



Individual and sex differences in learning abilities of ravens

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Abstract

Behavioral and physiological characteristics of individuals within the same species have been found to be stable across time and contexts. In this study, we investigated individual differences in learning abilities and object and social manipulation to test for consistency within individuals across different tasks. Individual ravens (*Corvus corax*) were tested in simple color and position discrimination tasks to establish their learning abilities. We found that males were significantly better in the acquisition of the first discrimination task and the object manipulation task, but not in any of the other tasks. Furthermore, faster learners engaged less often in manipulations of conspecifics and exploration of objects to get access to food. No relationship between object and social manipulation and reversal training were found. Our results suggest that individual differences in regard to the acquisition of new tasks may be related to personalities or at least object manipulation in ravens.

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1. Introduction

In the last decade, progress has been made in understanding individual behavioral differences. It has been found that individuals cope behaviorally and physiologically with environmental and social challenges, irrespective of life history, sex, or motivational state ('coping style theory'; Koolhaas et al., 1999). Several animal species, as well as humans, have shown a similar range of coping styles (Wilson et al., 1994; Holst, 1998; Koolhaas et al., 1999). For example, in rats (*Rattus norvegicus*), mice (*Mus musculus*) and great tits (*Parus major*), aggressive individuals ('proactive' or 'fast copers') spent less time exploring novel objects and were less alert to changing stimuli in known environments than less aggressive individuals ('reactive' or 'slow copers') (Koolhaas et al., 1999; Benus et al., 1990; Verbeek et al., 1996; Drent and Marchetti, 1999). Also, reactive individuals are more glucocorticoid-responsive than proactives (Koolhaas et al., 1999). These individual differences may directly affect attention, readiness to learn and central learning mechanisms (Brown, 1994; Holst, 1998; Koolhaas et al., 1999; Bolhuis et al., 2004; Drent and Marchetti, 1999). However, there were also reports

that learning abilities did not vary with coping style (Bolhuis et al., 2004; Carere et al., cited in Groothuis and Carere, 2005).

Juvenile ravens (*Corvus corax*) assemble in non-kin groups (Parker et al., 1994) and later on form stable breeding pairs (Heinrich, 1989). They are scavengers that feed mainly on ephemeral carcasses or kills, but also exploit various man-made food resources (Ratcliffe, 1997) at garbage dumps or game parks (Ratcliffe, 1997; Hauri, 1956; Drack and Kotrschal, 1995). Nevertheless, ravens are extremely wary of novel feeding situations. Such neophobia could hamper exploration of new food sources for days, weeks or even months (Kijne and Kotrschal, 2002).

To overcome monopolization of food by dominant conspecifics (Heinrich, 1988) and/or non-conspecific competitors such as wolves (*Canis lupus*; Bugnyar and Kotrschal, 2002a), ravens use a variety of tactics of social manipulation, such as recruitment of conspecifics at roosts and by food calling (Marzluff and Heinrich, 1991; Heinrich and Marzluff, 1991), scrounging (Bugnyar and Kotrschal, 2002a), misleading (Bugnyar and Kotrschal, 2004), and pilfering caches (Bugnyar and Kotrschal, 2002b; Heinrich and Pepper, 1998). Some of these tactics might require cognitively demanding skills (Bugnyar et al., 2004) and might partially be learned by experience as it has been found for Western Scrub jays (*Aphelocoma californica*; Emery and Clayton, 2001; Emery et al., 2004). Thus, learning and behavioral flexibility might play an essential role in successful coping with social and ecological challenges in ravens.

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In this study, we investigated individual learning abilities in relation to explorative behavior towards novel objects containing food and manipulation of conspecifics handling preferred items. Using two simple discrimination tasks (color and position) and their reversals, we first attempted to establish a measure for individual learning ability (acquisition) and flexibility (reversal). In a second study, we tested explorative behavior and motor skills in an object manipulation task. These are parameters also used in the coping style theory to characterize individuals into different personalities. Finally, we analyzed manipulative behavior within the social group using focal observations. The aim was to test whether individuals that were faster in the individual learning task were also more manipulative in the motor tasks and more proficient in manipulating their conspecifics. In addition, we wanted to investigate whether the individual differences were in line with predictions from the coping style theory.

2. General methods

2.1. Subjects and setting

Subjects of this study were eight zoo-bred ravens (four males, four females) and four wild-caught (three males, one female) raven nestlings that were hand-reared from 12–40 days after hatching to fledging at the Konrad Lorenz Research Station, Gruenau, Austria. Most of the birds tested were juveniles in their first year (8 months at the beginning of the study) except one zoo-bred male who was already 9-year-old. Unfortunately, two juvenile males (one zoo-bred and one wild-caught) died during the study due to predation. All ravens were marked with colored rings for individual identification. The birds had access to water and were fed once or twice a day. The diet consisted of various kinds of meat, milk products and fruit. The ravens were housed together in a large outdoor aviary situated in the Cumberland game park in the Austrian Alps (Fig. 1). During experiments, individuals were called into the back compartments where they could be tested in physical and visual isolation from conspecifics. All juvenile birds had previously been tested on gaze following, exploration, neophobia and imitation, but not on any discrimination or individual learning task.

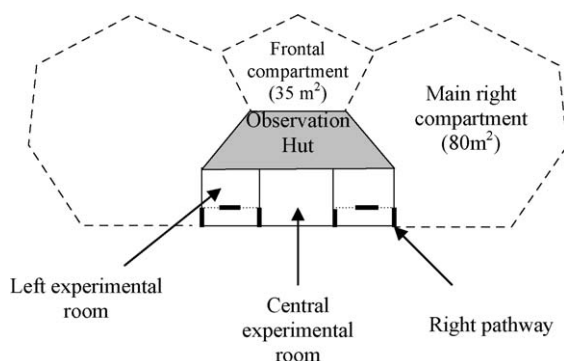


Fig. 1. Sketch of the aviary. Dashed lines indicate wire mesh and bold lines indicate doors in the back.

2.2. Study 1: discrimination learning tasks

2.2.1. Methods and materials

2.2.1.1. Color discrimination. The experimental set-up as well as the discrimination learning per se was completely new for all juveniles in the first discrimination test. In this first task birds had to learn to differentiate between two differently colored plastic tubes (11 cm long, 3 cm diameter). The tubes were red, yellow or blue and randomly assigned to the birds so that each color combination was present at least twice. One of the colored tubes was filled with cheese—a highly valued food by ravens. No cue was given in the beginning as to which color would be rewarded. Olfactory cues are unlikely to be important in ravens [Heinrich and Pepper \(1998\)](#); however, to avoid any such possibility, both tubes had contained cheese before the experiment started. Individuals received 10 trials per session, one session every other day. In order to reach the first part of the criterion, individuals had to choose the rewarded color five times in a row in the same session. If this criterion was reached before the 10 trials were over, the session was terminated. In the session after the first part of criterion was reached, the subjects had to choose the rewarded color again in the first three trials in order 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 vice versa. The reversal training was terminated when animals chose the rewarded (previously unrewarded) color five times in a row. If animals did not choose correctly on the first three trials in the session after the criterion was reached, they would resume normal testing until they reached the criterion 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. Since ravens easily loose interest in tasks, we chose thus a relatively lax criterion to ensure their participation.

2.2.1.2. Position discrimination. In the right-left discrimination task, we used two identical cylindrical white 500 g yoghurt cups (12 cm high, 9 cm diameter) and baited either the right or the left one according to the assignment. 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. Otherwise the design of the experiment was the same as for the color discrimination test. Individuals were tested in visual isolation from others and all received the color discrimination task before the right/left discrimination task.

The right/left discrimination task was conducted 8 weeks later, after all birds had received training with three other discrimination tasks and their reversals (shape, size and social; [Range et al., submitted for publication](#)). This last test of the

right/left discrimination was used to examine whether experience with the general set-up of the experiments would affect the results.

2.2.2. Data analyses

We used two dependent measures. The number of trials to reach criterion indicates how quickly the ravens learned the tasks. We also analyzed the number of errors to reach criterion.

2.3. Study 2: motor task

2.3.1. Methods and materials

In the object manipulation task, ravens had to handle an open 1/2 l plastic bottle (green, but slightly transparent so that ravens could see the content) baited with highly valued food (a dog food pellet). To receive the food, the ravens had to lift the bottle so that the opening (diameter 2 cm) pointed to the ground or shake/throw the bottle. Prior to the experiments, ravens were habituated to the bottle to decrease the effects of neophobia (each bird had touched the bottle).

In the test trials, individuals were visually isolated from conspecifics either in the back or in one of the side compartments of the aviary. Tests began when the subject perched between 2 and 3 m away from the experimenter and watched what the experimenter was doing. The food was placed into the bottle and placed on the ground for the bird to manipulate. Experiments were videotaped for later analysis. Each bird received five sessions of 10 min each. Birds were tested only once a day and motor tasks were alternated with discrimination learning trials.

2.3.2. Data analysis

We analyzed: (1) the total number of actions performed on the object by each individual across the five sessions, (2) the latency to touch the object defined as the time from the beginning of the experiment until the bird touched the bottle for the first time, (3) the average number of times food was gained and (4) the number of different methods used by the subject in the five sessions. Since not all individuals participated in each of the five sessions, we calculated the *s* score, which is defined as (number of occurrences of behavior)/(time on test before occurrences) where the divisor includes the periods of observation in which the behavior does not occur (Theobald and Goupillot, 1990).

2.4. Study 3: dominance rank and social manipulation

2.4.1. Methods and materials

The ravens were observed in the morning and in the late afternoon each day either by C. Schlögl or C. Pribersky-Schwab. Data on social interactions ('who' does 'what' to 'whom') were collected in a semi-random order by 5 min focal samples (Altmann, 1974). Each raven was sampled approximately the same number of times in the morning and in the afternoon. Results reported are based on data collected by C. Schlögl unless otherwise indicated. He collected between 21 and 30 focal samples per individual between November 2004 and February 2005. The two individuals who were killed were sampled 9 and 10 times, respectively.

For this study, we analyzed dominance interactions on the basis of retreat interactions and social manipulation on the basis of interactions over favoured items. *Retreat* was defined as moving out of the 1 m perimeter of an approaching reactor. In *retreat after aggression* the actor moved out of the 1 m perimeter of the reactor who threatened or pecked the actor. *Social interactions over items* refers to any situation where an individual tries to get access to a piece of food or an object that another individual is manipulating (kleptoparasitism, scrounging; Brockmann and Barnard, 1979; Giraldeau and Caraco, 2000). These interactions could involve displacing the conspecific from the item (i.e., actor takes the item and reactor has to leave), stealing the item (i.e., actor takes and leaves with the item while the reactor is inattentive) or getting the other to share the item (i.e., both individuals manipulate the same item; Bugnyar and Kotrschal, 2002a). Since the ability of displacing others from items is strongly affected by dominance rank, we confined our analysis to the parameters stealing (18% of interactions) and sharing (72% of interactions).

2.4.2. Data analyses

Dominance rank was defined according to the direction of submissive behavior (*retreat + retreat after aggression*). To determine the dominance relationships among all individuals in the group, we pooled the focal animal data of the two observers (CS and CPS; the same results were obtained as when data were analyzed separately). Individuals were ordered to reduce the number of circular triads (Vries de, 1995). If a relationship between individuals was unclear, the average rank was assigned to both. The highest-ranking individual was ranked 1, the lowest ranking individual 12. For the category *social manipulation*, we calculated the frequency of the parameters stealing and sharing per minute.

2.5. Statistics

Statistical analyses were performed with SPSS (Version 10.0.5, 1999), with MATMAN (Version 1.0, Noldus Technologies), or by hand according to Siegel and Castellan (1988). We used Mann–Whitney *U*-tests to investigate sex differences, Kruskal–Wallis tests to look for individual differences and Spearman rank correlations to test for relationships between data sets. If sex was highly predictive in regard to certain behavior or learning abilities, we statistically controlled for the effect of sex in our analyses. α was set at 0.05, trends were reported for $0.1 > \alpha > 0.05$. All tests were two-tailed.

Due to the loss of two juvenile males, sample sizes differed between experiments. Additionally, the one adult male was excluded from the analysis of the color discrimination task and the bottle-opening task since he had prior experience with those tasks.

3. Results

3.1. Study 1: discrimination learning tasks

Individual differences in the number of trials to reach criterion and errors made were profound both in the acquisition and reversal of the two discrimination tasks. Interestingly, we found

Table 1
Sex differences in color and positional discriminations both for the acquisition and reversal phase (Mann–Whitney *U*-tests)

	Males, median (quartile 1; 3)	Females, median (quartile 1; 3)	N_M	N_F	W_x	P
Color acquisition						
Trials	12 (5.5; 18.5)	32 (29; 37)	6	5	40.5	0.041
Errors	4 (3; 6.5)	11 (11; 11)	6	5	45.0	0.002
Position acquisition						
Trials	21 (0.29)	4 (1.5)	5	5	24.0	NS
Errors	7 (0.8)	1 (1.2)	5	5	24.5	NS
Color reversal						
Trials	37.5 (31.25; 50.5)	60 (50; 65)	5	5	35.0	NS
Errors	19 (15.5; 25.5)	27 (27; 32)	5	5	35.0	NS
Position reversal						
Trials	21 (11; 30)	23 (20; 35)	5	5	29.0	NS
Errors	15 (9; 19)	10 (8; 18)	5	5	26.0	NS

M: male; F: female; NS: $P > 0.1$.

that overall, males were significantly better than females in the acquisition phase of the color discrimination task both in the number of trials to reach criterion as well as in the number of errors they made (Table 1). In contrast, there was no sex difference in the acquisition phase of the positional discrimination task or in the reversal phase of the color and the position discrimination (Table 1). If we statistically controlled for the effect of sex on the color discrimination task (males were faster than females), acquisition in both discrimination tasks was highly correlated with each other (partial correlation coefficient = 0.91; d.f. = 7, $P = 0.01$), suggesting that males got worse, but individual performance was consistent in relation to others over tasks. No such relationship was found between the reversal tasks.

3.2. Study 2: motor task

The number of actions performed was positively correlated with shorter latency to touch (Spearman-rank correlations: $N = 11$, $r_s = 0.76$, $P = 0.01$), average food received ($N = 11$, $r_s = 0.92$, $P < 0.001$) and number of methods used ($N = 11$, $r_s = 0.82$, $P = 0.005$); hence, we used the number of actions performed as the variable in all further analyses. We found an overall significant difference in the number of actions performed between individuals (Kruskal–Wallis: $\chi^2 = 30.459$; d.f. = 10; $P = 0.001$). Moreover, we found that males manipulated the bottle significantly more often than females did (Table 2).

3.3. Study 3: dominance rank and social manipulation

Ravens formed by and large a linear dominance hierarchy ($h' = 0.69$; 1 would be complete linearity). The probabil-

ity that the observed linearity resulted from a random process was $P < 0.0003$. In our group, all males outranked the females (Table 2), which led to interdependency between rank and sex. We found no difference in the frequency of social interactions over items between males and females (Table 2).

3.4. Individual consistency across studies

Individuals who took fewer trials and made fewer errors to reach criterion in the discrimination tasks (statistically controlled for the effect of sex) were less often engaged both in exploration of the bottle and in manipulating conspecifics (Table 3). Even though not significant, correlations with rank (statistically controlled for the effect of sex) were positive and quite high considering the small sample size in the color and position acquisition phase, indicating a tendency for high-ranking individuals to be better in the individual learning tasks than low ranking individuals. Reversal learning did not show any significant relationship with the same parameters as the original acquisition (Table 3).

4. Discussion

The aim of this study was to investigate the extent to which learning abilities of ravens differ between individuals and whether individual ravens are consistent in performance across different problems. We found that individuals were consistent in their performance in the two discrimination tasks, but that sex had a strong influence on acquisition in the color discrimination. Males were also more manipulative in the motor task but not in social interactions than females. Finally, individuals who were better/faster learners in the individual learning tasks were less

Table 2
Sex differences in social manipulation, object manipulation and rank in ravens (Mann–Whitney *U*-tests)

	Males, median (quartile 1; 3)	Females, median (quartile 1; 3)	N_M	N_F	W_x	P
Rank	4 (25; 5.5)	9.5 (9.5; 12)	7	5	50.0	0.001
Motor task (number of actions)	479 (190; 662)	29 (9; 109)	6	5	18.0	0.015
Social manipulation	0 (0; 0.06)	0.04 (0.01; 0.07)	7	5	32.5	NS

Social manipulation was defined as stealing and sharing of food or objects per hour. Motor task was defined as the number of actions performed on a bottle filled with food during 20 min. Rank was defined according to the direction of submissive behavior. M: male; F: female; NS: $P > 0.1$.

Table 3

Spearman rank correlations (r_s) and partial correlations (p_c) between the number of trials needed and errors made to reach criterion in the discrimination tasks and social manipulation, rank and object manipulations

Behavior	N/d.f. ^b	Trials		Errors	
		r_s/p_c	P	r_s/p_c	P
Acquisition CD					
Rank ^a	8	0.59	0.072	0.47	NS
Motor task (number of actions) ^a	8	0.52	NS	0.63	0.049
Social manipulation ^a	8	0.15	NS	0.82	0.004
Acquisition PosD					
Rank [*]	7	0.50	NS	0.42	NS
Motor task (number of actions) [*]	6	0.88	0.004	0.80	0.018
Social manipulation	10	0.79	0.006	0.84	0.002
Reversal CD					
Rank ^a	7	0.20	NS	0.23	NS
Motor task (number of actions) ^a	7	−0.26	NS	−0.33	NS
Social manipulation	10	−0.01	NS	0.21	NS
Reversal PosD					
Rank ^a	7	0.27	NS	0.38	NS
Motor task (number of actions) ^a	6	0.34	NS	0.29	NS
Social manipulation	10	0.35	NS	0.08	NS

CD: color discrimination; PosD: position discrimination; NS: $P > 0.1$. Corrected α -value = 0.016.

^a Parameters controlled for sex (partial correlations).

^b N for spearman rank correlations and d.f. for partial correlations.

often engaged in physical and social manipulations (motor task and scrounging) than individuals who took more trials to reach criterion and made more mistakes.

Interestingly, our data revealed that sex might influence individual learning abilities in ravens, at least with respect to newly encountered tasks. The sex difference in performance in the acquisition phase of the color discrimination task disappeared after similar tasks were conducted, suggesting that males grew less accurate (they needed more trials and made more mistakes) when repeatedly confronted with the same kind of problems. Actually, the main difference between the color and position discrimination in our study was that males and females were equally good in the position but not in the color discrimination task. Sex has been shown to influence responsiveness to environmental stimuli, to correlate with levels of interest in novel items, and to define the extent of participation in activities in primates (Fragaszy and Visalberghi, 1990). If that is true also for ravens, sex effects should be found across different problems. In fact, we also found sex differences in the object manipulation task with males being more manipulative and showing shorter latencies to approach the object. The latter differences might be explained by males being more willing to take risks. For example, in wild ravens co-feeding with wolves at the local Cumberland game park, more young males were killed by the wolves than females (of 12 killed, 9 were male and only 3 were females, Bugnyar and Kotrschal, unpublished data). Another explanation for the sex differences could be due to the rank difference between males and females, preventing the females from showing that they learn or manipulate to reduce retaliation by males (see Drea and Wallen, 1999 for difference in performance of high- and low-ranking monkeys). However, since we tested the ravens in visual isolation and all animals had prior experience

with individual testing before these experiments, this explanation is unlikely.

Several individuals in our study solved the first task in three to five trials. Four animals showed one-trial learning in the positional discrimination. Good individual learning abilities are likely to be useful for species that feed on many different food resources, especially if accessing food is dangerous (e.g., in the case of wolves or humans as competitors). Interestingly, the slower learners engaged more in interactions with conspecifics over items, suggesting that they tried to reach their goals more often by social means than fast learners. Observations of wild ravens suggest that ravens are quite flexible in adjusting their scrounging frequency in regard to the difficulties to access food, but also show individual consistency in whether or not to use scrounging across different foraging sites (Bugnyar and Kotrschal, 2002a).

According to the coping style theory (Koolhaas et al., 1999; Sih et al., 2004), proactive individuals should be faster than reactive animals in the acquisition of simple discrimination tasks, but are more prone to form routines. Thus, reactive animals should be faster than proactive individuals in more complex tasks, for example reversal learning (Drent and Marchetti, 1999). Proactive individuals are usually categorized by short approach latency and quick explorative behavior towards novel objects, whereas reactive individuals show the reversed pattern. Although we did not test for it per se, we found quick explorers (motor task) to be faster learners. These data are in line with the results reported for great tits by Drent and Marchetti (1999) and suggest that there may be differences in acquisition of simple discrimination tasks between explorative and less explorative individuals. Nevertheless, in contrast to published studies investigating the relationship between reversal learning

and personality (Benus et al., 1987, 1990; Verbeek et al., 1996; Teskey et al., 1998; Marchetti and Drent, 2000), we found no correlation between the trials needed to reach criterion or errors made and any of our other measures. One explanation for this discrepancy could be the inherent sequence of acquisition and reversal tasks with reversals always being last. Ravens become inattentive if too many similar tests are performed, which could have masked any differences in learning abilities. However, in the position discrimination, acquisition for most animals was rather short, rendering this explanation unlikely.

In further studies, the link between further behavioral characteristics, physiological parameters and learning abilities in ravens should be investigated to reveal whether the relationships of explorative behavior and learning abilities reflects personality traits, or if slow learners are simply less motivated to learn, but more motivated to play. Furthermore, individuals that make little use of their conspecifics via scrounging would also be expected to be less attentive, and probably even less successful in social learning tasks, than individuals that scrounge more often (Fritz and Kotrschal, 1999; but see Giraldeau and Lefebvre, 1987; Giraldeau and Caraco, 2000). Thus, it would be interesting to examine the relationship between individuals' coping styles and their social learning abilities.

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