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Ontogeny of object permanence in a non-storing corvid species, the jackdaw (*Corvus monedula*)

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Abstract

The aim of the present study was to investigate the ontogeny of object permanence in a non-caching corvid species, the jackdaw (*Corvus monedula*). Jackdaws are often presented as typical examples of non-storing corvids, as they cache either very little or not at all. We used Uzgis and Hunt's Scale 1 tasks to determine the age at which the certain stages set in and the final stage of this capacity that is reached. Our results show that the lack of food-storing behaviour is not associated with inferior object permanence abilities in the jackdaw, as our subjects ($N = 19$) have reached stage 5 competence (to follow successive visible displacements) at the average age of 61 days post-hatch and showed some evidence of stage 6 competence (to follow advanced invisible displacements) at 81 days post-hatch and thereafter. As we appreciate that object permanence abilities have a very wide ecological significance, our positive results are probably the consequence of other, more fundamental ecological pressures, such as nest-hole reproduction or prey–predator interactions.

Keywords

Object permanence; Jackdaw; Ontogeny; Non-storing; Corvids

Introduction

In the physical world that we share with countless organisms, both animate and inanimate objects tend to move through space. The ability to follow these appearing, disappearing and perhaps reappearing objects is of unquestionable advantage to virtually any organism; indeed, it is crucial for any animal's survival. When following the movement of an object,

an individual may rely on a number of signals, visual, olfactory, auditory (Etienne 1984). However, when an object disappears without leaving such perceptual cues, following its movements requires some cognitive tools, such as mental representation of the object as a distinct entity and the ability to understand that objects continue to exist, even when temporarily out of sight of the observer.

In children, object permanence develops over the first 2 years of life in a staggered manner. Piaget (1954) has shown that children develop their understanding about temporarily invisible objects in distinct stages, which each correspond with a specific age. Before children start to search for an object that they have seen disappear, they are still in stage 1 according to Piaget. At stage 2, children become capable of visual pursuit a moving object, while at stage 3, they can retrieve a partially covered object. At the beginning of stage 4, infants are only able to find a hidden object if a grasping movement has been initiated at the time of disappearance (stage 4a), while later (stage 4b), this condition is no longer a prerequisite to recover the object (single visible displacement). However, in stage 4b, infants remain unable to solve a sequential visible displacement (where the object is fully visible during the manipulations). They are prone to the so-called A-not-B error, as they search for the object where they previously found it even though they saw the object hidden in another location. In stage 5, the A-not-B error has disappeared, and infants solve problems with a sequential visible displacement (stage 5a) and successive visible displacement (stage 5b). In stage 6, infants master first (stage 6a) problems with a single invisible displacement (when the object is hidden first in the hand or in a container and then is moved behind a cover). Then, in stage 6b, problems involving sequential invisible displacement and successive invisible displacements are mastered.

Object permanence is a fundamental cognitive skill that may serve as basis for more complex cognitive mechanisms in animals as well as humans. Moreover, the comparative study of infant development and animal cognition might be very useful in gaining information on the nature and evolution of cognition (Gomez 2005), while it is undoubtedly important to keep in mind the possibility that similar abilities in different species may be based on different mechanisms. The presence of object permanence capacity has been extensively studied in many species, including several avian species (Dumas and Wilkie 1995; Etienne 1973; Funk 1996; Funk and Matteson 2004; Pepperberg et al. 1997). Some of these studies (Gomez 2004; Doré and Goulet 1998) have revealed that many species develop object permanence skills in the same sequence as children, only at different speeds. Though in some aspects criticised by some researchers (Bower 1982; Baillargeon 1987; Doré and Dumas 1987), the Piagetian framework has been recognised as a very useful tool tracking the existence of the developmental stages, and also for comparative research, as the tasks involved may be administered with minimal variation to very different species, so differences revealed cannot simply be explained by different experimental procedures (Pepperberg 2002).

Corvid cognition is generally considered quite advanced. According to recent views, it may even parallel primate cognition in several aspects (Emery and Clayton 2004). Most of the intriguing evidence of these highly specialised mechanisms come from studies conducted in a food-storing context (e.g. Balda and Kamil 1992; Bednekoff and Balda 1996a, b; Clayton

and Krebs 1994; Dally et al. 2005; Heinrich and Pepper 1998). These studies show that food-storing corvid species have an excellent spatial memory; some are capable of recalling cache sites even many months after the cache was made; moreover, some can recall also the type of item cached at the particular places as well as when the cache was made, suggesting the presence of “episodic-like memory” (Clayton and Dickinson 1998). They also seem quite capable of handling the social aspects of caching, as there is a growing amount of evidence in corvids for phenomena such as gaze following (Bugnyar et al. 2004), visual perspective taking (Bugnyar and Heinrich 2005; Dally et al. 2006) and tactical deception (Bugnyar and Kotrschal 2002). The capacity to remember numerous cache sites for sometimes extended periods of time, in sum excellent performance in studies of spatial memory, has been associated with a relatively larger hippocampus in food-storing corvids (Healy and Krebs 1992; Shettleworth 2003).

Considering all this information on a wide range of food-storing species, we know surprisingly little about the cognitive capacities of non-storing corvids. Jackdaws are one of the few Old World corvids caching very little or no food and have been shown to have a relatively smaller hippocampus (Healy and Krebs 1992) than their caching relatives, which might affect their performance in spatial memory tasks. Scheid and Bugnyar (2008) have shown that foodcaching ravens are much more efficient in observational spatial memory tasks than non-caching jackdaws. However, very little attention has been paid to how these differences may affect other related cognitive abilities. Among many others, the development and final stage of object permanence has so far only been studied in food-storing corvids. Eurasian jays (*Garrulus glandarius*) (Zucca et al. 2007) and ravens (*Corvus corax*) (Bugnyar et al. 2007) have been shown to have stage 6 competence, while magpies (*Pica pica*) (Pollok et al. 2000) also reached stage 6 while showing a particular anomaly.

To assess the ontogeny of object permanence and the final stage reached in a non-storing corvid species, we have conducted a series of experiments on 19 hand-raised jackdaws (*Corvus monedula*). In order to obtain comparable data to recent studies on caching species (Pollok et al. 2000; Bugnyar et al. 2007; Zucca et al. 2007; Salwiczek et al. 2009), we have used the same methodology, namely the Scale 1 series of tasks from Uzgiris and Hunt (1975) (see also Pepperberg et al. 1997 and Pepperberg 2002) and one additional test, the so-called “Shell game” to further assess the question of stage 6 competence (Sophian and Sage 1983, Sophian 1985). Despite criticism of this method, mainly on the “face-to-face” nature of the testing and the possible training of subjects (habituation or learning) in the course of testing, we have decided in favour of using it primarily for the sake of comparability. Another positive aspect of Scale 1 is that specific subsets of these tasks directly correlate with Piagetian stages, but provide finer divisions of these stages, possibly yielding more detailed information.

Methods

Subjects

We hand-raised 20 young jackdaws (*C. monedula*) to participate in this and some other experiments in spring, 2005. The hand-raising and the testing took place at the Konrad Lorenz Research Station in Grünau, Austria. The jackdaws were taken from nests in

Stralsund and in Baden-Württemberg, Germany, with appropriate licences, in between the age of 13 and 20 days post-hatch. After their capture, they were kept in cardboard boxes, 2, 3 or 4 birds together, lined with hay and kitchen towels, until they fledged at between 26 and 31 days of age. A few days after fledging, they were moved to a spacious outdoor aviary, approximately 12 m × 10 m and about 4–5 m high. The aviary was fully equipped with perches, sheltered shelves, a tray of bathing water, and the floor was covered by natural vegetation. A small experimental complex, consisting of 5 compartments, was connected to the main aviary by a wooden door and a wooden window, so the experimental areas could be fully visually separated from the main aviary (for rough plan of the premises see Fig. 1). The floor of the experimental complex was covered with fine-grained gravel. During most of the day, when no testing was in progress, the birds were free to roam in the entire main aviary and the experimental complex as well.

While still in the nest, the birds were fed with a wet mix consisting of ground beef, hard boiled egg yolk, cottage cheese and a commercially available dry insect mix. Bird vitamins and ground cuttlebone were mixed into the food. On hot days, additional water was provided through syringes. After moving to their outdoor aviary, the birds continued to be fed on this mix, but gradually other various foods were introduced such as fruits, vegetables, pasta, rice, potatoes, milk products, mealworms, crickets and dry cat food as treats.

All of the subjects participated in object permanence testing except as noted below, for exact number of subjects in each task, please see Table 1. One very shy bird, Dominique, had to be excluded from testing before task 5, as it became extremely reluctant to enter the experimental complex. From this point on, the total number of subjects was 19.

To assess criticisms of “Scale 1” concerning training and learning throughout the testing procedure, we divided our subjects randomly into 3 groups. The subjects of our first group ($N = 8$) were tested on all tasks. The subjects of our second group ($N = 5$) were tested on only every second task from task 4 onwards (namely on tasks 6, 8, 10, 12 and 14), while in the third group ($N = 6$), subjects skipped tasks 5–9 and resumed testing on task 10. All birds ($N = 19$) were tested on task 15. The aim of this was that if there is a training effect altering the age at which a certain task is passed, then we should be able to find a difference in the performance of our groups, due to the different amount of testing.

A total of 10 subjects ($N = 10$) participated in this task “S”, the Shell game, five from Group 1, one subject from Group 2, and four from Group 3.

Procedures

Tasks

Stage 2 (*visual pursuit*)

Task 1: Subject succeeds in this task if it is able to track an object moving slowly around the bird in a horizontal plane through an arc of 180°.

Task 2: A moving object disappears behind a screen. Success is demonstrated in this task if the bird looks at the point of disappearance or returns its glance to the starting point, after several presentations.

Stage 3 (simple visible displacements-partial hiding)

Task 3: An object is partly hidden under a single cover that is laid on the table. The criterion of success is met when the subject obtains the object either by pulling it from under the cover or by removing the cover and then taking the object.

Stage 4 (simple visible displacements-complete hiding)

Task 4: An object is completely hidden under a single cover laid on the table. The criterion of success is met if subject removes the cover and picks up the object. Search was only allowed to begin when the hiding process was completed.

Stage 5 (simple and complex visible displacements-multiple covers)

Task 5: Two covers, A and B, were used. The object was hidden three times under one cover (A in the case of 10 birds and B in the case of the other 10), and then, it was hidden under the other cover. Criterion performance was immediate search under the cover where the object has been last hidden. Errors in this task, namely continued search under the first cover (so-called A-not-B errors), characteristically precede stage 5 competence in human infants.

Task 6: Two covers, A and B, were used, but the object was hidden alternately under the two different covers. Criterion performance was to search immediately under the cover where the object was last hidden.

Task 7: Three covers, A, B and C, were used. The hiding place of the object varied between the three covers. Criterion performance was to search immediately under the cover where the object was last hidden.

Task 8: In this task, the object was held visibly in the hand of the experimenter, was passed successively under two of the covers, and then was finally hidden under the third cover. Success in this task is demonstrated only if the subject searches directly under the final hiding place. Searching in the order of the hiding is incorrect.

Task 9: In this task, the three covers were laid on top of each other and the object was hidden under them, so to meet criterion the subject had to remove all three superimposed covers to obtain the object. This task is meant to test the subjects' persistence.

Stage 6: (invisible displacement tasks, in which only the implementing cover is visible, thus inferential abilities are required to track object)

Task 10: One standing screen (set up perpendicular to the plane of the table) and a small non-transparent container were used. The object was placed into the container, then the container with the object inside was moved behind the screen and the object was hidden there. Finally, the empty container was shown to the bird. Criterion performance was

indicated if the subject checked the container, then retrieved the hidden object from behind the screen, or went straight to the screen to retrieve the object.

Task 11: Two standing screens (A and B) and a small non-transparent container were used. As in task 5, the object, concealed in the container, was hidden three times behind one screen and then hidden behind the other screen. The hiding was similar in other ways to the hiding in task 10. Success is demonstrated by the subjects if they immediately start searching behind the screen where the object was hidden.

Task 12: The container concealing the object was moved alternately behind the two screens (A and B), where the object was then hidden. The hiding was similar in other ways to the hiding in task 10. Criterion performance was immediate search behind the screen where the object was hidden.

Task 13: The object travelling in the container was hidden behind one of three screens (A, B or C). The hiding was similar in other ways to the hiding in task 10. Criterion was immediate search behind the screen where the object was hidden.

Task 14: Three standing screens (A, B and C) were used. The object was placed visibly in the palm of the experimenter, who then closed her hand thus concealing the object. The closed hand was passed behind two screens, and then finally, the object was left behind the last screen. The empty hand was shown to the subject. The sequence of the displacement was either ABC or CBA. The criterion was searching all screens in the same order as the hand moved and finding the object under the last screen. If the subject has previously found the object under the last screen, in this situation, going only to the last screen and finding the object was also acceptable.

Task 15: Very similar to task 14, except that it is a “trick”, as the object was left under the first screen visited by the closed hand, but the hand moved on, leading the subject to believe that the object will be hidden under the last screen. The criterion here was to search the screens in reverse order. For alternatives in the interpretation of performance in this task, please see “Results” and “Discussion”.

Task S (“Shell game”): We also tested our birds on a task, testing for attention, spatial cognition and different memory types, as well as object permanence abilities, similar to the one suggested by Doré et al. (1996). This procedure was initially introduced in infant studies by Sophian and Sage (1983) and Sophian (1985). Three non-transparent containers were used in this task, with the object visibly hidden in one of them. After hiding the object, the experimenter visibly changed the position of the baited container relative to the other two. Task S included seven trials, in five of which the baited container changed its relative position, while in the remaining two, the baited container remained in place and another container was moved to a different position, so unlike the first five trials, the subject had to choose a container that remained in place in order to obtain the reward. These two trials were intended to control for stimulus/local enhancement.

Exact manipulations involved in the trials of task S are shown in Fig. 2.

Apparatus

When we started our experiments, our subjects were still in the nest boxes and were unable to feed on their own. Apart from this, they were unable to ingest relatively large and hard items, which would have been suitable to use as search items. For this reason, we have started testing with non-food objects, namely pieces of shiny tin foil (approx. 1 cm × 3 cm) in which the birds were particularly interested. After task 4 was passed, we found that our birds became less interested in non-palatable objects, but were increasingly motivated by cat food treats, so we used these treats as search objects from that task onward. We used brown cardboard squares (10 cm × 10 cm) as screens. They were slightly bent and crumpled in the middle to give full coverage, so the baited screen provided no visual cue to the position of the hidden object. All the screens used were identical without any markings. Where several screens were used, they were placed approximately 30 cm from each other. On tasks testing invisible displacements, we used a small brown cardboard container (5 cm × 4 cm × 3 cm) and the screens were set up perpendicular to the plane of the table, as we found it easier and less confusing to subjects to pass behind them with the container, rather than trying to pass under them. For the Shell game, we used 3 small cardboard containers similar to that used previously in invisible displacement tasks.

Although the relative importance of the sense of olfaction to birds seems to vary greatly between avian species (e.g. Harriman and Berger 1986), and for example, Gagnon and Doré (1992) argue that odour cues are unimportant even for creatures with an olfactory sense as sensitive as dogs', we wished to control for this possibility due to such criticism in connection with Scale 1 (Pepperberg et al. 1997). In order to do this, when starting to use food as search items, we stored all the objects used in the tasks in actual physical contact with the search items (cat food), so that all objects acquired the odour of the treats, to avoid the possibility of olfactory cueing.

Procedure of testing

Testing began 12 days after acquiring the birds (at age 25–32 days old), when they were still in their nest boxes, prior to fledging. The testing for the first tasks (1, 2 and in some cases 3) was conducted while the subjects were still in their nest boxes. After the birds moved to their outdoor aviary (ages 21–36 days post hatch), the testing was conducted in one of the compartments of the experimental complex on a table (100 cm × 70 cm) put there for this purpose.

Testing sessions took place every day when the weather allowed, but subjects were never tested on a particular task on two consecutive days, and in general, we attempted to expose each individual to a given task as few times as possible to avoid trial-and-error learning or conditioned responses. On the other hand, we aimed at testing each subject at least every 3 or 4 days as not to miss the exact onset of capability of passing a certain task or stage.

At the beginning of each testing session, the birds were called (vocally and offering treats) into the experimental complex through the door. Usually, more than one subject entered initially, as some birds were especially keen on participating. The door was then closed. The birds that entered were allowed to stay in the first compartment, and only one subject at a

time was allowed to enter the actual compartment where the testing took place. Testing for a particular subject was terminated for the day if it performed an incorrect response. On making a wrong choice, the subject was immediately shoed out and was never allowed to continue searching, so it could never observe where the item had actually been hidden. In order to pass a task, the subject had to respond correctly on 3 consecutive trials in one session without errors. From task 5 onwards, we considered a task passed if the bird had made 3 correct responses and no errors. This change was made as the tasks became increasingly complicated and we wished to accurately pinpoint the onset of a certain stage as well as aiming to avoid training (learning, habituation) due to overexposure to a task.

When testing was finished for the day for a subject, it was let out into the central part of the experimental complex until all subjects had completed their testing, and then, the whole flock was allowed back to the main aviary. Calling the subjects in from the main aviary was repeated when all the birds in the first compartment had completed testing and transferred into the central part, until eventually all the birds had their testing session. The birds were physically, but not visually separated from their flock mates at the time of testing, but neither the birds in the first compartment, nor the birds already in the central part had a direct view of the table and the manipulations taking place there. The voluntary nature of testing and the lack of total visual separation from the others resulted in the birds being relaxed and motivated in the testing situation, which is very important when trying to assess cognitive abilities, as stress may impair performance in such experiments (e.g. de Kloet et al. 1999; Weir and Kacelnik 2006).

The experimenter was seated while she manipulated the objects, and the birds were sitting on a perch level with the height of the table and about 15 cm away from the edge of the table and altogether approximately 50 cm away from the set-up. The manipulations took place when the bird was paying attention and was seated on the perch. When the manipulations were complete, the experimenter lowered both of her hands to her lap and looked up, away from the set-up and directly at the bird. If the bird initiated search before this position was taken by the experimenter, it was not allowed to make the choice. Bearing in mind the dangers of experimenter cueing in this face-to-face testing situation, the outmost care was taken as not to influence the choice of the bird in any way. When the experimenter had taken up this neutral position, the bird was allowed to jump onto the table and search freely.

Data analysis

We used Kolmogorov–Smirnov tests to check normality of our data for each group and each test (data were grouped by task and by group). As we found that some of our datasets were not normally distributed, we proceeded to use non-parametric analyses. To compare the performance of three groups, we used Kruskal–Wallis tests with a Dunn’s Multiple Comparisons test where necessary, while when comparing only two of our groups, we used Mann–Whitney *U* tests. To assess possible correlations between the numbers of sessions when birds have committed errors and their performance in object permanence tasks, we used Spearman’s Rank Correlation test. To determine the mean age of passing a task, data from all three groups were pooled.

Results

Mean age of the subjects at passing Scale 1 tasks

For detailed results on the mean age of passing each task, please see Table 1.

The subjects were generally able to master all the tasks of Scale 1 administered to them. An exception from this is the heterogeneous performance showed in task 15, as will be explained later in this section. The onset of competence in a certain task occurred roughly at the same age in all subjects, although there was considerable age difference in the flock.

In summary, we found that our birds were capable of comprehending single visible displacements (task 4, stage 4b) by the mean age of 41.45 ± 6.09 (SD) days, successive visible displacements (task 8, stage 5b) by the mean age of 57.64 ± 7.44 (SD) days, single invisible displacements (task 10, stage 6a) by the mean age of 61.21 ± 6.84 (SD) days and successive invisible displacements (task 14 stage 6b) by the mean age of 74.3 ± 7.72 (SD) days. See Fig. 3.

Describing the results in more detail, we can say that all of the subjects ($N = 20$) were able to master task 1 (tracking movement of an object through an 180° arc) and task 2 (looking at the point of disappearance when object disappears behind a screen) when testing began (at age 25–32 days old, in nest boxes, prior to fledging).

Task 3 (partly hidden object) was mastered at the mean age of 36.6 days (± 4 SD) post-hatch, while task 4 (completely hidden object) was mastered at the mean age of 41 days (± 6.1 SD); in the case of both these tasks, the number of subjects was 20. Passing task 3 mainly occurred on the second session, so on the first possible occasion according to our criterion.

As mentioned before, after passing task 4, we randomly assigned our subjects into 3 groups. All birds, except the one that was excluded, were tested on task 15. Table 1 shows the number of subjects participating in certain tasks and the mean age at which tasks 5–15 were mastered by the birds. Regarding task 5, it is important to note that some of our subjects (2 birds out of the 8 subjected to this particular task) made characteristic A-not-B errors, meaning that they kept searching under the first cover even when they witnessed the bait being hidden under the second cover. We feel that it is important to state this fact, keeping in mind that the issue of A-not-B errors is a key question of object permanence related studies; however, we find that our data are not sufficient to draw any conclusions as to the possible causes of this phenomenon.

As we have mentioned before, and similarly to the findings of Pollok et al. (2000) in the case of magpies, our subjects showed inhomogeneity in their performance in task 15. Out of our total 19 birds subjected to this task, 14 birds eventually passed this task according to our original criterion, searching the screens in reverse order. However, 5 individuals did the same in this task, as they had done in the previous one, attempting to follow the route of the hand concealing the desired item, and thus, they found the item straight away under the first screen. This is exactly the same as Pollok et al. (2000) found in case of caching magpies. As this trick task only makes logical sense if performed following task 14, we attempted to retest these subjects after administering task 14 again, but they did not change their original

strategy even after the third such session. As this response is just as logical as the criterion response from another point of view, we abandoned their testing. However, due to the uncertainty concerning task 15, we proceeded to perform task S, to further assess stage 6 competence.

Task S (“Shell game”)

As described before in the “Procedures” section, this extra task was designed to test for attention, spatial cognition and different memory types, as well as for stage 6 object permanence abilities. As mentioned in the “Subjects” section, 10 subjects ($N = 10$) participated in this task, five from the original Group 1, one subject from Group 2, and four from Group 3. Three of these 10 were the birds showing particular difficulties with task 15 (as mentioned above), so these birds were by no means excluded from further investigations into stage 6 competence. As the five trial types are identical in their logic, and so are the two stimulus/local enhancement controls, the performance of each bird was calculated as a percentage of correct responses per the total amount of trials in both test and control trials. Their performance was then compared to a 33 % chance level, using Wilcoxon’s signed rank test (Thas et al. 2005), as there were three possible boxes to choose from in this task. We found that the performance of the birds in the Shell game was significantly better than chance ($T+ = 55.00$, $P = 0.002$). Their performance in the stimulus/local enhancement control trials was also significantly above chance ($T+ = 55.00$, $P = 0.002$). See Fig. 4. These data suggest that jackdaws are capable of following complex invisible displacements, as well as being able to track and remember (at least for a short duration) spatial information about hidden objects, so this result may be considered as further evidence of stage 6 competence.

Comparing the performance of the three groups

Our hypothesis was that if there is a training effect altering the age at which a certain task is passed, then we should be able to find a difference in the performance of our groups, due to the different amounts of testing. We compared performance of the groups in all tasks performed after their division following task 4. In the case of tasks which all three groups participated in, such as tasks 10, 12, 14 and 15, we used a Kruskal–Wallis test. In case of tasks 10, 14 and 15, we did not find a significant difference in the performance of our groups, while in task 12, there was a marginally significant difference ($\chi^2 = 6.287$, $P = 0.043$), but this result was not affirmed by the Dunn’s Multiple Comparisons test. See also Fig. 5a–d. In the case of those tasks where only two groups participated, such as tasks 6, 8, 11 and 13, we used a Mann–Whitney U test, but failed to find a significant difference between the performances of our groups. This lack of difference shows that the uneven amount of experience in testing situations had no effect on the age of passing a task. Becoming capable of such performance follows the birds’ ontogenic development, rather than being an effect of training.

Testing for possible correlations between the number of sessions when an error was made and age of passing a task

The number of sessions with errors before passing a certain task may be found in Table 2 for each individual. This confounding variable may potentially influence the age at which an individual passed a task, or reached a stage. To more precisely assess the possibility of learning and habituation during the testing procedures, we calculated the cumulative number of sessions when at least one manipulation was made, and thus, one search was initiated by the bird, but an error was made and session the was terminated. Theoretically each of these sessions would give an opportunity for the subject to gather information about the testing situation and so could alter the age of passing a certain task. To assess potential correlations, we used Spearman's Rank Correlation for nonparametric data. As no significant difference between the groups had been found, data from all groups were pooled.

We found no significant negative correlations between the number of sessions with errors and age in days at passing a task, meaning that birds with more experience did not reach a stage sooner. On the contrary, some significant positive correlations were found in case of task 3 ($r_s = 0.638$, $P = 0.002$, $N = 20$), task 5 ($r_s = 0.783$, $P = 0.022$, $N = 8$), task 7 ($r_s = 0.925$, $P = 0.001$, $N = 8$), task 8 ($r_s = 0.859$, $P < 0.001$, $N = 14$), task 9 ($r_s = 0.988$, $P < 0.001$, $N = 8$), which means that in some cases, the more prior experience birds had, at the later age were they able to master a certain task. This phenomenon may be caused by the fact that the birds were developing considerable neophobia (see also Zucca et al. 2007), which affected some individuals more/sooner than others. For example, 5 birds out of the 14 needed as many as 5 or 6 sessions before being able to pass task 81. This task is the first task in Scale 1 with successive displacement, thus by nature is considerably more complicated than those preceding it. Therefore, this task is also a sub-step of the Piagetian stage 5. Given our testing procedure (testing subjects every 2–3 days), we may have started testing for this ability at too early an age, aiming not to miss out on the onset of this capacity. However, the rest of the birds (9 individuals) needed two or less sessions. This heterogeneity in the performance leads us to think that perhaps this is again an issue of some of our birds being affected by increasing neophobia.

Discussion

We found that, interpreted at a group level, jackdaws achieve stage 6 object permanence abilities relatively quickly. In order to test the hypothesis that the birds' development follows the Piagetian stages, we would have had to have subjected our birds to all the tasks at all ages, which was naturally not practicable. Our data suggest that the birds passed most tasks roughly as soon as they were faced with them. An exception from this is task 8, where it may well be possible, that we had to wait for the birds' cognitive maturation to catch up with our testing schedule. Because of the above, our data do not provide sufficient evidence that jackdaws progress through the stages in a fixed sequence, as using the sequential tasks of Scale 1 had given us no opportunity to explore this question. Thus, our findings neither corroborate nor refute the hypothesis that jackdaws acquire object permanence abilities in a fixed sequence, following the Piagetian stages.

However, we have shown the maximum ages by which jackdaws become capable of passing Scale 1 tasks. We suggest that our results reflect a process of maturation rather than training and experience during trials, as our subjects in the three groups had different amounts of experience, yet still they developed object permanence abilities at roughly the same ages. We attempted to assess the possibility that the number of sessions with errors prior to the certain tasks may have affected the age of passing them, and we found no evidence that more “practice” had any effect on the performance. This confirms our results from comparing the performance of the three groups, namely that the performance in the tasks of Scale 1 reflects a maturation process and is indeed not an effect of some kind of training, learning or habituation.

Jackdaws acquired object permanence abilities similar to those found in children (Piaget 1954; Baillargeon and DeVos 1991) and some other animal species (Gagnon and Doré 1994; Gomez 2005; Dumas and Wilkie 1995; Funk 1996).

Unlike parrots (Pepperberg et al. 1997; Funk 1996) but similarly to other corvids (Bugnyar et al. 2007; Pollok et al. 2000), jackdaws reach stages 4 and 5 relatively quickly. Our subjects ($N = 19$) have developed stage 5 competence (the ability to follow successive visible displacements) at an average age of 61 days post-hatch and showed evidence of stage 6 competence (the ability to follow advanced invisible displacements) at 81 days post-hatch and thereafter. Only Eurasian Jays have been reported to acquire stages quicker than jackdaws (Zucca et al. 2007). The relatively early development of object-related competence is in accordance with the generally faster maturation and overall development of jackdaws compared to food-storing corvid species, such as magpies (Pollok et al. 2000) and ravens (Bugnyar et al. 2007). Like great apes (Call 2001), kakarikis (Funk 1996) and grey parrots (Pepperberg et al. 1997), but unlike cats and dogs (Doré et al. 1996), and most interestingly magpies (Pollok et al. 2000) and Eurasian jays (Zucca et al. 2007), two out of eight of our jackdaws subjected to task 5 committed characteristic A-not-B errors. The differences in this matter might possibly be due to slight methodological differences in the numbers of times (in our case 3) the object was hidden under a certain cover before moving the hiding to the other cover. The A-not-B errors observed might be caused by a local enhancement effect rather than object permanence related issues; however, we feel that based on our data, it would not be possible to draw any conclusions regarding this question.

Some of our subjects had a continuing problem with passing task 15 according to our original criterion, which is particularly interesting as magpies (Pollok et al. 2000) had very similar difficulties. Out of the 19 subjects, 5 individuals did not pass task 15 according to our original criterion; however, their response was not illogical when seen from another point of view, so their actions did not reveal any implications of behaviour inconsistent with stage 6 competence. However, to further assess this issue, we proceeded to test the subjects on the Shell game, and based on these results, we argue that jackdaws do actually acquire stage 6 competence.

As the method we chose has sometimes been criticised (criticisms and strong points reviewed in Pepperberg 2002) on the issue of possible training during the administration of the sequentially more and more difficult tasks, we divided our birds into three groups which

each received different amounts of testing, but we could not find any significant differences in their development, nor in their competence at the final stage. For this reason, we feel that the results we acquired by using Scale 1 were not in any way artificial. By using the same method, we were able to compare our results with data on food-storing ravens and magpies. Finally, we administered an extra task, task S, or the “Shell game” to assess not only object permanence abilities but also some other cognitive capacities, such as attention and spatial memory. Our birds performed significantly better than chance in these trials. All these data suggest that jackdaws develop an ability in object permanence corresponding to the Piagetian stage 6 competences.

A further criticism of the Scale 1 method lies in the face-to-face nature of testing (Collier-Baker et al. 2004, 2005; Fiset and Leblanc 2007) so we took the utmost care not to bias or cue our animals in any way (the birds were not allowed to choose or search until the experimenter had taken up the neutral position mentioned in the procedures). Of course, the possibility of cueing could not be completely eliminated given our face-to-face testing procedure. On the other hand, we feel that when testing animal cognition it is also of very high importance that the subject is in no way stressed when subjected to a cognitive task, as stress may impair their performance considerably (e.g. Weir and Kacelnik 2006). Having the person who had raised the birds by hand as experimenter had very favourable effects on the stress level of our subjects.

A question of considerable interest is whether the lack of caching behaviour in jackdaws is an ancient trait, inherited from a non-caching common ancestor, or represents the loss of a skill as a secondary specialisation to a less demanding ecological environment, with the common ancestor of corvids being a food-storer. In this latter case, we should expect to find no differences in the performance of food-storing and non-storing corvids on non-spatial tasks (De Kort et al. 2006). Our findings are not contradictory to this hypothesis, but as object permanence has evident values in various respects other than food-storing, it is difficult to draw any conclusions regarding this issue.

Based on the above data, we suggest that the lack of food-storing behaviour in jackdaws is not associated with inferior object permanence abilities. This is not surprising as sophisticated object permanence skills have a very wide ecological significance and are a prerequisite of various other behaviours, more fundamental than caching. Having a considerably smaller hippocampus relative to their brain size (Healy and Krebs 1992) seems to be connected with poorer spatial memory (Scheid and Bugnyar 2008), but this did not impair performance in our task S.

We know that jackdaws hardly ever make food caches in the wild (Henty 1975); however, we argue that advanced object permanence abilities may be of several other advantages in the ecological context, as these birds are known to raid caches made by other species, and also to carry objects in their throat pouches, where those are temporarily invisible to others, but the ability to track them is undeniably favourable for conspecifics who are observing. Object permanence abilities have a wider ecological significance, for example, in prey–predator interactions and in connection with nest-hole reproduction, which may underlie the unimpaired capacity.

In general, we can conclude that corvid cognition does not seem to be advanced only in food-storing species. Non-storing species, such as jackdaws, also have some quite impressive cognitive abilities “up their sleeve”. We feel that it is very interesting to study corvids’ object-related and social cognition in contexts other than food caching, as this way non-caching species may be included for further comparison.

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Fig. 1.
The jackdaw aviary and the experimental rooms

Fig. 2.

Trial and control situations in our task S, the Shell game. In trials the baited containers moved to change their relative position, while in the controls the baited container remained in the same place and empty containers moved. (*Dots* indicate baited containers, *dark outlines* indicate moving containers)

Fig. 3.

Mean age of passing single visible, successive visible, single invisible, successive invisible displacements (Piagetian stages 4b, 5b, 6a and 6b)

Fig. 4.

Performance of jackdaws ($N = 10$) in the Shell game (task S) and Controls for local/stimulus enhancement. Figure shows per cent of correct responses per individual and the group mean. Chance level is at 33 %. (*Signals birds showing anomaly in task 15)

Fig. 5.

a–d Age at which birds in the three groups (Group 1—all tasks given, Group 2—tasks 5–9 skipped and Group 3—every second task given between 4 and 14) reached criterion on tasks 10, 13, 14, 15. *Box plots* show medians and interquartile ranges. We found no significant differences

Table 1
The mean age ($\pm$ SD) of the birds in days when passing each task and the number of subjects taking part in the tasks

Task	3	4	5	6	7	8	9	10	11	12	13	14	15
N=	20	20	8	14	8	14	8	19	13	19	13	19	14
Age (days)	36.6	41	43.5	47	48.4	57.6	61	61.2	68.4	69.1	74.3	74.3	80.7
SD	4	6.1	5	4	4.2	7.4	9.1	6.8	7.6	7.2	6.3	7.7	7.9

Table 2

The number of sessions ending with errors received by each bird before passing each task

Group	Name	Task 3	Task 4	Task 5	Task 6	Task 7	Task 8	Task 9	Task 10	Task 11	Task 12	Task 13	Task 14	Task 15
1	Woody	0	0	0	0	0	5	0	0	0	1	2	0	0
1	Clever	0	1	1	0	0	5	0	0	0	0	0	0	0
1	Rózi	0	1	0	0	0	6	0	0	0	0	0	0	2
1	Borso	0	0	2	0	0	0	0	2	0	0	1	1	2
1	Stini	0	1	1	0	0	1	0	0	1	2	0	0	0
1	Csuri	0	1	3	0	0	1	0	1	2	0	0	0	0
1	Novak	0	1	1	0	2	5	0	0	2	0	0	0	3
1	Gonzo	0	1	1	0	0	2	0	1	0	0	2	1	4
2	Phoebe	0	1 xxx	xxx	xxx	xxx	xxx	xxx	0	5	0	1	0	1
2	Liberó	0	0 xxx	xxx	xxx	xxx	xxx	xxx	0	0	1	2	0	np
2	Ortiga	0	0 xxx	xxx	xxx	xxx	xxx	xxx	0	2	0	0	0	np
2	Domin.	1	1 xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx
2	Fraulein	2	0 xxx	xxx	xxx	xxx	xxx	xxx	0	0	0	0	2	np
2	Jacques	0	0 xxx	xxx	xxx	xxx	xxx	xxx	0	2	0	1	0	0
3	Smart	0	2 xxx	0 xxx	0 xxx	1 xxx	1 xxx	1 xxx	1 xxx	1 xxx	1 xxx	0	1	1
3	Puck	2	0 xxx	1 xxx	1 xxx	6 xxx	6 xxx	0 xxx	0 xxx	2 xxx	2 xxx	2	0	0
3	Finci	1	1 xxx	0 xxx	0 xxx	2 xxx	2 xxx	0 xxx	0 xxx	0 xxx	0 xxx	0	0	np
3	Berci	1	0 xxx	2 xxx	2 xxx	1 xxx	1 xxx	0 xxx	0 xxx	4 xxx	4 xxx	4	2	2
3	Marci	1	1 xxx	1 xxx	1 xxx	0 xxx	0 xxx	0 xxx	0 xxx	1 xxx	1 xxx	3	1	1
3	Sundan.	2	0 xxx	0 xxx	0 xxx	0 xxx	0 xxx	0 xxx	0 xxx	0 xxx	0 xxx	0	0	np

All attempts where at least one manipulation was executed by the experimenter while the bird was present in the experimental compartment are considered a session. After making an error, the session was terminated. xxx = bird has not been subjected to the task; np = did not fulfil criterion in task even after 5 sessions