less than four trials to reach criterion in the first discrimination task), making only a few mistakes. The average trials to reach the criterion in the acquisition phase across the four discrimination problems was 31.05 and thus slightly below the level reported for stump-tailed macaques (Macaca arctoides) and rhesus macaques (M. mulatto) who averaged 13.6 and 19.7 trials, respectively, to reach the 9/10 acquisition criterion across 36 problems (Essock-Vitale 1978). However, all monkeys of that study had extensive previous experimental histories, including many learning set-related problems, which could have provided positive transfer. Another study that provided data on five preliminary discrimination problems (Harlow 1944) showed that the errors made by monkeys were in the same range as the ravens (monkeys 14, 24, 13, 38, 26; ravens 7, 18, 17, 4). However, the learning curves of two new-world monkey species trained with five discrimination problems (Callicebus/Samiri) were considerably steeper than the learning curves of our ravens (Fig. 3) at least in the feature discriminations (Fragaszy 1981). In addition, the percentage correct, especially in the feature discriminations, often does not reach more than 80% in the individual birds, indicating that ravens still made mistakes when they are about to reach criterion in contrast to the new-world monkeys.

Reversal phase

We found no indication that ravens learned a concept of reversal discriminations over the few presented problems. A high level of performance would have implied the adoption of a win–stay, lose–shift (WSLS) strategy (Harlow 1949). In the WSLS strategy, the subject consistently chooses a stimulus if it is rewarded on the first trial (win–stay) but consistently chooses the other stimulus if the stimulus chosen on the first trial is not rewarded (lose–shift). The speed of reversal learning in this study is difficult to interpret due to the small number of qualitatively different tasks (color, shape, size and position) and the same order of presentation. Moreover, we used a laxer criterion during the tests for the reversal compared to the acquisition phase. In previous studies, animals have been given learning sets of between 50 and 1,000 problems over which to investigate the rates of acquisition. However, such testing would be impossible to conduct in the semi-natural situation we chose for this study. Even after the few tests we conducted, some birds became less and less interested (see above). Conducting further tests or choosing a stronger criterion

might have led to the refusal to work on the side of the birds. One possible solution might be to test birds only every 2 or 3 months with one problem at a time (keeping the quality of the task constant and randomizing the order of presentations between birds) instead of conducting one test after the other. This might lead to a better performance of the animals, but still allow for testing in a semi-natural environment.

General discussion

This pilot study differed from other published data on learning in several factors. First, our feature discrimination tasks were quite difficult in the sense that the spatial position changed randomly between trials (e.g. not just right/left). Second, none of our animals were trained in discrimination learning before the experiment except the adult male. Third, our criterion was relatively easy compared to other published studies (e.g. 18 correct choices out of 20) and also different between the acquisition and reversal phases. Fourth, we presented the animals with four qualitatively different discriminations that were presented in the same order. These differences and shortcomings of this study make a comparison with results from other studies difficult, if not impossible. Nevertheless, this preliminary study suggests that at least some ravens might learn discrimination tasks very fast (two males learned the colour discrimination after four and four trials, several birds showed one-trial learning in the fourth discrimination task). This fast learning is comparable to the speed of task acquisition in other corvid studies (e.g. Tebbich et al. 2006). Further studies with a larger discrimination set will allow more profound comparisons with other species and with corvids tested in the laboratory.

References

Bond AB, Kamil AC, Balda RP (2003) Social complexity and transitive inference in corvids. Anim Behav 65:479–487

Brown C, Dooling RJ (1992) Perception of conspecific faces by budgerigards (*Melopsittacus undulatus*): I. Natural faces. J Comp Psychol 106:203–216

Brown C, Dooling RJ (1993) Perception of conspecific faces by budgerigards (*Melopsittacus undulatus*): I. Synthetic models. J Comp Psychol 107:48–60

Bugnyar T, Kotrschal K (2002a) Scrounging tactics in free-ranging ravens, *Corvus corax*. Ethology 108(11):993–1009

Bugnyar T, Kotrschal K (2002b) Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? Anim Behav 64:185–195

Bugnyar T, Kotrschal K (2004) Leading a conspecific away from food in ravens (*Corvus corax*)? Anim Cogn 7(2):69–76

Bugnyar T, Stowe M, Heinrich B (2004) Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. Proc R Soc Lond B Biol Sci 271(1546):1331–1336

Chappell J, Kacelnik A (2002) Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). Anim Cogn 5(2):71–78

Chappell J, Kacelnik A (2004) Selection of tool diameter by New Caledonian crows *Corvus moneduloides*. Anim Cogn 7:121–127

Clayton NS, Dickinson A (1999) Motivational control of caching behaviour in the scrub jay, *Aphelocoma coerulescens*. Anim Behav 57:435–444

Drack G, Kotrschal K (1995) Aktivitätsmuster und Spiel freilebender Kolkraben Corvus corax im inneren Almtal/Oberösterreich. Monticula 7:159–174

Drea CM, Wallen K (1995) Gradual acquisition of visual-discrimination tasks in a social group of rhesus monkeys (*Macaca mulatta*). Anim Learn Behav 23(1):1–8

Emery NJ, Clayton NS (2001) Effects of experience and social context on prospective caching strategies by scrub jays. Nature 414(6862):443–446

Emery NJ, Dally JM, Clayton NS (2004) Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. Anim Cogn 7(1):37–43

Essock-Vitale S (1978) Comparison of ape and monkey modes of problem solution. J Comp Physiol Psychol 92(5):942–957

Fragaszy D (1981) Comparative performance in discrimination learning tasks in two New World primates (*Saimiri sciureus* and *Callicebus moloch*). Anim Learn Behav 9(1):127–134

Grant D (1946) New statistical criteria for learning and problem solution in experiments involving repeated trials. Psychol Bull 43:272–282

Harlow HF (1944) Studies in discrimination learning by monkeys: 1. The learning of discrimination series and the reversal of discrimination series. J Gen Psych 30:3–12

Harlow HF (1949) The formation of learning-sets. Psychol Rev 56:51–65

Hauri R (1956) Beiträge zur Biologie des Kolkraben (*Corvus corax*). Ornithol Mitt 53:28–35

Heinrich B (1995) An experimental investigation of insight in common ravens (*Corvus corax*). Auk 112(4):994–1003

Heinrich B (1999a) Mind of the raven. New York, Harper

Heinrich B (1999b) Planning to facilitate caching: possible suet cutting by a common raven. Wilson Bull 111(2):276–278

Heinrich B, Pepper JW (1998) Influence of competitors on caching behaviour in the common raven, *Corvus corax*. Anim Behav 56:1083–1090

Hunt GR (1996) Manufacture and use of hook-tools by New Caledonian crows. Nature 379(6562):249–251

Hunt GR (2000) Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. Proc R Soc Lond B Biol Sci 267(1441):403–413

Hunt GR, Gray RD (2003) Diversification and cumulative evolution in New Caledonian crow tool manufacture. Proc R Soc Lond B Biol Sci 270(1517):867–874

Hunt GR, Gray RD (2004) The crafting of hook tools by wild New Caledonian crows. Proc R Soc Lond B Biol Sci 271:S88–S90

Hunter MW III, Kamil AC (1971) Object discrimination learning set and hypothesis behaviour in the northern bluejay (*Cynaocitta cristata*). Psychon Sci 22(5):271–273

Kamil AC, Balda RP, Olson DJ (1994) Performance of 4 seed-caching corvid species in the radial-arm maze analog. J Comp Psychol 108(4):385–393

Kamil AC, Hunter MW III (1970) Performance on object discrimination learning-set by the greater hill myna (*Gracula Regiliosa*). J Comp Physiol Psychol 73:68

Kenward B, Weir A, Rutz C, Kacelnik A (2005) Tool manufacture by naive juvenile crows. Nature 433:121

Lipp HP, Pleskacheva MG, Gossweiler H, Ricceri L, Smirnova AA, Garin NN, Perepiolkina OP, Voronkov DN, Kuptsov PA, Dell'Omo G (2001) A large outdoor radial maze for comparative studies in birds and mammals. Neurosci Biobehav Rev 25(1):83–99

Mackintosh NJ, Wilson B, Boakes RA (1985) Differences in mechanisms of intelligence among vertebrates. Philos Trans R Soc Lond B Biol Sci 308(1135):53–63

Olson D, Kamil AC (1995) Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory. J Comp Psychol 109(2):173–181

Pavlov IP (1927) Lectures on conditioned reflexes. International, NewYork

Pepperberg IM, Lynn SK (2000) Possible levels of animal consciousness with reference to grey parrots. Am Zool 40:893–901

Pepperberg IM, Gordon JD (2005) Number comprehension by a grey parrot (*Psittacus erithacus*), including a zero-like concept. J Comp Psychol 119(2):197–209

Range F, Bugnyar T, Schlögl C, Kotrschal K (2006) Individual and sex differences in learning abilities of ravens. Behav Processes 73:100–106

Ratcliffe D (1997) The raven. A natural history in Britain and Ireland. Poyser, London

Schlögl C (2005) The ontogeny of gaze following in common ravens (*Corvus corax*). Thesis, University of Bayreuth, Germany

Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences. Boston, McGraw-Hill

Smirnova AA, Lazareva OF, Zorina ZA (2000) Use of number by crows: investigation by matching and oddity learning. J Exp Anal Behav 73(2):163–176

Tebbich S, Seed A, Emery NJ, Clayton NS (2006) Non tool-using rooks, *Corvus frugilegus*, solve the trap-tube task. Anim Behav 10:225–231

Troje NF, Huber L, Loidolt M, Aust U, Fieder M (1999) Categorical learning in pigeons: the role of texture and shape in a complex static stimuli. Vision Res 39:353–366

Warren JM (1966) Reversal learning and the formation of learning-sets by cats and rhesus monkeys. J Comp Physiol Psychol 61:421–428

Weir AS, Chappell J, Kacelnik A (2002) Shaping of hooks in New Caledonian crows. Science 297:981

Wilson B, Mackintosh NJ, Boakes RA (1985) Transfer of relational rules in matching and oddity learning by pigeons and corvids. Q J Exp Psychol B Comp Physiol Psychol 37 (4):313–332