HOODED CROWS SOLVE A TRANSITIVE INFERENCE PROBLEM COGNITIVELY

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We investigated the ability of hooded crows to form transitive inferences. Subjects were trained to discriminate a series of overlapping pairs of stimuli: A+ B-, B+ C-, C+ D-, D+ E, where the letters stood for colour stimuli and plus and minus for rewarded or non-rewarded choices. The stimuli were cards of different colours with a circle of the same colour on the reverse side and diameters decreased from A to E. To preclude an influence of the reinforcement history on choices with the test pair BD, an overcompensation phase was instituted after training. It consisted of the presentation of all training pairs with frequencies selected so that the reward to non-reward ratios for stimulus D would be between 1.5 and 2.0 times greater than for B. If, during the BD test, the bird chose the stimuli according to these ratios they should prefer D. If they chose according to diameter relation they should prefer B. During these tests, the crows strongly preferred B over D (83.1%). In a second experiment, subjects were trained with the same procedure except that the diameters of the circles were all the same. During this test, the performance of two crows was not significantly different from chance level (53.1%), and the other two crows preferred D (80.0%). We conclude that crows can solve transitivity tests using cognitive mechanisms if they are offered additional information (in this case circle diameter) which, presumably, allows them to represent the relevant stimuli in an ordered series.

Keywords: *animal welfare, hooded crow, transitive inference, visual discrimination*

Introduction

A transitive relationship holds if, when a relationship *Rl* binds together stimuli *a* and *b*, and *b* and *c*, it also links stimuli *a* and *c*. Stimuli related in such a way yield a transitive series: *a Rl b Rl c*. If a subject is able to deduce from the two premises *a Rl b* and *b Rl c* the new relationship *a Rl c*, then we say that this subject is capable of transitive inference.

Transitivity-competent subjects should derive relationships between stimuli in a transitive series without any direct training of the transitive relationship. For example, if we know that Ann is taller than Betty and Betty is taller than Kate we can infer that Ann is taller than Kate even if we have never seen them together. Also, if Ann is the mother of Betty and Betty is the mother of Kate we can conclude that Ann is certainly not the mother of Kate. Moreover, if Ann is next to Betty and Betty is next to Kate, what we can say about Ann and Kate? If

they are standing in a line then Ann is not next to Kate, but if they are forming a circle then Ann is next to Kate (Evans *et al* 1993). This implies that competent subjects should be able to distinguish relationships which allow transitive inferences from relationships that are non-transitive.

An important application of inferential reasoning in the natural environment can be found in social group contexts (Kummer 1982). Some observations indicate that primates (eg hamadryas baboons [*Papio hamadryas*], Java monkeys [*Macaca fascicularis*] and chimpanzees [*Pan troglodytes*]) are able to comprehend the linear dominance rankings that exist within their group by observing dominance interactions among the members of the group (Rowell 1974; de Waal 1977). If a subordinate animal sees that B loses to A, and he himself has lost to B, he could conclude that A is superior to him and thus reduce the number of contests.

Birds are promising subjects for the comparative investigation of animal cognition in that they possess a specific type of brain structure characterized by the development of the hyper- and neostriatum nuclei instead of the neocortex in mammals. Nevertheless, the birds' hyperstriatum appears to be not only a functional analogue but also a morphological homologue of the mammalian neocortex (Karten 1991; Medina & Reiner 2000). Can we find similar cognitive abilities among representatives of primates and birds? To address this question we chose hooded crows (*Corvus cornix*), a species of corvid.

Corvids are characterized by a relatively high brain structure complexity (Stingelin 1958; Obukhov 1995) and by an ability to solve various types of complex cognitive tests (Koehler 1950; Kamil 1985; Wilson *et al* 1985; Mackintosh 1988; Krushinsky 1990; Zorina 1997). Further, their cognitive abilities appear to be comparable to those of monkeys in a number of tasks (Kamil 1985; Zorina 1997). Pigeons, the standard laboratory avian subjects, on the other hand, are not able to solve a number of complex cognitive tests which corvids can perform successfully (Wilson *et al* 1985; Krushinsky 1990; Zorina 1997).

Thirty years ago, Bryant and Trabasso (1971) devised a simplified method for presenting transitivity tests to very young children, and thereafter this paradigm was adapted into a fully non-verbal method by many researchers using different animals (pigeons [*Columba livia*] – von Fersen *et al* [1991]; Zentall & Sherburne [1994]; Zorina *et al* [1996]: crows [*Corvus cornix*] – Zorina *et al* [1996]: rats [*Rattus norvegicus*] – Davis [1992]; Roberts & Phelps [1994]: rhesus monkeys [*Macaca mulatta*] – Rapp *et al* [1996]; Treichler & van Tilburg [1996]: squirrel monkeys [*Saimiri sciureus*] – McGonigle & Chalmers [1977]; Harris & McGonigle [1994]: chimpanzees – Gillan [1981]; Boysen *et al* [1993]). It has been shown that all the species listed above were able to respond transitively. Nevertheless, the mechanisms that are responsible for the solution of non-verbal transitive tests still remain in dispute. Some researchers suppose that transitive responses are based on comparisons between internal representations of the stimuli's transitive interrelations (Gillan 1981; Davis 1992; Rapp *et al* 1996; Zorina *et al* 1996). Other investigators are inclined to believe that the mechanism involved is associative in nature and based on the reinforcement history accrued during the training (von Fersen *et al* 1991; Couvillon & Bitterman 1992; Wynne 1995; for a review see Siemann & Delius [1998]).

Experiment 1: transitive inference in hooded crows

The purpose of this experiment was to test the ability of hooded crows to derive the relationship between two stimuli B and D from a series of overlapping stimulus pairs and to

establish whether an associative or cognitive mechanism was responsible for the solution to this problem.

Subjects, apparatus, stimuli and statistical analysis

Four hooded crows, all more than 1 year old were used as subjects. Crows were caught when about 6 months old and housed in outdoor aviaries in small groups (2–3 birds). All birds were experimentally naive. Throughout the experiment, the birds had free access to water. Mealworms were used as a reinforcement, two worms for each trial, up to a maximum of 120 daily. Mealworms are the crows' favourite food and food deprivation was not necessary, though sometimes it was used at the beginning of the training. If crows refused to work during the training, they received food without animal proteins for 1 or 2 days. Daily experimental sessions were conducted 6 days a week and consisted of 40–60 trials.

A

B

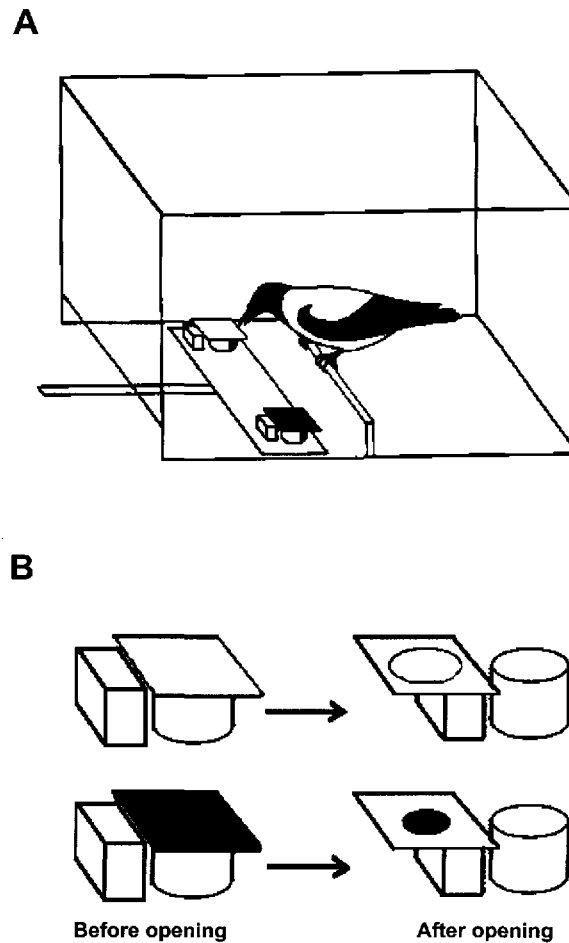Before opening   After opening

Figure 1   Schematic representation of the apparatus used: (a) bird in the experimental cage; (b) two cups with stimulus lids before and after opening.

Figure 1a shows the experimental apparatus. During an experimental session, a bird was placed into an experimental cage. At the beginning of the trial, a tray with two cups covered with lids was slid into the cage. One of the cups contained two mealworms. Both cups were covered with cards that served as lids. The upper surface of each card was of one of five colours (red, yellow, green, blue or black). This colour cue served as the primary stimulus. A circle of the same colour was drawn on the underside of each card (feedback stimulus). When the bird turned over a card it came to rest on a block placed behind the corresponding cup. The bird then saw a circle of the same colour as the upper side of the card (Figure 1b). The diameter of the circles decreased from red (6.5cm) to black (3.5cm; Figure 2a). After a correct choice, the birds usually also turned over the card on the wrong cup; if not, the experimenter turned this card for the bird. In the case of a wrong choice, the tray was immediately angled so that the crow could not reach the correct cup. The experimenter then turned over the correct card and left the tray in the bird's field of vision for 3–5 s before withdrawing it.

The differences between the number of correct responses in blocks of 10 trials and the chance level was assessed using the binomial test. Percentage choice score pairs were compared with t-tests. Different experimental groups were compared with Mann-Whitney U tests. The Statistica® (version 5.01) package (StatSoft Inc, Tulsa, USA) was used to do the analysis.

Training procedure

In order to have them form a transitive series, the birds were trained on a multiple discrimination task. It consisted of overlapping pairs of the stimuli: A+ B-, B+ C-, C+ D-, D+ E- where the letters stand for stimuli of different colours and the plus and minus symbols indicate that choices of the corresponding stimuli were either rewarded or non-rewarded (Figures 2a; 2b). During the training, a correction procedure (repeating the same trial until the right choice was made) was sometimes used. The number of correction trials was recorded at all phases of training. During the test phases, this procedure was not employed. The training was continued until a criterion of 80 per cent correct or better over 30 consecutive trials was reached within each training phase (binomial test; $P < 0.001$).

The four subjects were randomly assigned to two groups in order to avoid possible colour preferences (Figure 2a). The stimuli A, B, C, D and E were represented by red, yellow, green, blue and black, respectively, for group 1 (Zosja and Kotja), and by black, blue, green, yellow and red for group 2 (Dascha and Zelenaja).

During the first training phase, the crows were trained to choose A and to avoid B (Figure 2b). During the second phase, a new pair of stimuli was presented in which B was rewarded and stimulus C was not rewarded. The third phase involved the two previous pairs (A+ B- and B+ C-) alternated qausirandomly. During this stage, birds were expected to learn that stimulus B was rewarded when paired with C and not rewarded when paired with A. The same scheme was followed until the birds met the 80 per cent criterion for all four pairs (A+ B-; B+ C-; C+ D-; D+ E-).

All subjects learned the four training pairs (Zosja needed 524 trials, Kotja 882, Dascha 816 and Zelenaja 685, mean of 727 trials). Statistical analysis did not reveal any difference between the two groups (Mann-Whitney U test; $P > 0.12$) and their results were therefore pooled.
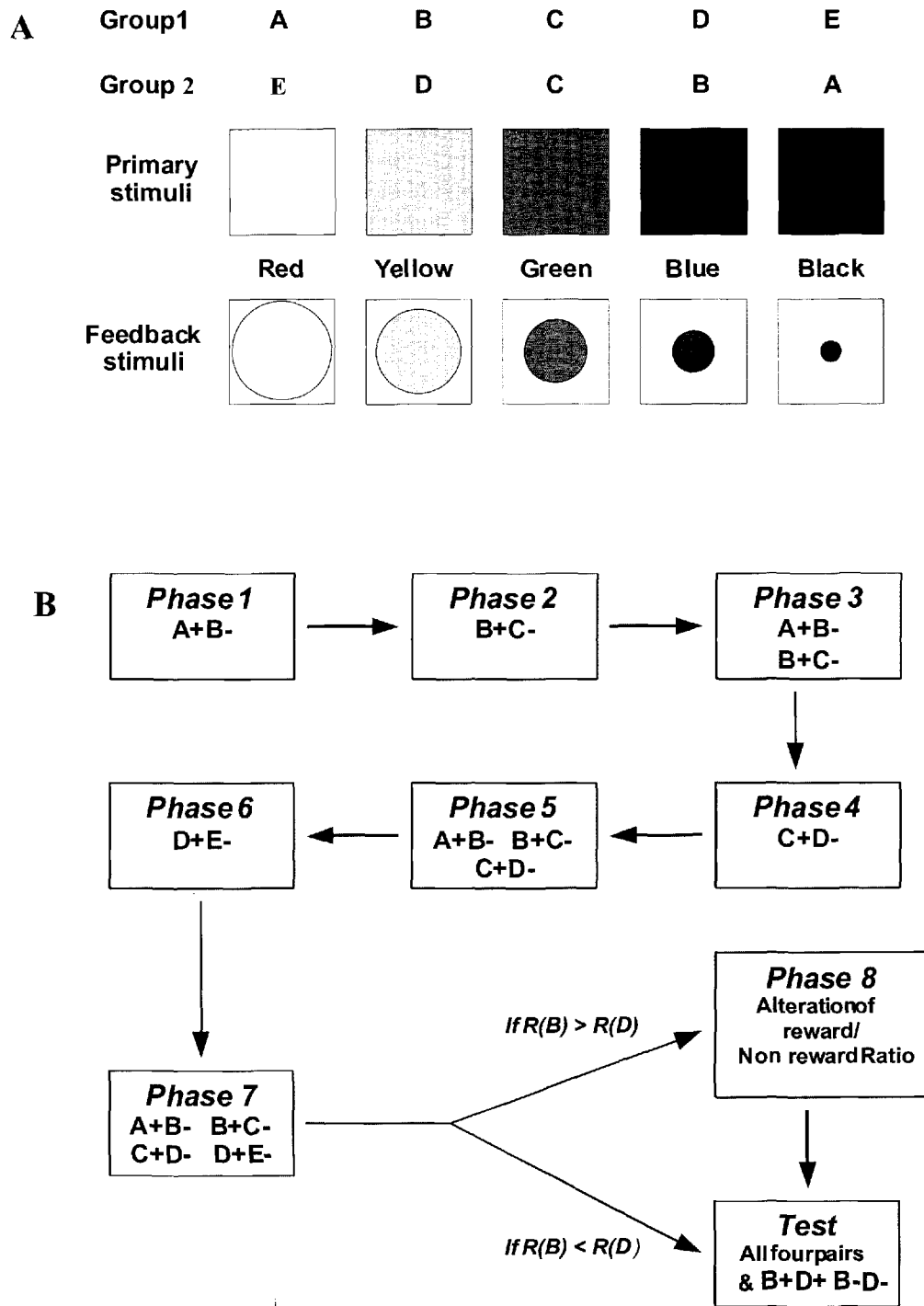
Figure 2   Design of the experiment: (a) primary and feedback stimuli for groups 1 and 2; (b) training and testing procedure for both groups.

Pre-test considerations and procedures

During training, the subjects were supposed to learn that the same stimulus may be rewarded or non-rewarded depending on the second stimulus in the pair. They could also learn that each primary stimulus was followed by a feedback stimulus (same colour circle of specific diameter) and that, within each pair, the larger (or smaller, depending on group) circle corresponded to the rewarded primary stimulus.

Transitive responding, by a generally accepted procedure, is tested with the B and D pair of stimuli, never presented together during training. This allows the researcher to test whether the subjects are able to deduce that, if B is larger (smaller) than C and C is larger (smaller) than D, then B must be larger (smaller) than D.

However, an alternative explanation is that birds may be able to solve the tests without using any such mental representation. They may simply choose from the test stimuli according to the different reward/non-reward ratios attached to the stimuli.

For instance, during Zosja's training stimulus B was rewarded 124 times and non-rewarded 58 times, whereas stimulus D was rewarded 54 times and non-rewarded 52 times, and the reward/non-reward ratio for B was therefore 2.1 and for D 1.0. Therefore, the subject could prefer B not because of comparing the internal representations of the stimuli, but because of the different probability of getting reinforcement for that choice. Many researchers (see Wynne [1995]; Siemann & Delius [1998] for reviews) have shown the presence of such a mechanism and its affect on stimulus choice in pigeons.

In order to assess the possible influence of the reinforcement history on the test pair BD, the number of rewards (N_r) and non-rewards (N_n) for each stimulus during all the training phases (including correction trials) was calculated. The reward/non-reward ratio ($R = N_r/N_n$) served to compare the value of the stimuli B and D. If the ratio for stimulus D was larger than that for stimulus B, the test phase was instituted: if not, the subjects were exposed to a so-called overcompensation phase (Figure 2b).

The overcompensation phase (phase 8) consisted of all four pairs of training stimuli presented with frequencies adjusted on the basis of the reward/non-reward ratios calculated before. In fact, the pair D+ E- had to be presented very frequently in order to augment the reward/non-reward ratio of D. As a result of this overcompensation phase, the reward/non-reward ratio of stimulus D was 1.5 to 2 times greater than that of stimulus B.

Following our example of Zosja: in planning the overcompensation phase we added 102 trials of D+ E-, and 10 trials with each of the three remained pairs (A+ B-, B+ C-, C+ D-). That would have adjusted the ratio of D to 3.0 if the subject had not made any mistakes during the phase. Actually, the subject performed at a high level (88.2%) but, because of some wrong choices, the final reward/non-reward ratio of D was 2.55.

Figure 3 shows the number of rewards and non-rewards for each bird before and after the overcompensation phase. After training, the reward/non-reward ratio for D was greater than for B for Kotja, Dasha and Zelenaja (Figure 3a) and they went directly to the test. As we mentioned above, Zosja was exposed to the overcompensation phase.

To summarize, if the birds choose the stimuli according to the reinforcement history during the test, they should all prefer stimulus D. If the birds compared the internal representations of the hierarchically organized stimuli stored in memory (in other words, used an inference-like process) then they should prefer stimulus B.
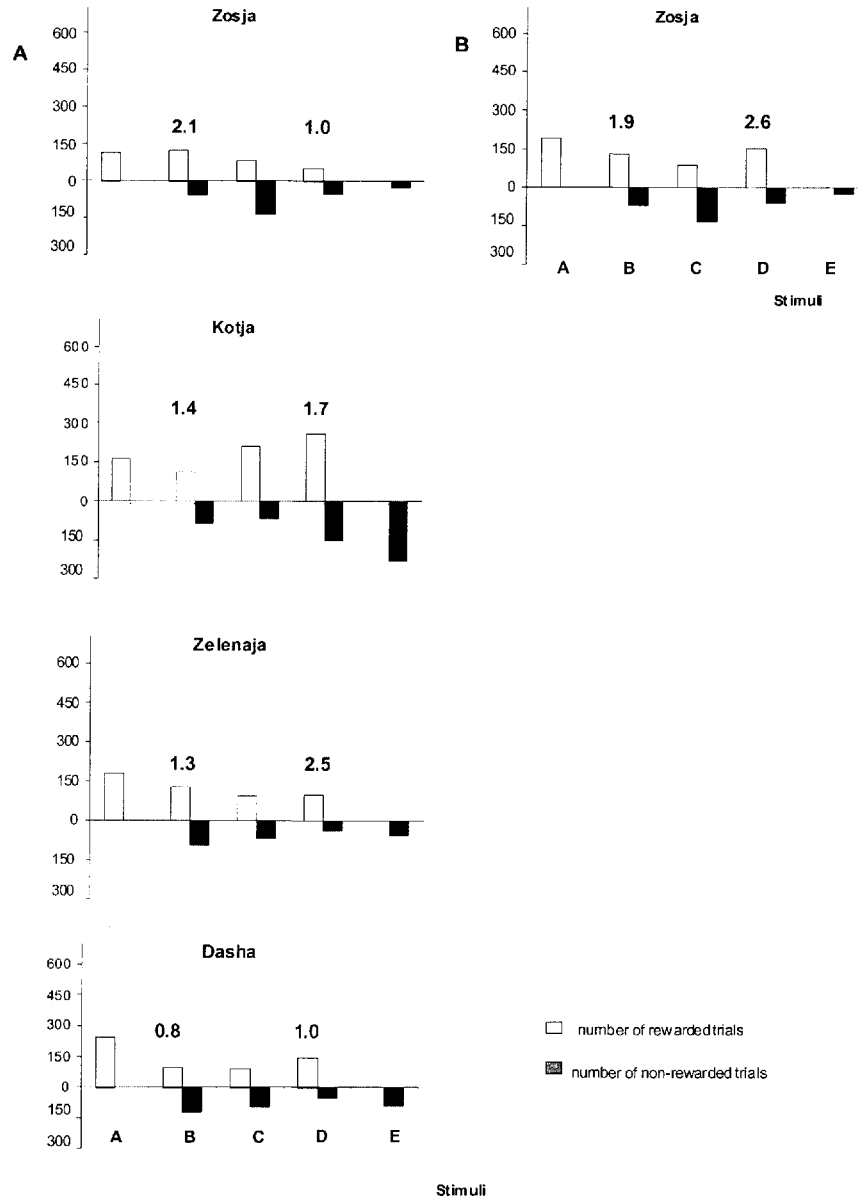
Figure 3   The number of rewarded (white columns) and non-rewarded (filled columns) trials in Experiment 1. Numbers above columns indicate the reward/non-reward ratio attached to the corresponding stimulus: (a) before the overcompensation phase; (b) after the overcompensation phase. Note that three subjects did not need an overcompensation phase (see text).

Test procedure and results

The test phase consisted of the presentation of all four training pairs and the new BD pair. Within the BD test, both stimuli were rewarded in half of the trials and not rewarded in the other half. Moreover, to prevent the birds from comparing the diameters of the circles during the test pair trials, both lids were never open at the same time. The test pair was presented 40 times, out of a total of 160 trials.

Figure 4a shows the performance with the training pairs and the test pair. All crows strongly preferred stimulus B over D (mean 83.1%) and this performance did not differ significantly from the performance with the training pairs (*t*-test; $P > 0.2$). Performance with all pairs was significantly above chance (*t*-test; $P < 0.01$).

It must be emphasized that the subjects could not explicitly respond to the diameters of the circles because they could only see these after choosing one of the primary stimuli. Remember that stimulus D had a much greater reward/non-reward ratio than stimulus B. The possible spontaneous preference of a colour also could not explain these results because for the first group stimulus B was yellow and D was blue, but for the second group the allocation was the reverse. It is concluded that crows solved the transitive tests on the basis of non-associative, cognitive mechanisms probably involving the construction of a mental series of the stimuli and comparing them during the test. For instance, crows of Group 1 were likely to remember that B was greater (by feedback stimulus diameter) than C and C was greater than D, then in the test compare representations of B and D (directly or using the intermediate C) and conclude that B was greater than D.

Experiment 2: are the feedback circle sizes important?

The purpose of this experiment was to find out whether the crows really could remember and use the information provided by the feedback stimuli to obtain a reward in the transitive test. The apparatus and procedures were the same as in Experiment 1 (Figure 2) except that all the feedback circles had the same diameter (6.5cm). Four new, experimentally naive subjects (Korsar, Solomon, Kondrat and Karolina) were used. As in Experiment 1, subjects were randomly assigned to two groups (Figure 2a) in order to avoid possible colour preference (group 1 consisted of Korsar and Solomon, group 2 of Karolina and Kondrat).

Training and test results

All subjects learned the four training pairs up to criterion (Korsar took 838 trials, Solomon 462, Kondrat 774 and Karolina 1050). The statistical analysis did not reveal any difference between the two groups (Mann-Whitney U test; $P > 0.12$) and their results were therefore pooled.

As shown in Figure 5, three subjects, Korsar, Solomon and Kondrat, were subjected to an overcompensation phase. With Karolina, the reward/non-reward ratios of B and D were 2.33 and 3.13 respectively. After the overcompensation phase, the reward/non-reward ratio of D was also greater than that of B in the three other subjects.

During the test, two of the four birds (Korsar and Kondrat) strongly preferred stimulus D over B (mean of 80.0%), whereas the performance of the other two (Solomon and Karolina) was not significantly different from chance level (mean of 51.3%).

Figure 4b shows the average performance with the training and test pairs during the test phase. The performance with the test pair BD was not significantly different from chance level (choices of B 35.6%; *t*-test; $P = 0.1$), nor was the performance with the training pair CD (mean of 63.1%; *t*-test; $P = 0.12$). The performance with the pairs AB, BC and DE was

significantly above chance (75.6%, 80.6% and 85.6% respectively; t-test; $P < 0.008$) and was not significantly different between pairs (t-test; $P > 0.13$). The performance with the test pair differed significantly from the performance with all training pairs (t-test; $P < 0.02$).
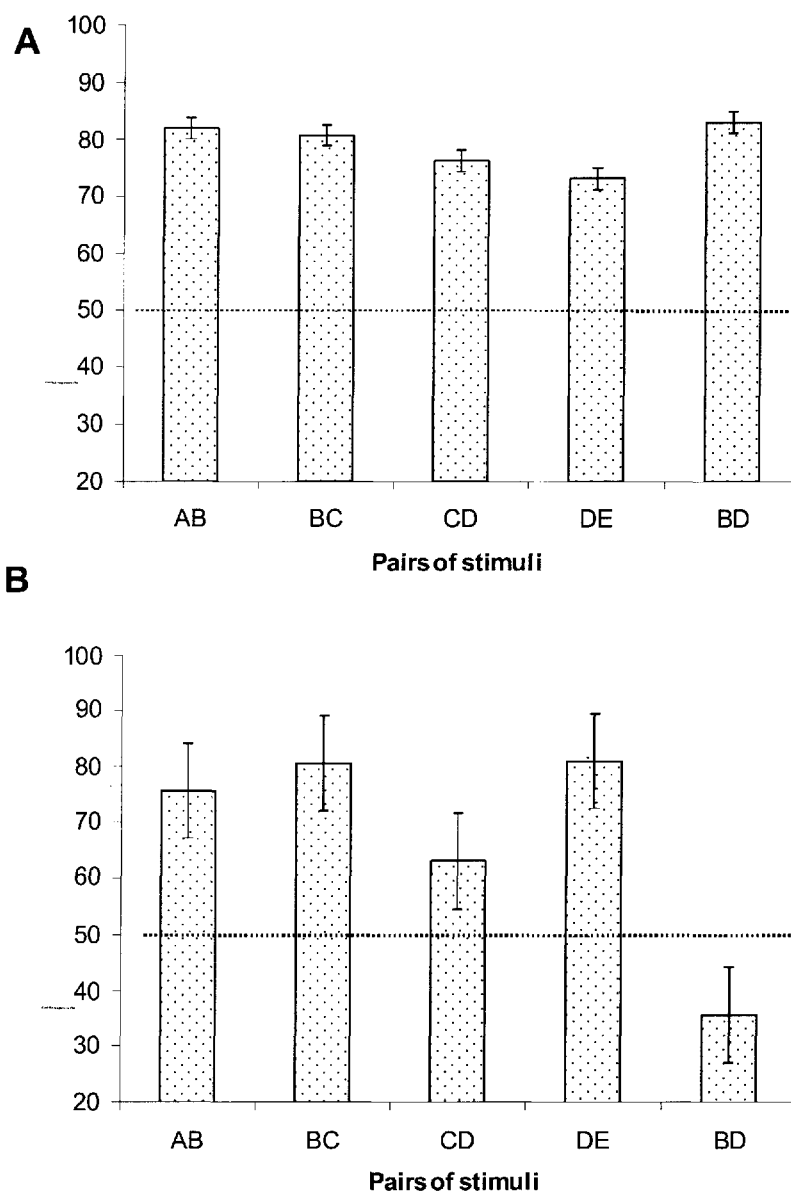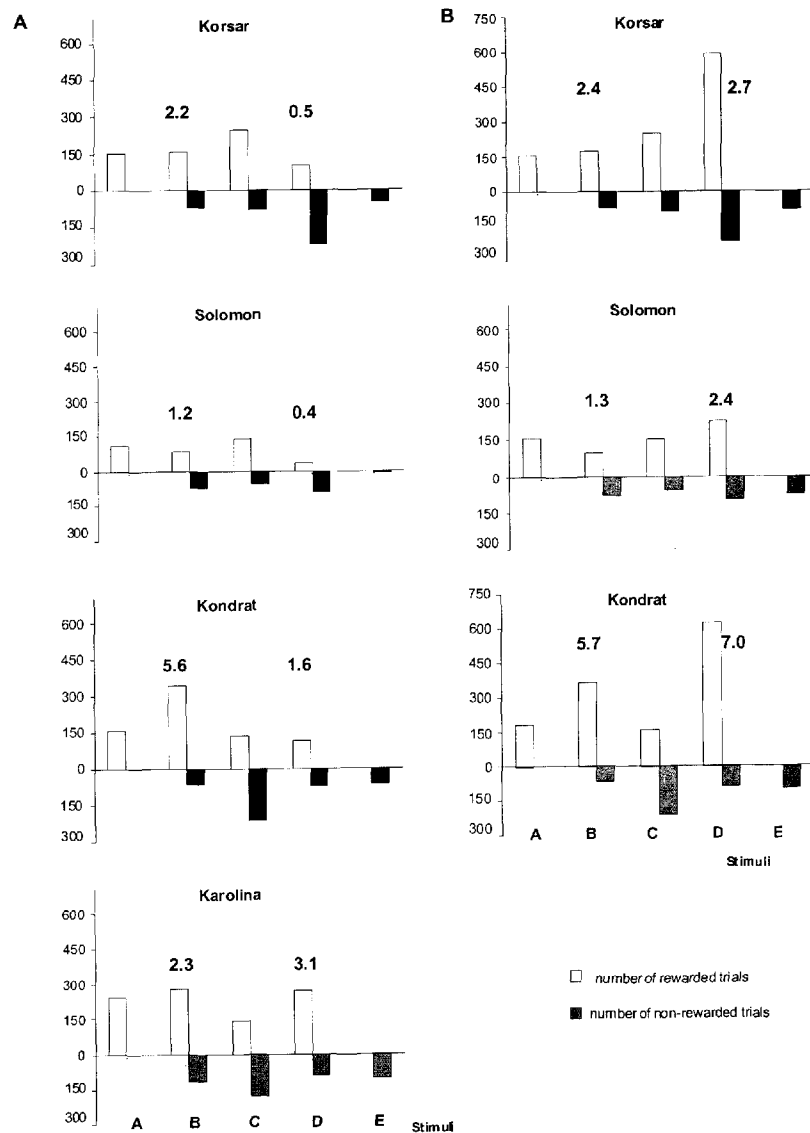

Figure 4   **Performance on training and test pairs: (a) Experiment 1; (b) Experiment 2.**

Figure 5 The number of rewarded (white columns) and non-rewarded (filled columns) trials in Experiment 2. Numbers above columns indicate the reward/non-reward ratio attached to the corresponding stimulus: (a) before overcompensation phase; (b) after overcompensation phase. Note that one subject did not need an overcompensation phase (see text).

Comparison of experiments

The acquisition of pre-test learning in both experiments did not differ significantly (Mann-Whitney *U* test; $P > 0.11$). We expected to find an end-anchor effect, ie a better performance

with the end pairs AB and DE than the middle pairs BC and CD, which has been observed in children and some animals (Bryant & Trabasso 1971; von Fersen *et al* 1991). For the first experiment, however, the statistical analysis did not reveal any difference between performance within the training pairs. In the second experiment, a significant difference was found between stimulus pairs AB and BD, BC and CD, BC and BD, and BD and DE (t-test for dependent samples; $P < 0.04$).

The performance with test pair BD was significantly better during the first experiment than during the second one (means of 83.1% and 35.6% respectively; t-test; $P = 0.03$). Note that in both of these experiments the design was the same except for the feedback stimuli: during the first experiment, the circles differed in diameter, whereas in the second they were equal. The crows appeared to be using the difference in feedback circle diameter to organize the primary stimuli into an ordered series. When this size cue was present they were capable of responding transitively but when it was absent they chose the stimuli randomly or according to the reward/non-reward ratio. Therefore, the transitive relationship between the stimuli seemed to be important for transitive inference formation in crows.

Conclusion

It seems unlikely that the results presented above could be explained using associative models; at least, not with those existing at present (von Fersen *et al* 1991; Couvillon & Bitterman 1992; Siemann & Delius 1998). Although they differ in some details, all of them predict very good performance with the end pairs AB and DE and poorer performance in the middle pairs BC and CD (end-anchor effect). However, in Experiment 1 there was no difference in performance between training pairs. It should be emphasized that associative models take into account the different stimulus values but not the differences in feedback stimuli, which seem to be essential in our experiments. But what happens if one removes from these the 'dimensional' cues, as we did in Experiment 2? Associative theories strongly predict that subjects should choose the stimulus with the greater reinforcement value, as did two of the crows. However, the performance of the two other birds (near chance level) can hardly be explained by the same kind of associative process.

Of course, we cannot exclude the possibility that some future associative learning model may explain the transitivity performance of our crows, but we suspect that it will need to incorporate some mechanism that implements an ordered linear representation of the stimuli. To work out a kind of model explaining the results obtained and to test it in a new experiment will be our goal for the next step of study.

Transitive inference formation is one form of inferential cognitive ability. Animals could use this type of reasoning in different everyday situations, which include comprehending the social interactions between the members of a social group and optimization of food searching. Our data support a hypothesis that not only humans and apes but also non-primates (crows) are capable of this rather high form of cognition. The extension of our understanding of animals' cognitive abilities can finally lead us from consumer-like treatment of different species to recognition of their rights.

Acknowledgements

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