Ontogeny of object permanence and object tracking in the carrion crow, Corvus corone

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Object permanence is a component of physical cognition and refers to the knowledge that an object still exists when out of sight or displaced. Many animal species develop object permanence skills in a similar sequence as human infants, but few master the most complex aspects, such as representing invisibly displaced objects. We tested six developing, hand-raised carrion crows on Piagetian object permanence applying a randomized presentation of Uzgiris & Hunt's (1975, *Assessment in Infancy: Ordinal Scales of Psychological Development*, University of Illinois Press) Scale 1 tasks. In addition, the birds were tested on transpositions, visible and invisible rotational displacement tasks. The results from this longitudinal study demonstrate that young carrion crows did develop full Piagetian object permanence skills including Stage 6 (with the exception of task 15). This ability developed gradually, albeit with slight changes in the order of mastery compared to human infants. Systematically different points in time at which same-aged crows mastered the tasks indicated interindividual cognitive differences. The crows showed perseverative searches at a previously rewarded location (the so-called 'A-not-B error'). They mastered visible rotational displacements consistently, but failed at more complex invisible rotational displacements. The overall pattern of the development and competence of object permanence in crows is similar to other corvid species. The absolute ages at which corvid species pass the tests seem to be a function of the hatching-to-fledging time. The findings may reflect maturing executive functions rather than being related to food-storing habits.

Object permanence is a simple component of physical cognition (Shettleworth 2009). It refers to the knowledge that an object still exists when out of sight and the ability to represent its unseen displacement trajectory (Piaget 1952, 1954). To test object permanence in animals, many of the cognitive tests devised by Piaget for young children are ideal for comparative studies because they rely on simple nonverbal behaviours (Doré & Dumas 1987; Gómez 2005). According to the Piagetian framework, more and more complex performance levels are reached along a fixed developmental succession in six stages. After an initial inability to follow moving objects (Piagetian Stage 1) at the earliest period of ontogeny, individuals later begin to track moving items (Stage 2), and recover partly (Stage 3) and fully (Stage 4) hidden objects. In the process of maturation, individuals develop more advanced skills and retrieve items that have been displaced visibly (Stage 5). Before accomplishing the tasks of Stage 5, subjects typically commit the 'A-not-B' error: when they see an object that they have repeatedly found in one location (A) hidden in another place (B), they still search in the previously rewarded location. Finally, individuals also master the retrieval of objects that had been displaced invisibly (Stage 6).

Keeping track of objects invisibly moving in space along a specific trajectory is a challenging task. It requires continuous updating of representations of the unperceived object and its position while maintaining a stable representation of the stationary surroundings (Sophian 1986). In Piagetian Stage 6, for instance, an object is placed in full view of the subject, hidden in the experimenter's closed hand or an opaque container and moved sequentially behind two or three occluders before being hidden behind one of them. Several species, including great apes (de Blois et al. 1998, 1999; Call 2001; Barth & Call 2006), psittacids (Funk 1996; Pepperberg et al. 1997) and corvids (Pollok et al. 2000; Bugnyar et al. 2007; Zucca et al. 2007) solve these tasks at progressive stages of their development. The evidence for other species, such as lesser apes, monkeys and prosimians, to master Piagetian Stage 6 is less convincing (Neiworth et al. 2003; Mendes & Huber 2004; Fedor et al. 2008; Deppe et al. 2009).

Even more demanding than simple displacements are rotations in which a subject witnesses a target object being hidden in one of

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several containers and the experimenter then changes the positions of the containers, including the one hiding the target object, by rotating a platform on which they are located. Task demand in rotation is typically a function of rotation angle, and both great apes (Beran et al. 2005; Okamoto-Barth & Call 2008; Albiach-Serrano et al. 2010) and human children (Sophian 1986; Okamoto-Barth & Call 2008) find such tasks hard. It remains elusive to what extent birds are able to solve transpositions and rotational displacements.

Object permanence is thought to be of particular importance for food-caching birds, such as corvids, because retrieving a hidden object requires some sort of internal representation of an invisible object. In corvids, development of full Piagetian object permanence has been studied so far in magpies, *Pica pica* (Pollok et al. 2000), Eurasian jays, *Garrulus glandarius* (Zucca et al. 2007), and ravens, *Corvus corax* (Bugnyar et al. 2007). They all achieved Piagetian Stage 6 and thus are able to represent invisible object displacement. During this developmental trajectory, however, conspicuous differences between species have been observed: Magpies and Eurasian jays show no A-not-B error before passing task 5 of Stage 5, which has been attributed to a particularly high resistance to interference owing to food-storing habits in these species (Pollok et al. 2000; Zucca et al. 2007). However, this hypothesis cannot explain why ravens, intensely object-storing corvids, do show this error (Bugnyar et al. 2007). We therefore tested the object permanence abilities of a closely related corvid species, the carrion crow. We hypothesized that if crows also showed an A-not-B error, such perseverative search at previously rewarded locations might indicate a lack of inhibitory control caused by immature executive functions, rather than being related to food-storing habits.

METHODS

Subjects

Six hand-reared birds were available for the study. Four of the crows (all siblings) were taken from the institute's breeding stock at the age of 18 days (day of hatching known) and the remaining two birds were taken from the wild at the age of 4 weeks (estimated from developmental status). They were marked with coloured rings for individual identification and carried leather jesses. One of the wild-caught birds never cooperated and was soon excluded from being tested. The remaining five birds, four males and one female (sex determined from feather material; Tauros Diagnostiks, Bielefeld, Germany), were all tested on the entire Scale 1 by Uzgiris & Hunt's (1975) object permanence tasks (experiment 1) and later on the rotation tasks (experiment 2). Licences for keeping, breeding and taking the birds from the wild, as well as an animal experimentation licence, were all provided by the local authority, the Regierungspräsidium Tübingen, Germany. After the study, all the birds were kept for use in other experiments.

Housing

After being taken from their nests, the nestlings were initially kept individually in transparent containers of the size of a crow's nest and later transferred to larger wooden containers in rooms with daylight. When fully fledged, all birds were transferred to large indoor aviaries (360 × 240 cm and 300 cm high) with daylight in which they were housed side by side in one group of four (the four siblings) and one group of two (the wild-caught birds). Each aviary was equipped with several wooden perches, cardboard boxes, a bath tub and several toys. The floors were covered with paper and chipped wood. The nestlings' and fledglings' diet consisted of chick meat, insects and insect larvae,

hardboiled eggs, vegetables, fruits and mashed birdseed (Beoperlen, Vitakraft, Germany). Water was initially delivered with plastic pipettes until the birds were able to take it from cups. In addition, mineral and vitamin supplements 'Vitakalk' (Marienfelde GmbH, Hamburg, Germany) and 'Korvimin' (WDT, Garbsen, Germany) were given.

General Procedure

All tasks were administered on a table inside an empty aviary next to the home aviaries of the birds. During testing, birds had full auditory contact with group mates, but visual contact was prevented by a large occluder between the test and the home aviaries. All birds had ad libitum access to water. Three hours before the test sessions, food was removed to increase the birds' motivation. All tests for all birds were carried out within 2 h during the morning. The sequence in which the birds were tested varied randomly across days. The tasks were presented three times a week, usually Mondays, Wednesdays and Fridays. The two experimenters (A.H. and V.R.) were present inside the experimental aviary during each session as camera operator and task presenter. The assignments of duties were switched between the experimenters on a regular basis. To avoid gaze cues, the presenter wore sunglasses during the sessions and avoided looking at the apparatus during the bird's choice.

A session started when an experimenter entered an aviary and displayed food items. This caused the tame birds to fly onto the experimenter's arm to be rewarded and carried over to the adjacent test aviary. The bird was then placed in front of the test apparatus (roll top box) on the table to attend the tasks. This transparent plastic roll top box (a round box for experiment 1 and a square box for experiment 2) prevented the crows from removing the occluders and searching for the hidden objects before task presentation was finished (Fig. 1a). Diverse occluders used in different tests are shown in Fig. 1c–g.

At the beginning of a trial, the experimenter showed a mealworm, *Tenebrio molitor*, to the bird. When the bird was paying attention, the experimenter presented the task and hid the mealworm. After the mealworm was hidden, the roll top box was opened. From that point on, the bird had 30 s to make its choice. A response was classified as correct if it was in agreement with the criterion for a given task (see Table 1). Each task consisted of six trials. Two incorrect answers led to the task being aborted. This procedure aimed at minimizing the risk of the bird learning the tasks, as it was the objective of the study to test for cognitive development and not for the ability to learn. No restraints were applied and the experimental protocol required the bird's cooperation. If the bird flew from the table during a session, it was lured back to continue the experiments. If the crow was persistently distracted and unwilling to attend to the tasks, it was carried back to the group without finishing them. After the test session, each bird was carried back to its aviary where it stayed with its group mates the rest of the day with food and water provided ad libitum.

The whole session in all experiments was videotaped. We did an offline evaluation and both experimenters decided separately whether a task was successful or not. Only tasks that were judged as correct by both experimenters independently were counted as mastered. To evaluate interobserver reliability, we calculated the kappa coefficient (Viera & Garrett 2005), which measures the agreement between two or more observers. In general, a kappa of 1 indicates perfect agreement, whereas a kappa of 0 indicates agreement equivalent to chance (Viera & Garrett 2005). Interobserver reliability in both experiments was high (Cohen's $\kappa = 0.91$ in experiment 1 and Cohen's $\kappa = 0.92$ in experiment 2).
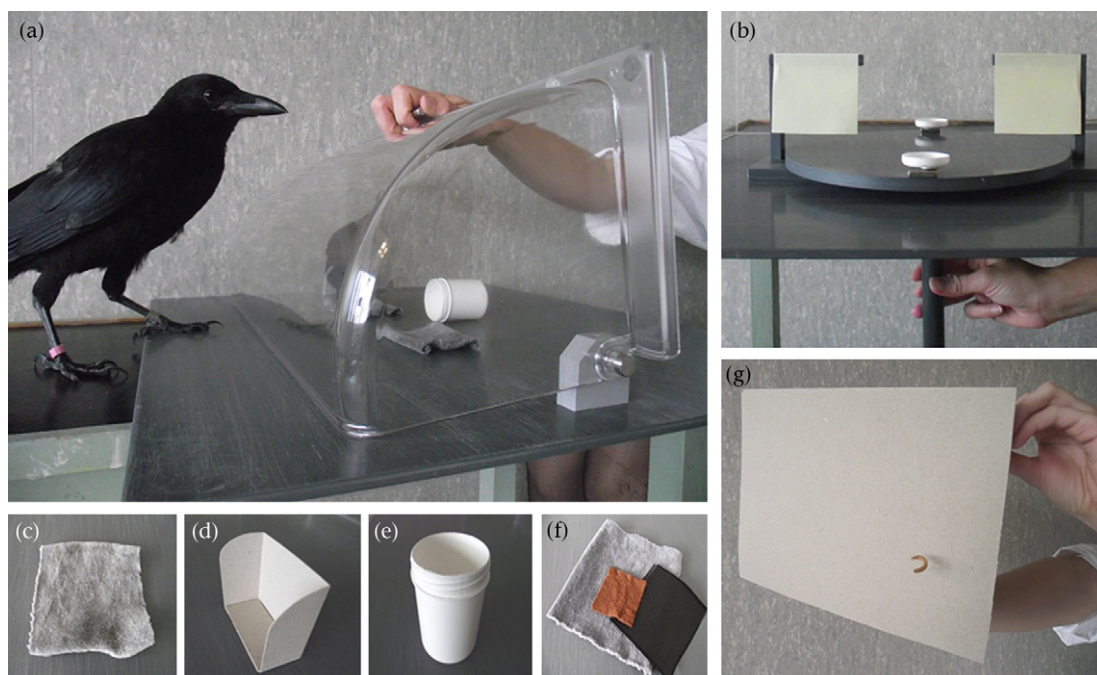
Figure 1. Test set-up and materials. (a) Roll top box used in experiment 1 (48 × 17 cm and 20 cm high). (b) Rotation platform (25 cm) used in experiment 2 (visible conditions shown). (c) Cloth cover (8 × 8 cm). (d) Cardboard screen (8 × 8 cm, side 3 cm). (e) Opaque plastic container (4.5 cm high, 4 cm diameter) used for invisible displacements in Scale 1 tasks and rotation tasks. (f) Grey (13 × 13 cm), black (8 × 8 cm) and brown covers (4.5 × 4.5 cm) for task 9. (g) Cardboard screen (27 × 19 cm) and mealworm attached to 20 cm long nylon thread used in task 2.

Experiment 1: Piagetian Object Permanence

The crows were tested with the complete Scale 1 tasks designed by Uzgiris & Hunt (1975). These tasks are suitable for interspecies comparison, as they have been used successfully in earlier studies of object permanence in corvids. Scale 1 consists of 15 tasks of increasing difficulty (Table 1). The tasks correlate with the Piagetian scheme. Even though they omit Piagetian Stage 1, they allow for a finer subdivision of the remaining Stages 2–6 by breaking the Piagetian stages into the 15 tasks of Scale 1.

A task of Scale 1 was mastered if the subject passed the first three trials in a row or made five correct trials out of six. Three different tasks were tested during one session. To determine precisely the ages of task mastery and to be able to compare them to other tested animal species, the first task tested within one session was the so-called sequence task. The sequence task was defined as the task that the birds had to master next in Scale 1; for example, if task 4 was accomplished, the sequence task was task 5.

To avoid the age of task mastery reflecting a predetermined sequence of tasks rather than actual developmental stages, two additional tasks were tested; these two tasks were pseudorandomly picked (using custom-made software) every session anew and for each bird individually from the set of the not yet mastered tasks.

Experiment 2: Transpositions and Rotational Displacements

The test period was 1 month. It started when the birds were 119 days of age, on average. At that time nearly all birds had mastered the Scale 1 tasks 1–14. Testing was carried out in the same sessions after testing for the remaining tasks of Scale 1.

Transpositions

We tested two transposition tasks, which were comparable to the 'shell game'. In the first variant, two screens were used: The worm was shown to the bird and placed behind one of the screens. Then the experimenter changed the positions of the screens, including the one hiding the worm. The subject had to keep track of the target screen and to search for the worm directly behind the correct screen. Three screens were used in the second variant. It was nearly the same procedure, but here the screens were switched twice, with the baited one changing position only once. To pass the transposition tasks, the bird had to master either the first three trials in a row, or five out of six trials.

Rotational displacements

Apparatus. A round PVC rotation platform (25 cm diameter) with two containers on opposite sides was placed in the centre of the roll top platform (see Fig. 1b). A rod was attached to the underside of the platform and passed downwards through a hole in the roll top platform. By turning the rod manually underneath the table, the experimenter could thus rotate the round platform with the containers without the bird noticing the cause of the action. For the visible conditions, a worm was placed on one of two small identical white plastic plates. Two yellow paper screens served as occluders for hiding the worm at its final destination after the rotation (see Fig. 1b). The same rotation platform was used for the invisible rotational displacements. However, larger containers (3.5 cm diameter, 4.7 cm high) served as opaque containers for the worm, ensuring that the bait was not visible throughout the rotation. Thus, while in visible conditions the worm was visible during rotation, the bait was fully occluded in the invisible conditions.

Visible rotational displacements. For the 90° rotation task, the rotation platform was aligned so that both containers were in line with the subject and one was directly in front of it (see Fig. 1b). A mealworm was placed in full view of the subject in the container closer to the subject. Then, the rotation platform was rotated to the left or to the right by 90° until the worm was finally hidden behind one of the screens. The criterion for passing the task was

Table 1
Experiment 1: description and criteria of tasks 1–15 of Scale 1 (Uzgiris & Hunt 1975) and their grouping into the Piagetian Stages

Task	Stage	Task description and passing criteria
Visual tracking of moving objects		
1	2	A mealworm attached to a thin nylon thread was brought in front of the bird and shaken to catch its attention. Then the worm was moved slowly in the horizontal plane through an arc of 180° around the bird. Criterion: the bird had to follow the worm continuously through the arc of 180°
2	2	A moving mealworm attached to a thin nylon thread disappeared at one side of a cardboard screen and reappeared at the opposite site (Fig. 1g). Criterion: after several presentations the bird had to return its glance to the point of reappearance before the worm reappeared
Search for simply hidden objects		
3	3	A worm was partly hidden under a single cover. Criterion: the bird had to obtain the partly hidden worm by pulling it out from under the cover or by taking it after removing the cover
4	4	A worm was completely hidden under a single cover. Criterion: the bird had to remove the cover and take the worm
5	5	Two covers were used in three subtrials: the worm was hidden twice under one cover (A) and then it was hidden under the other cover (B). Criterion: the bird had to search for the hidden worm in the place of its final disappearance. Searching under the first cover (A) in the third subtrial instead of searching under the second cover (B) would indicate the Piagetian 'A-not-B error'
6	5	Two subtrials: the worm was hidden alternately under the two covers. Criterion: the bird had to search for the worm under the cover where it was last hidden
7	5	Three covers were used. The worm was hidden randomly under the three covers. Criterion: the bird immediately had to search for the worm under the respective cover where it was hidden
Search for more complex hidden objects		
8	5	The worm was visibly presented with forceps, passed successively under each of the three covers and was finally hidden under the cover where it disappeared last. Criterion: the bird had to search for the worm under the last cover
9	5	The worm was hidden under three superimposed covers of different colours and sizes. Covers were placed in such a way that it was not possible to remove all covers at the same time (Fig. 1f). Criterion: the bird had to obtain the worm after removing all the covers
Search for invisibly displaced objects		
10	6	The worm was visibly presented with forceps and then placed into a small opaque plastic container. The container was then passed under a cover and the worm was hidden under it. The empty container was removed and then shown to the bird. Criterion: the bird had to search for the worm inside the container and then under the cover or immediately under the cover Control task: same procedure as in task 10, but the worm was left in the container. Criterion: the bird had to search for the worm in the container
11	6	The worm was visibly presented with forceps and placed into the container. Then the procedure was the same as in task 5. Criterion: the bird had to search for the hidden worm in the place of its final disappearance
12	6	The worm was visibly presented with forceps and placed into the container. Then the procedure was the same as in task 6. Criterion: the bird immediately had to search for the worm under the respective cover where it was hidden
13	6	The worm was visibly presented with forceps and placed into the container. Then, the procedure was the same as in task 7. Criterion: the bird had to search for the worm under the cover where it was hidden
Search for successive invisibly displaced objects		
14	6	The worm was visibly presented in the palm of the experimenter's hand, which was then closed. The hand passed behind three screens and the worm was left behind the last one. Then the experimenter showed her empty hand to the bird. Criterion: the bird had to search for the worm directly behind the last screen or behind all three screens in the same order as the experimenter's hand passed behind them
15	6	The worm was visibly presented in the palm of the experimenter's hand, which was then closed. The hand passed behind three screens and the worm was left behind the first one. Then the experimenter showed her empty hand to the bird. Criterion: the bird had to search for the worm systematically in reverse order: final screen, second screen and finally first screen

that the bird had to search behind the screen where the worm was hidden.

For the 180° rotation task, the rotation platform was positioned so that both containers were equidistant from the subject. A mealworm was hidden in full view of the subject in the container behind one of the two screens. Then, the rotation platform was rotated by 180° so that the container passed in front of the bird until the worm was finally hidden behind the other screen. The criterion for passing the task was that the bird grasped the worm from the baited container.

Invisible rotational displacements. In the 'No-rotation' task, the rotation platform was aligned so that both occluders were equidistant from the subject (see Fig. 2a). A mealworm was hidden in full view of the subject in one of the two occluders. The criterion for passing the task was that the bird had to search for the worm in the occluder where it was hidden.

In the 90° rotation task, the rotation platform was aligned so that both occluders were in line with the subject and one was directly in front of the bird (see Fig. 2b). A mealworm was hidden in full view of the subject in the occluder closer to the subject. Then, the rotation platform was rotated to the left or to the right by 90°. The criterion for passing the task was that the bird had to search for the worm in the occluder where it was hidden.

In the 180° rotation task, the rotation platform was aligned as in the 'No rotation' condition (see Fig. 2). A mealworm was hidden in
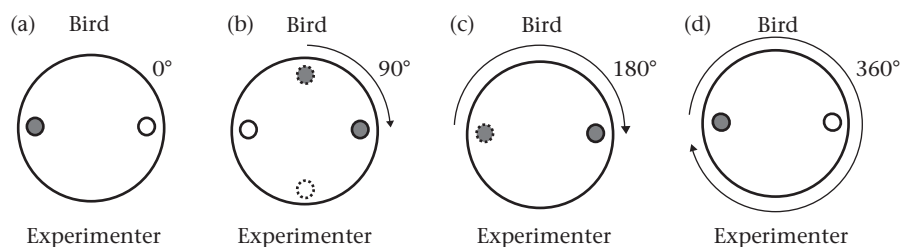

Figure 2. Schematic diagram of the rotation tasks (top view, not to scale). Large circles indicate the rotation plate; small circles represent the possible locations of the visible worm (visible displacement condition) or the plastic containers (invisible displacement condition). Filled circles indicate baited locations/containers, dashed circles locations/containers before rotation and solid circles locations/containers after rotation. (a) No rotation task, (b) 90° rotation, (c) 180° rotation and (d) 360° rotation.
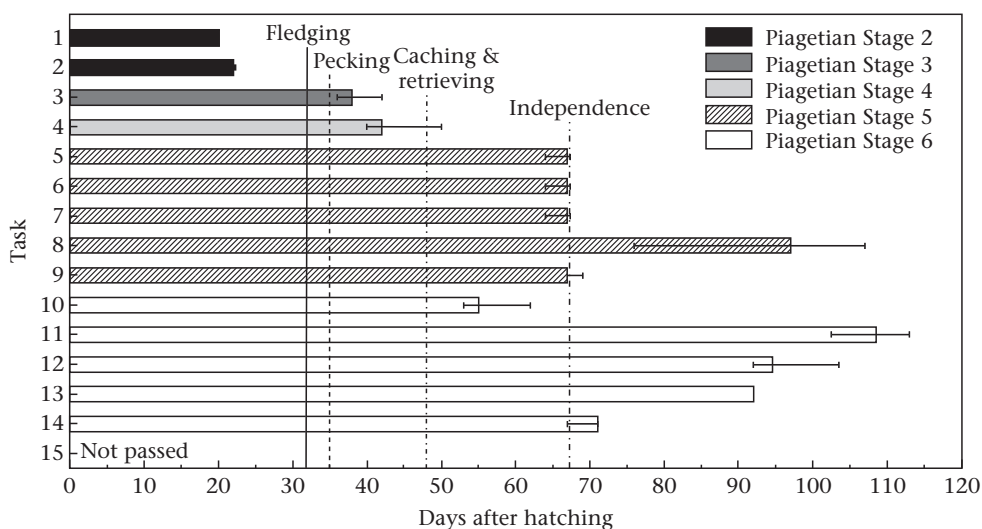
Figure 3. Median age at which the crows mastered the tasks of Scale 1 (Uzgiris & Hunt 1975). Data are based on five birds, except for tasks 1, 2, 11 and 12 (N = 4). Time point of independence is derived based on the data provided by Bauer et al. (2005). Error bars indicate first and third quartiles, respectively.

full view of the subject in one of the two occluders. Then, the rotation platform was pseudorandomly rotated to the left or to the right by 180°. The criterion for passing the task was that the bird had to search for the worm in the occluder where it was hidden.

In the 360° rotation task, the rotation platform was in the same basic position as in the 'No rotation' and '180° rotation' conditions (see Fig. 2d). A mealworm was hidden in full view of the subject in one of the two occluders. Then, the rotation platform was rotated to the left or to the right by 360°. The criterion for passing the task was that the bird had to search for the worm in the occluder where it was hidden.

In the control condition, the task administration and procedure were identical to the rotational displacement task described above, except that an opaque piece of paper was fixed to the front of the roll top box serving as a visual barrier during task presentation. This control was applied immediately after a bird passed a criterion to investigate the possibility that nonvisual cues were used to detect the hidden worm.

Procedure. First, the two visible rotational displacements were administered. Only if subjects mastered at least one of these two tasks were all invisible rotational displacements carried out. The birds were given a maximum of six trials per task. A trial started when the bird was attentive. Baiting of the containers was pseudorandomized: Within the six trials the worm was hidden at random three times in the left and three times in the right container. This pseudorandomized scheme was also carried out for the process of rotation: The platform was rotated three times to the left and three times to the right within the six trials. After each task presentation, the top of the roll top box was opened so that the bird had access to the test stage and could make its choice. Any touching of the occluder, or inspection of its content, was considered a choice. If the subject did not pass the criterion, we prevented the bird from getting the worm by rapidly closing the top of the roll top box or by keeping the occluder shut. A task was considered as mastered when the subject performed at least five out of six trials without error. As 50% is the probability that the bird's choice is correct, the chance probability with this criterion is below 0.05 ($0.5^5 = 0.03125$). If the bird made any two incorrect choices within one task, the session was counted as a failure and testing was aborted. Statistical tests were calculated using SPSS (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Experiment 1: Piagetian Object Permanence

All five crows mastered almost all 15 tasks of Scale 1 at some point during development. Task 15 was a striking exception because all birds continued to search behind the final screen rather than reversing their search sequence back to the first screen. In addition, one out of the five crows never mastered tasks 11 and 12. The onset of mastery for a given task occurred at comparable ages of the birds, but, as shown in Fig. 3, the median age at which the tasks were mastered differed strongly (Friedman test: $P < 0.001$). The differences in cognitive demand are also indicated by the fact that the number of (pseudorandom) task presentations across the tasks of Scale 1 differed significantly (Friedman test: $P = 0.003$), with tasks 5, 11 and 13 being particularly difficult (Table 2). In a few instances, the temporal sequence of task competence was not quite as predicted from previous studies. Overall, however, the order of mastery of the tasks of Stage 1 was still significantly correlated with human ordinality (Spearman rank correlation: $r_S = 0.815$, $P < 0.001$). Thus, the temporal sequence of the six Piagetian Object Permanence stages was found valid in the crows.

Visual tracking of moving objects

All four tested birds mastered task 1 on the first day of testing (day 20) and the second task 2 days later (day 22). The fifth bird was

Table 2
Number of task presentations until successful passing of test

'Scale 1' task	Median number of task presentations±SE	N
1	1±0	4
2	2±0.25	4
3	4±1.38	5
4	4±1.12	5
5	12±2.42	5
6	5±1.36	5
7	2±0.77	5
8	9±4.61	5
9	2±0.32	5
10	1±0.4	5
11	13±2.79	4
12	9±3.55	4
13	11±0.63	5
14	6±2.4	5

already much older at that time and therefore was not tested. Visual tracking of a target (task 1) was thus present at day 20 or younger. The nestlings also tried to peck after the moving mealworm.

Search for simply hidden objects

On average, the birds mastered task 3 (finding partly hidden objects) at 5.5 weeks of age, and task 4 (finding completely hidden objects) a few days later. The youngest bird mastering task 3 was 33 days of age. The oldest bird (59 days) was the only wild-caught bird that had just started to participate in the experiments at that time; it succeeded in both tasks on the first day of testing.

Before mastering task 5, all five tested crows showed the 'A-not-B error', that is, after searching under cover A after the mealworm was hidden there twice in a row, they continued to search under cover A, even though the mealworm was placed consecutively under cover B. The birds often hesitated before choosing a location when making the 'A-not-B error'. Indicating an increased cognitive demand, task 5 required (together with task 13) the largest number of 11 test sessions, on average, until the birds finally mastered it at 9 weeks of age (see Supplementary video S1). After succeeding with task 5, all birds immediately mastered tasks 6 and 7 within the very same session.

Search for more complex hidden objects

In task 8, the object was successively but visibly displaced under three covers. Unexpectedly, this seemed to be very demanding for the birds because they only succeeded after 10 weeks of age, long after they had mastered tasks 9 and 10. The birds seemed to have problems staying attentive throughout the relatively long displacement period, causing many errors.

Task 9, in contrast, was mastered at 9 weeks of age, long before task 8. The test was passed when the crows first removed the outer large cover, then the middle cover, and finally the inner small cover to get the mealworm. Often, the birds pecked under all three covers at once, in which case the trial was aborted and repeated.

Search for invisibly displaced objects

Even though task 10 is the first task belonging to the final Piagetian Stage 6, the birds had surprisingly little difficulty solving it (see Supplementary video S2). The crows both searched first in the container and then under the cover, as well as directly under the cover. On average, they succeeded after passing task 4, before any of the tasks of Stage 5, thus jumping from Piagetian Stage 4 to Stage 6. In other words, all five birds mastered task 10 out of sequence, long before it would have been presented based on the predefined task succession. We designed an additional control task to exclude the possibility that the birds saw the cover as the only possible hiding place. The control for task 10 was mastered by all birds immediately after passing task 10.

In contrast to task 10, task 11 seemed particularly demanding for the birds. One bird never passed it and the other four crows succeeded only at 15 weeks of age, on average. Similar to task 5, the birds make the 'A-not-B error' before succeeding. Often, the birds seemed more interested in the plastic container than the mealworm.

Tasks 12 and 13 were passed almost in parallel, at 13.5 weeks of age. Only one bird (the same that failed task 11) never succeeded. Task 13 required 11 session repetitions (median), before the birds accomplished it (Table 2).

Search for successive invisibly displaced objects

Task 14 was mastered by all five birds 2 weeks after task 10, at a mean age of 10 weeks (see Supplementary video S3). The birds both searched directly behind the screen that the hand last passed and in the same sequence as the hand passed behind the screens.

There was no significant difference in the average age at which the crows mastered the tasks of Stage 5 and Stage 6 (Wilcoxon test comparing the birds' mean age for all Stage 5 tasks with the mean age for all Stage 6 tasks: $P > 0.05$). The ages at which the birds mastered the tasks of Scale 1 was different for individual subjects (Friedman test on ranks of age of mastery: $P = 0.001$), indicating that certain individuals mastered the tasks faster than others. This effect was also present when only the four siblings were compared.

The last and final task of Stage 6, task 15, was never passed by any bird. The crows repeatedly searched behind the screen where the hand had disappeared last. After not finding the object, the subjects stopped searching altogether. The failure for task 15 provides additional evidence for the absence of social or sensory cues that might have been exploited by the birds, because if they had, they should have succeeded in this final task.

Experiment 2: Transpositions and Rotational Displacements

At the onset of experiment 2, the birds were on average 17 weeks (119 days) old and had passed nearly all tasks of Stage 6, except for task 15.

Transpositions

None of the birds reached the criterion for both administered transposition tasks in the test period of 1 month.

Rotational displacements

Visible rotational displacements. To prevent the birds from peeking into the plastic container, we used a slightly larger roll top box. Unfortunately, this new device scared one of the five test birds off and caused it to stop attending the experiments. As a consequence, only four birds (the four siblings) performed the tests of experiment 2. Of these four crows, three mastered the 90° visible rotation task at an average age of 16.5 weeks (116 days). Moreover, two of the four crows also passed the 180° visible rotation task (see Supplementary video S4). In the control conditions in which the birds could not see where the worm was hidden, they performed at chance level (50%), indicating that they were not able to exploit unintended cues to solve the tasks.

Invisible rotational displacements. During the invisible rotational displacement tests, one further bird stopped working and had to be excluded from the experiment. Of the three remaining crows, all three birds passed the No rotation task, confirming the crows' understanding of the plastic containers as hiding places in which objects became invisible, but still remained existent. In addition, two out of three birds mastered the 90° invisible rotation task (see Supplementary video S5). At the time of passing these two tasks, the birds were between 116 and 120 days old. The two successful birds failed when they could not witness the hiding process and performed at chance level. This again confirmed the absence of unintended cues the birds might have been able to exploit to master the tasks. None of the crows, however, passed the 180° and 360° invisible rotation tasks. Experiment 2 was discontinued when the birds reached an age of 20 weeks (140 days).

DISCUSSION

The results from this longitudinal study demonstrate that young carrion crows developed full Piagetian object permanence skills including Stage 6 (with the exception of task 15), as described by Uzgiris & Hunt (1975). Just as in other birds, mammals and human infants, this ability developed gradually, albeit with slight changes in the order of mastery of some visible and invisible displacement tasks. Just like ravens, but in contrast to magpies and Eurasian jays,

the crows also performed perseverative (A-not-B) searches at a previously rewarded location. In general, the crows mastered visible rotational displacements. Transpositions and invisible rotational displacements, however, showed the limits of object permanence capacities in young carrion crows.

Comparison of Corvid Species

We hypothesized that object permanence abilities would be a function of the duration of development. We took the hatching-to-fledging time as an indicator for development in corvids; other indexes, such as the time of independence, were less suited because of the broad time ranges found in the literature (Bauer et al. 2005). This assumption is supported by findings in the order Primates: here, object permanence competence is positively correlated with development (Dixon 1998), that is, object permanence develops faster the faster development to adulthood takes. For instance, macaques, *Macaca mulatta*, reach Stage 5 competence earlier than gorillas, *Gorilla gorilla*, which develop faster than humans (Gómez 2005).

Among the four corvid species tested for mastering Piagetian Stages 2–6, Eurasian jays have the shortest duration of the hatching-to-fledging time (21 days, Glutz von Blotzheim 1994; Bauer et al. 2005), followed by magpies (27 days, Birkhead 1991), carrion crows (32 days, own observations) and finally ravens (40 days, Bugnyar et al. 2007). In agreement with our hypothesis, Eurasian jays needed by far the shortest time for passing Stage 5 (6 weeks of age) and Stage 6 (7 weeks of age; Zucca et al. 2007). The carrion crows of the current study (Stage 5: 11 weeks of age; Stage 6: 13 weeks of age) and ravens (Stage 5: 11 weeks of age; Stage 6: 14 weeks of age; Bugnyar et al. 2007) followed several weeks later (Fig. 4a). A developmental index was defined as the average age of each of the four corvid species when passing the Piagetian stages divided by the species' duration of nestling period. With the exception of the magpies (Pollok et al. 2000), the data of the remaining corvids are superimposed (Fig. 4b), suggesting that the time of cognitive development is proportional to the time of physical development. Only magpies have been reported to pass Stages 5 and 6 at a much older age (17 and 26 weeks of age, respectively; Pollok et al. 2000). Given that the magpies' behavioural repertoire (in terms of foraging, caching and social intelligence) seems to be fundamentally similar to that of the other investigated members of the corvid family, such a prolonged development seems unusual. Perhaps methodological factors account for this discrepancy: From task 8 on, magpies were tested only once a week (Pollok et al. 2000), whereas Eurasian jays (Zucca et al. 2007), carrion crows (current study) and ravens (Bugnyar et al. 2007) were tested two or three times per week. In addition, magpies were strictly tested according to the predefined task sequence of Scale 1 by Uzgiris & Hunt (1975), whereas Eurasian jays (Zucca et al. 2007) and our carrion crows were presented with two additional and randomly picked tasks of Scale 1 in each session, which might increase the chance of passing higher-order tasks at an earlier age.

Sequence of Mastering Tasks

The carrion crows in the current study mirrored human subjects in their object permanence development in terms of the order of mastering the Piagetian Stages 2–6. However, the crows differed slightly from human subjects (Uzgiris & Hunt 1975) and the other tested corvids (Eurasian jays, magpies and ravens) in their object permanence development when considering individual tasks of Scale 1 (Table 3). Some of the invisible displacements of the later tasks were performed before the earlier visible displacement tasks.
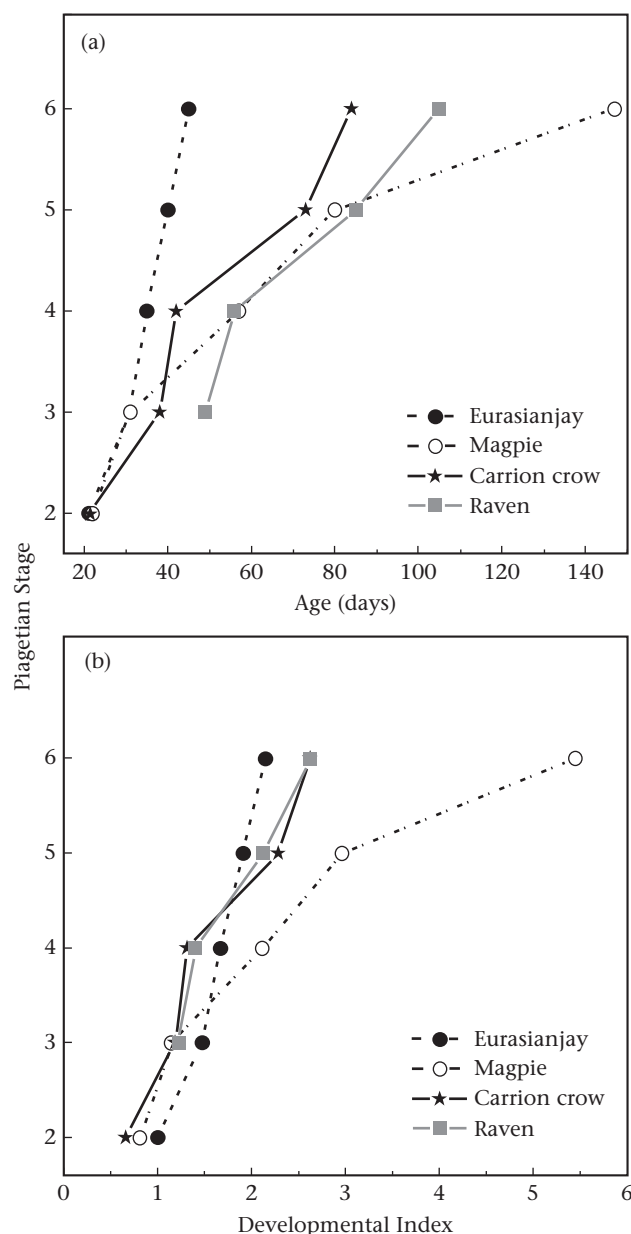

Figure 4. Comparison of the ontogeny of Piagetian object permanence abilities in four corvid species: Eurasian jays, *Garrulus glandarius* (data from Zucca et al. 2007), carrion crows, *Corvus corone* (current study), ravens, *Corvus corax* (data from Bugnyar et al. 2007) and magpies, *Pica pica* (data from Pollok et al. 2000). (a) Ontogeny of Piagetian object permanence as a function of absolute age. Each data point is the average time of mastery across all tested birds and all respective Scale 1 tasks for a given Piagetian Stage. (b) Development of object permanence relative to duration of nestling period.

In particular, the crows mastered task 10 (the first task of Piagetian Stage 6) prior to all the tasks of Piagetian Stage 5 (tasks 5–9). Moreover, task 8 of Piagetian Stage 5 was mastered later than all tasks of Piagetian Stage 6, with the exception of task 11, which was the last task the crows passed in their development. Overall, however, the order of mastery of the tasks of Scale 1 was still significantly correlated with human ordinality.

This temporal pattern of object permanence development in crows is reminiscent of the performance of another bird species, the New Zealand parakeet, *Cyanoramphos auriceps*, for which similar deviations from scale ordinality have been reported (see

Table 3
Sequence of passing tasks 1–15 of Scale 1 (Uzgiris & Hunt 1975) in various corvid species

'Scale 1'	Eurasian jays*	Magpies†	Carrion crows	Ravens‡
1	1	–	1	–
2	2	–	2	–
3	3	3	3	3
4	4	4	4	4
5	5, 6, 7	5, 6, 7	10	5
6			5, 6, 7	6, 7
7				
8	8, 9, 10	8		8, 9
9		9	9	
10	10	10	14	–
11	–	11	13	–
12	–	12	12	–
13	13	13	8	13
14	14, 15	14	11	14
15		15: Criterion not met	15: Criterion not met	15: Criterion not met

Tasks mastered at the same time are listed in one row. Omitted tasks are marked with a dash.
* Data from Zucca et al. 2007.
† Data from Pollok et al. 2000.
‡ Data from Bugnyar et al. 2007.

Table 3 in Funk 1996). Just as in our carrion crows, task 8 of Scale 1 was mastered surprisingly late and task 10 unexpectedly early by the parakeets (Funk 1996). Similar deviations from the standard task ordinality, particularly in relation to the challenges of task 8, have also been reported in primates. Just like the carrion crows, two young rhesus monkeys, *Macaca mulatta*, performed task 10 before tasks 9 and 7, and all of these tasks were performed before task 8 (Wise et al. 1974). Redshaw (1978) and Wood et al. (1980) found that apes (four infant gorillas and two young chimpanzees, *Pan troglodytes*, respectively) and human infants performed task 9 prior to task 8. And while most human results have followed the Uzgiris & Hunt (1975) scales of ordinality, Miller et al. (1970) reported that human subjects performed tasks 9, 10, 11, 12 and 13 before task 8. These mixed results in mammals and birds raise questions about whether cognitive capacities required for simple invisible displacements really do have such a delayed development in human and nonhuman animals (Funk 1996).

Rotational Displacements

Transpositions ('shell game') and invisible rotational displacement tasks, in particular, require cognitive resources such as attention, spatiotemporal working memory and mental updating. While visible rotations of 90° and 180° were still mastered by three or two (out of four) birds, respectively, none of them succeeded with transpositions or items invisibly displaced by 180° or 360°. Invisible rotational displacements thus clearly showed the limits of object permanence capacities in carrion crows.

Rotational displacement tasks seem to be very challenging to many animals. Adult dogs, *Canis familiaris*, also seemed to be able to track visually rotationally displaced objects and objects invisibly displaced by 90°, but failed to track a 180° invisible rotation task (Miller et al. 2009). The authors argued that conflicting contextual information (the scene appeared the same before and after the rotation) might have caused this poor performance. In contrast to young crows and adult dogs, several adult ape species succeeded in invisible rotational tasks of different degrees of difficulty (Albiach-Serrano et al. 2010). Apes and 3–9-year-old children seem to benefit from landmarks (Beran et al. 2005; Okamoto-Barth & Call 2008).

Based on the results in dogs, apes and children, two aspects need to be explored in crows in future studies for comparative reasons: First, would the capacity to master invisible displacement emerge at a later stage of ontogeny or even not before adulthood? Second, are crows able to exploit landmarks or other visual cues to solve invisible displacement tasks? Given the current results in young crows, better performance later in ontogeny and in different contexts cannot be excluded.

The A-not-B Error, Caching and Executive Skills

When subjects see an object that they have repeatedly found in one location (A) hidden in another place (B) and still search in the previously rewarded location, they commit the 'A-not-B' error. The carrion crows, like ravens (Bugnyar et al. 2007), New Zealand parakeets (Funk 1996) and a grey parrot, *Psittacus erithacus* (Pepperberg et al. 1997), but in contrast to their corvid relatives magpies (Pollok et al. 2000) and Eurasian jays (Zucca et al. 2007), showed a reliable A-not-B error before mastering task 5 of Piagetian Stage 5. Corvids are known to cache food items to various degrees, and the lack of the A-not-B error in magpies and Eurasian jays had been attributed to a particularly high resistance to interference owing to the food-storing habits in these species (Pollok et al. 2000; Zucca et al. 2007). Magpies and jays seem to be scatter hoarders (Birkhead 1991; Zucca et al. 2007) and store single items in many different places; a lack of the A-not-B error in these birds would be ecologically sound. However, even primates (such as apes) that typically do not cache food items at all and human infants show an A-not-B error. We speculate that the presence of the A-not-B error might actually reflect the maturing of specific executive functions in these intelligent birds rather than being related to food-storing habits.

Gómez (2005) hypothesized that the cause of object permanence differences during ontogeny in human infants is more related to a mismatch between object knowledge (which seems to be developed much earlier) and its use in action. He therefore suggested that object permanence, and the overcoming of the A-not-B error in particular, might be an index not of representational change, but of the growth of executive faculties that allow the application of object knowledge that already exists (Gómez 2005). The perseverative search at previously rewarded locations might indeed indicate a lack of inhibitory control and task-switching abilities necessary to adapt flexibly to a changing environment, a hallmark of executive function. Our crows often hesitated before choosing when making the 'A-not-B error', an observation compatible with immature inhibitory control in goal-directed behaviour.

The hypothesis that maturing executive functions might play a role in overcoming the A-not-B error is supported by the finding that mammals endowed with a particularly high degree of executive control, simian primates, also show this error early in their ontogeny, whereas cats, *Felis catus* (Dumas & Doré 1989) and dogs (Gagnon & Doré 1994) seem to lack the A-not-B error. In primates, the prefrontal cortex is implicated in providing executive control function. It would be interesting to see whether and how the avian nidopallium caudolaterale, the proposed analogue of the mammalian prefrontal cortex, contributes to object permanence tasks.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi:10.1016/j.anbehav.2011.05.012.

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