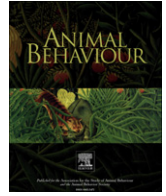




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New Caledonian crows' responses to mirrors

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Recent mirror studies with two corvid species have reported contrasting findings. Jungle crows, *Corvus macrorhynchos*, showed no self-contingent behaviour when confronted with mirrors, whereas Eurasian magpies, *Pica pica*, reportedly passed the 'mark' test for self-recognition. We investigated mirror-induced behaviour in wild-caught New Caledonian crows, *Corvus moneduloides*. We first documented the response of 10 naïve crows to a 50 × 40 cm vertical mirror. The crows responded to their mirror image with social displays and engaged in search and mirror-directed exploratory behaviour. Their agonistic social displays towards the mirror did not decrease in frequency over time. We then gave two of these crows and two naïve ones a mirror-mediated spatial location task with a horizontal mirror. All four crows successfully used the horizontal mirror to locate hidden food. Therefore, they were able to exploit the correlation between an object's mirror reflection and its location in the real world. This suggests that New Caledonian crows may also have the ability to develop an understanding of how mirrors represent objects in the environment, despite the lack of self-directed behaviour in front of mirrors. Our study fills an important gap in mirror studies on corvids, which are considered to be the primate equivalents of the avian world.

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Mirror image stimulation (MIS) has become a standard test in comparative animal psychology ever since Gallup (1970) conducted the first objective 'mark' test for mirror self-recognition. In the mark test, animals have to touch marks (e.g. coloured dots) on their bodies that are only visible in a mirror. In this article, we use the term mirror self-recognition (MSR) to define the objective behaviour an animal performs when passing such mark tests (i.e. animals that touch the mark in front of a mirror have MSR). Originally, however, this test was specifically designed to test the long-held view in primatology that chimpanzees, *Pan troglodytes*, 'realised that their behaviour was the source of the behaviour being seen in the mirror' (Gallup & Povinelli 1993, page 327). In spite of the ongoing debate on whether animals that show MSR possess human-like self-awareness (Gallup & Povinelli 1993; Mitchell 1993a, b, 1995, 1997a; Heyes 1994, 1995, 1996; Gallup et al. 1995; Swartz 1997; Bard et al. 2006), mirror-induced responses in animals continue to be reported. Such reports range from animals that continuously exhibit species-specific social behaviours to those that spontaneously engage in self-exploratory behaviour in

front of mirrors (Pepperberg et al. 1995; Reiss & Marino 2001; Gallup et al. 2002; de Waal et al. 2005; Reznikova 2007).

Until recently, animals other than the great apes were thought to view mirror images only as conspecifics (Gallup 1970; Kusayama et al. 2000). Nonprimates now reported to pass the mark test are one bottlenose dolphin, *Tursiops truncatus* (Reiss & Marino 2001), one Asian elephant, *Elephas maximus* (Plotnik et al. 2006) and two Eurasian magpies, *Pica pica* (Prior et al. 2008). Animals that cannot be tested or do not conclusively pass the mark test nevertheless show other interesting, but less controversial, intermediate mirror-induced responses (Gallup 1970; Povinelli 1989; Pepperberg et al. 1995; de Waal et al. 2005). For example, mirror-triggered search is a basic task in which animals in the presence of mirrors search for hidden food (visible in the mirror) that is placed in fixed, familiar places (Menzel et al. 1985; Anderson 1986; Povinelli 1989). As food is always hidden in the same location, subjects may use the mirror only as a cue to start searching rather than to obtain information of the food's precise whereabouts (Povinelli 1989; Pepperberg et al. 1995). In contrast, in the mirror-mediated object discrimination task (Menzel et al. 1985; Pepperberg et al. 1995) subjects are required to look at mirror images of hidden objects that are either aversive or rewarding. They must then consistently choose to move towards them or move away from them. Animals can do this by exploiting the correlation between an object and its reflection, but they do not need to

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understand that the object is being represented in the mirror or use the mirror to guide their actions (Pepperberg et al. 1995).

The mirror-mediated spatial location task requires more sophisticated cognition (Menzel et al. 1985; Anderson 1986; Povinelli 1989; Pepperberg et al. 1995). Subjects must use mirrors without recourse to trial and error to find a reward that is hidden in one of several novel locations. To do so, they must understand the implicit correspondence between an object's location in the mirror and its location outside the mirror, that is, understand that the object reflected in the mirror is in the real world, in the exact same location as shown in the mirror. However, Povinelli (1989) has argued that animals capable of understanding the duality between mirrored objects and the environment may not necessarily perceive the duality between their own body movements and the image of those body movements in the mirror. In other words, an animal may understand that objects reflected in a mirror have the exact same spatial location in the environment (i.e. understanding mirror duality or mirror correspondence), but it may not understand that the reflected object and the real object are one and the same.

The more elaborate mirror-guided reaching task (Menzel et al. 1985; Anderson 1986) has been designed to test whether animals understand how mirrors can be used in synchrony with their own body movements. While animals that possess self-recognition should pass this test without training, others incapable of self-recognition may do so only after intensive, sequential training (Povinelli 1989). This training would involve an animal continuously monitoring the correspondence between its body parts and the reward object when both are visible only in the mirror (see Itakura 1987).

The heterogeneous taxonomic origin of animals reported to pass the mark test suggests, if rigorously confirmed, that this type of mirror use is an exceptional example of convergent cognitive evolution between primate and nonprimate animals (Reiss & Marino 2001; Plotnik et al. 2006; Prior et al. 2008). As mirror responses in children are well documented and provide cues to their developmental stages (Amsterdam 1972; Bertenthal & Fischer 1978; Anderson 1983; Asendorpf & Baudonnière 1993; Asendorpf et al. 1996), most animal studies have focused exclusively on mirror-triggered behaviour with potential self-awareness implications. However, they continue to ignore two nontrivial issues: (1) passing the mark test does not imply self-recognition, and (2) MSR does not imply self-awareness (sensu Gallup 1987; Mitchell 1993a; Swartz 1997). Children able to recognize themselves in a mirror or a video recording should touch the mark only when they see it on their face. Instead, children often wipe nonexistent marks off their noses when they see another person with a mark on her/his nose (Lewis & Brooks-Gunn 1979; Johnson 1983). This behaviour casts doubts on self-awareness in very young children who pass the mark test. Also, self-awareness is not the only proposed explanation behind MSR. For example, Mitchell (1993a, b, 1995, 1997a, b, 2002) has proposed that MSR may also initially develop without self-recognition via kinaesthetic–visual matching (i.e. the ability to match the visual experiences of our body movements with the proprioceptive representation of our body; for a complete list of the theoretical explanations of MSR, see Bard et al. 2006).

Regardless of the ambiguous nature of animal MSR, studies often fail to recognize that MIS holds a broader unexploited potential for cross-species comparison of cognitive abilities, especially those related to the perception and processing of mirror information (Pepperberg et al. 1995). Thus, researchers may overlook the more basic aspects and levels of mirror-contingent behaviour if they hold an all-or-nothing view of self-awareness (Swartz 1997; Reznikova 2007).

The two mirror studies that have been conducted with corvids are of particular interest regarding MIS in avian species. In

agreement with other published studies (Pickering & Duverge 1992 with lesser flamingos, *Phoeniconaias minor*; Pepperberg et al. 1995 with African grey parrots, *Psittacus erithacus*), four captive jungle crows, *Corvus macrorhynchos*, viewed their mirror image as a conspecific and showed no self-contingent behaviour during 150 min of mirror exposure (Kusayama et al. 2000). In contrast, three hand-raised Eurasian magpies showed self-contingent behaviour: two after 150 min of open mirror exposure and one during the mark test (Prior et al. 2008). Two of the Eurasian magpies were also reported to pass the mark test after 250 min of cumulative exposure to mirrors. Methodological issues in the above-mentioned studies could partly explain the differences in performance between jungle crows and the Eurasian magpies for two reasons. First, while the jungle crows were immediately tested in a small confined area (90 × 90 cm), the Eurasian magpies were tested only after 150 min of open mirror exposure in a 4 × 4 m room. The following 100 min of testing were carried out in a cage with open compartments (60 × 100 cm) which gave them free access to a mirror. Second, the jungle crows could not explore behind the mirror as it was up against a wall or floor. The Eurasian magpies could explore freely behind the mirror during the initial MIS but not during the mark tests. Thus the methodology used by Kusayama et al. (2000) may have restricted the jungle crows to developing social mirror responses and prevented the appearance of other, perhaps more interesting, mirror-contingent behaviours.

New Caledonian crows, *Corvus moneduloides* (NC crows hereafter) have remarkable tool skills in the wild (Hunt 1996; Hunt & Gray 2003, 2004). Wild-caught NC crows also show problem-solving skills in captivity that rival those of primates (Weir et al. 2002; Taylor et al. 2007, 2009, 2010a; Wimpenny et al. 2009). Here, we tested wild-caught NC crows for their responses to mirrors in two ways. We first gave the crows MIS using a vertical mirror in a large cage where birds could look behind the mirror. We predicted that NC crows would engage in similar social (aggressive) displays described in other avian studies when first confronted with their mirror image. However, with ample opportunity to explore both sides of the mirror and to search freely for the 'mirrored crow' in the cage, we expected that their social responses would be extinguished over time. Exposure to both reflective and nonreflective vertical mirror surfaces should lead to increasingly more mirror-directed exploratory and self-contingent behaviour (Pepperberg et al. 1995; Prior et al. 2008). We then gave the crows a mirror-mediated spatial location task to see whether they could use visual feedback in a horizontal mirror to locate hidden food. As tool-using NC crows search for larvae cached in dead wood (Hunt 2000), we expected them to learn rapidly to use the mirror as a tool to locate a hidden food reward. Birds were first trained to extract hidden food in a two-box apparatus. They were then tested on a more difficult four-box apparatus where only one compartment was baited. We predicted that if NC crows were using the mirror to locate food they would consistently search for it only in the baited compartment. However, if they usually first searched in any of the unbaited compartments it would suggest that they were instead using strategies such as mirror-triggered search.

EXPERIMENT 1: VERTICAL MIRROR IMAGE STIMULATION

Methods

Subjects

We carried out the experiment with 10 New Caledonian crows captured on the island of Maré, New Caledonia, in August/October 2007. We captured the birds using a 'whoosh net' (8 × 4 m; SpiderTech Bird Nets, Helsinki, Finland). We aged the crows by mouth colour, which is reliably related to age. Adults were over 2 years old

and juveniles were under 2 years old. All the crows were housed in a five-cage outdoor aviary situated in primary inland forest. The cages were 3 m high and at least 4 × 2 m in area. All cages were provided with ample perching space, branches and feeding logs. The crows were left to get accustomed to the aviary and human presence for 3 days before any experimental procedures began. They were fed a main meal in the evening consisting of soaked dog biscuits, bread or rice and occasionally raw egg. Papaya and clean drinking and bathing water were available throughout the day. Crows were given a half ration of food ca. 15 h prior to their participation in the experiment. Their body weights were closely monitored to maintain them at or above capture weight. All birds were captured before the breeding season (November–January) and kept in the aviary for up to 5 months. All 10 crows were presumed to be naïve to mirrors before the experiment began.

Experimental procedure

Experiments were conducted in a cage measuring 4 × 5 m and 3 m high. In the top corner of the cage was a small observation cage (0.5 × 2 m and 0.5 m high), which had a single perch in front of an observation window (25 × 25 cm). A vertical mirror (40 cm wide × 6 mm thick and 50 cm high) was fixed to a wooden base and positioned on top of a table (1 m high × 70 cm wide) in the middle of the large cage. Crows could easily reach the table from either the perches or the ground. A test crow was first moved into the observation cage and remained there for 2 min, with free access to the observation window from which it could see the back of the mirror in the large cage. After 2 min had elapsed the crow was moved into the large cage.

Crows were given a single 10 min mirror session per day, and up to six daily sessions. To control for effects of exposure to a novel set-up (i.e. the mirror on the table), we (1) reversed the mirror after each session and (2) assigned the crows pseudorandomly to two experimental groups ($N = 5$ per group). When reversed, the back of the mirror faced the crows instead of the reflective side. The mirror's reflective surface at the back was covered with cardboard to prevent crows from seeing their image in it if they inspected behind the mirror. Each group had an equal mix of crows of different ages (Table 1). Group 1 started with the reflective surface (R) of the mirror, and Group 2 started with the nonreflective surface (nR). At the end of the experiment each crow had been exposed to three reflective and three nonreflective vertical mirror sessions as follows: (1) Group 1: R₁, nR₂, R₃, nR₄, R₅, nR₆; (2) Group 2: nR₁, R₂, nR₃, R₄, nR₅, R₆.

In each session the front of the mirror was baited four times with small meat cubes (ca. 1 cm³) to ensure crows interacted with the reflective or the nonreflective mirror surface. One minute after a session had started, the experimenter entered the cage and left one meat cube on the table in front of the mirror (ca. 5 cm from the ledge) and immediately left the cage. One and a half minutes later, the experimenter repeated this procedure. Again, 1.5 min later the experimenter re-entered the cage and after leaving six meat cubes

in front of the mirror (five along the mirror ledge and one on the table) left the cage. Finally, 2.5 min later the experimenter entered the cage and left five meat cubes in front of the mirror (along the mirror ledge). The experimenter then left the cage and the session was terminated once 10 min had elapsed. Thus, each crow was offered a total of 13 meat cubes per session. We increased the number of meat cubes over the session to try to ensure a standard period of time in front of the mirror across individuals. Crows left the table as soon as the cage door was opened, and did not return until the experimenter had left the cage. Therefore they could have not seen the experimenter in the mirror. However, crows could see the camera lens reflected in the mirror when standing in front of it. Mirrors were thoroughly cleaned before each session to preclude possible responses to cues (olfactory, gustatory and/or visual).

Data analysis

All trials were recorded on video camera through a small hole in the opaque walls of the experimental cage. A total of 10 h of video footage was analysed by F.S.M. and the total frequency of nine mirror responses listed in Table 2 was scored (see Supplementary Movie S1). Similar responses have been described for children (Amsterdam 1972; Brooks-Gunn & Lewis 1984), chimpanzees (Lin et al. 1992), gibbons (Suddendorf & Collie-Baker 2009), macaques (Straumann & Anderson 1991), marmosets (Eglish & Snowden 1983), talapoins (Posada & Collel 2005), elephants (Povinelli 1989; Plotnik et al. 2006), dolphins (Marino et al. 1994), pigs (Broom et al. 2009), parrots (Pepperberg et al. 1995), chickadees (Censky & Ficken 1982), finches and parakeets (Gallup & Capper 1970), Eurasian magpies (Prior et al. 2008) and jungle crows (Kusayama et al. 2000). We did not witness any self-contingent (i.e. 'contingent' behaviour sensu Prior et al. 2008) or self-directed (sensu Bard et al. 2006) behaviours during the MIS sessions.

An independent scorer coded half of the reflective mirror sessions using only behavioural descriptions from Table 2. Scorer

Table 1
Study crows and their assigned groups for experiment 1

Group 1			Group 2		
Subject	Sex	Age	Subject	Sex	Age
Español	Male	Adult	Robin	Male	Adult
Angel	Female	Juvenile	Egg	Female	Juvenile
Boxer	Male	Juvenile	Slevin	Male	Juvenile
Sisu	Female	Juvenile	Ronia	Female	Juvenile
Cuba	Male	Juvenile	Tiga	Male	Juvenile

An adult is > 2 years old; a juvenile is < 2 years old.

Table 2
Mirror responses and definitions

Behaviour	Description
Social responses	
Vocalization	Bird makes a 'caw' call, sometimes accompanied by subtle wing flapping
Rapid head movement (RHM)	Bird does a series of six or more quick head movements in front of mirror, generally with stretched neck and accompanied by short series of non-'caw' calls
Tail-up	Acute tail lifting, usually after a sudden opening of wings
Attack	Bird jumps at mirror image, usually with claws up in frontal position
Exploratory responses	
Peck	Bird pecks at the surface of mirror or mirror image (not associated with attack)
Peekaboo	Bird stares at mirror image and then quickly moves its head out of view and then back, within 3s
Search responses	
Look under table (LUT)	While at the edge of the table, bird orients its head towards the ground, usually bending the whole upper body (including turning of the eye towards ground)
Look behind mirror (LBM)	Bird moves from front area to the back area of the table* or while perching on the mirror top ledge, turns its head or body from facing towards the front to towards the back of the mirror
Other responses	
Startle	Sudden wing flapping usually followed by a backwards jump or by flight, or any other sudden aversive reaction to the mirror image (i.e. leave table before eating bait)

* The table is divided by an imaginary line into 'front' and 'back of the mirror'.

consistency was measured with Spearman rank correlation tests (Martin & Bateson 1986). To detect any trend or habituation to vertical MIS, we used nonparametric Friedman's ANOVA. We carried out nonparametric Mann–Whitney *U* tests with SPSS version 15.0 (SPSS Inc., Chicago, IL, U.S.A.). We calculated Wilcoxon signed-ranks tests manually because of low sample sizes. The alpha level for the above tests was set at 0.05, unless otherwise indicated.

Results

We scored a total of 1246 and 110 behavioural responses during reflective (R) and nonreflective (nR) mirror sessions, respectively (Tables 3, 4). Scores between observers were highly correlated (two-tailed Spearman correlation tests: vocalization: $r_s = 1.0$; rapid head movements: $r_s = 0.923$; tail-up: $r_s = 0.949$; attack: $r_s = 1.0$; peck: $r_s = 0.986$; peekaboo: $r_s = 0.935$; look under table: $r_s = 0.931$; look behind mirror: $r_s = 0.997$; startle: $r_s = 0.949$; all $P < 0.001$).

We found no significant difference in both the R and nR conditions between groups in the frequency of the behaviour responses in Table 2 (Mann–Whitney *U* tests: all *P* values > 0.05). Therefore, we combined the data for each condition across groups 1 and 2.

With the exception of the search response 'look under table', crows made fewer responses to the mirror when it was reversed (Wilcoxon signed-ranks tests: rapid head movement: $W = 0$, $N = 9$, $P = 0.004$; tail-up: $W = 0$, $N = 10$, $P = 0.002$; attack: $W = 0$, $N = 6$, $P = 0.031$; peck: $W = 0$, $N = 6$, $P = 0.002$; look behind mirror: $W = 8$, $N = 10$, $P = 0.049$; startle: $W = 0$, $N = 10$, $P = 0.002$; look under table: $W = 15.5$, $N = 8$, $P = 0.74$; Fig. 1). We were unable to test for significant differences in 'vocalization' and 'peekaboo' frequencies across mirror conditions because of the low sample size ($N = 3$, $N = 5$, respectively). However, three birds made a total of 69 vocalizations during R sessions and only seven during nR sessions. Also, five birds made 61 peekaboos exclusively during R sessions.

The crows' social, exploratory, search and startle behaviours were not extinguished completely over time, as was predicted (Fig. 2). However, the frequency of the social responses across all crows tended to decrease over the 10 trials in the R sessions and the frequency of the exploratory responses tended to increase, but these trends were not significant (Friedman's ANOVA tests; social responses: $\chi^2_2 = 1.895$, $P = 0.42$; exploratory responses: $\chi^2_2 = 0.176$, $P = 0.95$; search responses: $\chi^2_2 = 1.947$, $P = 0.41$; startle: $\chi^2_2 = 1.600$, $P = 0.48$).

Birds approached the baited table as soon as the experimenter left the cage. With few exceptions, a crow immediately viewed its reflection as a threat and reacted agonistically (rapid head movement, tail-up, attack). As a consequence, birds often perched on the

Table 4
Cumulative number of responses to vertical MIS: Group 2

Responses	Robin		Egg		Slevin		Ronja		Tiga	
	nR	R	nR	R	nR	R	nR	R	nR	R
Social										
Vocalization	0	0	0	0	0	0	0	0	0	0
RHM	0	13	0	3	0	0	0	6	0	9
Tail-up	0	16	0	6	0	2	0	12	0	18
Attack	0	0	0	0	0	0	0	1	0	9
Exploratory										
Peck	0	8	0	2	0	1	0	1	0	48
Peekaboo	0	2	0	0	0	0	0	0	0	19
Search										
LUT	10	4	25	7	2	2	5	4	0	0
LBM	4	7	6	2	3	0	2	6	1	8
Other										
Startle	0	20	0	6	0	2	0	5	0	2

RHM: rapid head movement; LUT: look under table; LBM: look behind mirror.

top mirror ledge or ended up close to the mirror's side (usually after an attack). In both cases, crows had free access to the back of the mirror and frequently examined it. Birds also searched behind the mirror right after their mirror image disappeared from view. Such exploratory responses increased in frequency across mirror sessions (Fig. 2, but see also Appendix Tables A1, A2).

On several occasions, a crow flew off the table as soon as it saw its mirror image (startle responses), but they usually returned to the table a few seconds later. Crows also initially ate the meat in between or after making social responses to their mirror reflection. As mirror sessions continued, they started social interactions only after all or most of the meat cubes had been eaten.

Important individual differences in mirror responses were observed during R sessions (see Appendix Tables A1, A2). For example, only three crows (Español, Cuba and Sisú) from Group 1 made 'vocalizations' during the entire experiment. During their first reflective (R_1) mirror session they made submissive begging-like calls in front of their mirror reflection. Only two of these three crows (Español and Cuba) continued to vocalize in subsequent reflective mirror sessions. Crows other than Español made no 'vocalizations' during reversed mirror sessions (Tables 3, 4). Prior to the mirror experiment we had never observed Español's surprising begging-like behaviour in mature male NC crows.

Table 3
Cumulative number of responses to vertical MIS: Group 1

Responses	Español		Angel		Boxer		Sisú		Cuba	
	R	nR	R	nR	R	nR	R	nR	R	nR
Social										
Vocalization	40	7	0	0	0	0	2	0	27	0
RHM	4	0	43	0	4	0	3	0	1	0
Tail-up	32	0	79	0	9	0	22	0	11	2
Attack	2	0	106	0	0	0	41	0	19	0
Exploratory										
Peck	1	0	59	0	2	0	96	1	9	0
Peekaboo	3	0	22	0	0	0	15	0	0	0
Search										
LUT	5	1	19	11	7	4	7	6	3	1
LBM	8	2	65	8	3	4	79	3	19	1
Other										
Startle	5	1	1	0	6	0	4	0	2	0

RHM: rapid head movement; LUT: look under table; LBM: look behind mirror.

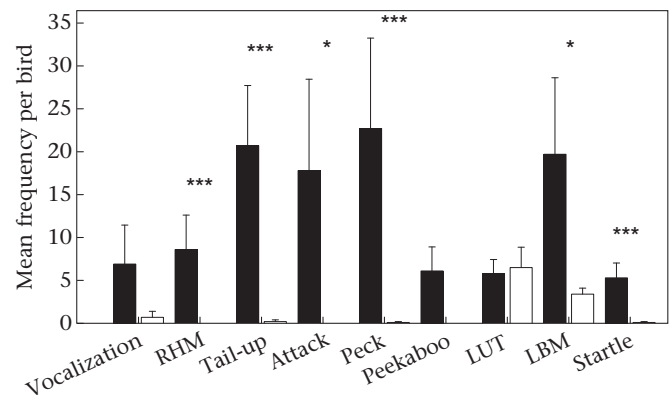


Figure 1. Comparison of responses to vertical mirror stimulation. Mean frequencies (group mean + SEM, $N = 10$) are shown. RHM: rapid head movement; LUT: look under table; LBM: look behind mirror. Black bars represent data from reflective mirror's surface (R) sessions and white bars show data from nonreflective mirror's surface (nR) sessions. * $P < 0.05$; *** $P < 0.005$ (Wilcoxon signed-ranks test).

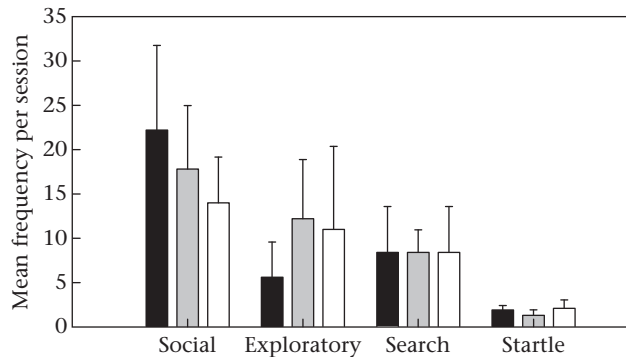


Figure 2. Frequency of behavioural categories during vertical mirror stimulation. Mean frequencies (group mean + SEM, $N = 10$) are shown. Social responses include vocalization, rapid head movement, tail-up and attack. Exploratory responses include peck and peekaboo. Search responses include look under table and look behind mirror. Startle responses only include startle. Black bars represent data from first reflective mirror's surface (R) sessions; grey bars, data from second R sessions; and white bars, data from third R sessions.

Discussion

Our study provides the first description of the initial reaction to a vertical mirror by captured corvids that had become independent in the wild. When first confronted with the mirror NC crows treated their mirror image as a conspecific. Their agonistic responses to their mirror image (e.g. rapid head movements, tail-up and attack) continued over the experimental sessions, with no significant decrease in frequency over time. However, the crows also engaged in search (look behind the mirror) and mirror-directed exploratory behaviour (peck and peekaboo) during reflective sessions. Therefore, after 30 min of exposure to a vertical mirror the NC crows that we tested did not show any of the self-contingent responses recently found in Eurasian magpies (Prior et al. 2008). As in the jungle crow study (Kusayama et al. 2000), our NC crows were probably not given enough mirror exposure to elicit any self-contingent behaviour. We could not give the crows extended exposure to a vertical mirror because of the limited time that we had use of the birds in the aviary.

Responses during MIS were significantly more frequent during reflective (R) than nonreflective (nR) sessions (Fig. 1). Therefore, other than 'look under the table', all responses were triggered by the reflection of 'another bird' in the mirror. The equally frequent 'look under the table' behaviour observed across mirror sessions can be explained if birds expected to find food when visiting the experimental table. Birds often search for objects of interest or food in the sand of cages, especially when they have just been rewarded with a small number of meat blocks. In the absence of the 'other bird' after they had eaten the meat bait on the table, crows immediately searched for food under the table. Thus, 'look behind mirror' appeared to be the only valid mirror-induced search behaviour.

Only three birds made 'vocalizations' during mirror sessions. We expected 'vocalizations' to be more evenly distributed across groups and individuals, given that begging in the wild is common in juveniles begging for food from adults and adult females begging for food from their partners in courtship behaviour. We were surprised that the dominant male adult among the study crows, Español, made submissive juvenile-like begging calls in front of his own mirror image. Other than Cuba, juveniles in this study made no 'vocalizations' in front of the reflective mirror (see Tables 3, 4). One possible explanation for the lack of begging by juveniles is that they might have recognized another juvenile in the mirror and therefore

did not beg to it. Most crows (adults and juveniles) did perform other forms of social displays (i.e. agonistic), though. Therefore, Español's begging might have been a submissive response to recognizing a high-ranking adult male crow in the mirror. He was also the only adult to attack the mirror, doing so twice. Nevertheless, we have never observed such begging when free-living dominant males are in close proximity at feeding sites.

We found no evidence that NC crows habituated to their mirror images over time. Other than for Egg and Slevin, agonistic social behaviours (tail-up, rapid head movement and attack) by crows restarted on the next session (see Appendix Tables A1, A2). Given that Egg and Slevin made almost no mirror-directed exploratory behaviours in the R sessions (Slevin made one peekaboo in R₃ session), they still appeared to have no understanding of mirror properties or showed any self-contingent behaviour in front of the mirror. Chimpanzees and orang-utans, *Pongo pygmaeus*, show a rapid extinction of social responses and initiate self-directed behaviour after 3 days of MIS (when given 8 and 5 h of mirror exposure per day, respectively; Gallup 1970; Suarez & Gallup 1981). Eurasian magpies also show transient social behaviours during the first 150 min of mirror exposure, and then start showing contingent behaviour in the following 100 min of exposure. Some gorillas, *Gorilla gorilla*, and orang-utans have become intensely curious about mirrors and have even grown attached to them, resisting attempts by experimenters to remove the mirrors from their cages (see Gallup 1968). Although three of five captive Eurasian magpies preferred compartments with mirrors (Prior et al. 2008), the wild-caught NC crows in our study did not spontaneously approach the mirror or stay in its proximity unless it was baited with food. However, this may have been because we placed the vertical mirror on a low table and wild-caught crows prefer to perch higher up in their cages.

Despite these differences, our study crows appeared to search actively for their mirror image in a similar way to that described in primates and children. They repeatedly searched behind the mirror during reflective mirror sessions (Fig. 1), and this often happened immediately after they lost sight of their mirror image (e.g. when they moved away from the mirror during social displays). Three juvenile NC crows in experiment 1 (Angel, Sisu and Tiga) reacted to their mirror image in a way similar to how primate infants react by repeatedly performing 'peekaboo' behaviours (see Appendix Tables A1, A2). Children and orang-utan infants start experimenting with mirror movement synchronism at 2 years of age (Robert 1986). Two-year-old children also actively seek their mirror image when they lose sight of it (Kleeman 1973; Modarressi & Kenny 1977), at about the time they recognize themselves in mirrors (Amsterdam 1972). They also search behind the mirror (Dixon 1957), probably in an attempt to re-establish contact with their mirror image. Two African grey parrots have also been reported to search behind mirrors, the juvenile (Karol) doing so more than the adult (Pepperberg et al. 1995). Similarly, monkeys (Anderson 1984) and apes (Suddendorf & Collie-Baker 2009) reach behind the mirror while in front of it as if to touch the monkey in the mirror.

EXPERIMENT 2: MIRROR-MEDIATED SPATIAL LOCATION TASK

Methods

Subjects

We used mirror-experienced birds Español and Sisu from experiment 1 and two new crows (Peel and Obo) kept in captive conditions as per experiment 1. Pelé was a male adult and Obo a female juvenile. Both Pelé and Obo were also presumed to be naïve to mirrors at the start of experiment 2.

We only had four crows available for experiment 2 at the time we carried it out. We could not use birds from experiment 1 other than Español and Sisu because they had been given mirror-mediated search experience for an unrelated experiment (Taylor et al. 2010b).

Experimental procedure

Experiments were conducted in a cage measuring 4 × 2 m and 3.0 m high. Crows could not see into this cage from the other aviary cages. A horizontal mirror (40 cm wide × 6 mm thick and 50 cm high) was set on top of a table (1.5 m high × 60 cm wide) at one side of the cage. As in experiment 1, mirrors were thoroughly cleaned before each session.

Habituation

Subjects were each given one 10 min habituation session with a horizontal mirror (same dimensions as in experiment 1) on the experimental table prior to training. This involved placing 10 target meat cubes (ca. 1 cm³) on the horizontal mirror at the start of the session. The crows either quickly ate all the bait while they were standing over the mirror or took them away to eat elsewhere in the cage. The following day we installed a perch 70 cm long and 11 cm above the horizontal mirror.

We then gave birds one session in which they had to retrieve a minimum of 10 target meat cubes from the perch and from the mirror's surface. The experimenter entered the cage and baited the apparatus four times. Birds were offered one, one, six and five meat cubes on each baiting event, respectively. A total of 11 meat cubes were left on the perch and two meat cubes on the mirror's surface (1 cm from the mirror's edge on the back side of the table). All sessions terminated before 10 min had elapsed. All crows showed some level of caution when approaching the mirror's surface. Their horizontal reflection caused initial startle responses that were quickly extinguished. Only one crow (Pelé) did not approach the mirror's surface after a startle, when it failed to retrieve the meat cubes there.

We then hung meat from the perch on a piece of cotton string 2 cm long. We gave birds three opportunities to retrieve a meat cube. All subjects readily bent their bodies over the perch to retrieve the cubes. As in the previous session, the crows only stayed perching over the mirror for up to a few seconds while they retrieved the meat. In some cases, when a crow would not approach the horizontal mirror or the new perch we placed smaller pieces of meat on top of the perch. We did not keep a record of how many of these extra small pieces of meat a crow received before it had taken the three meat cubes on the hanging string.

Next we introduced a wooden two-box choice apparatus (32 × 9 cm and 10 cm high) into the cage. It was placed on the horizontal mirror under the perch. The front of the apparatus consisted of two separated, open compartments (15 × 8 cm and 9 cm high; Fig. 3a). Each compartment had a piece of occluding board 3 cm deep at the top front of the compartment that could be used gradually to obstruct a crow's view of the meat baits (by manipulating the length of the string, see below). A crow could at all times clearly see the meat bait reflected in the horizontal mirror. When the food was hidden behind the occluding board a crow had to bend its head below the board to see it directly. Furthermore, crows could only see their heads in the mirror while searching for food inside the boxes because their bodies were completely occluded by the reflection of the apparatus. The aim of this habituation phase was to get birds comfortably extracting hidden meat bait before they moved on to testing with the training phase.

The experimenter entered the experimental cage and baited one of the two compartments at random. To do this, a 1 cm piece of

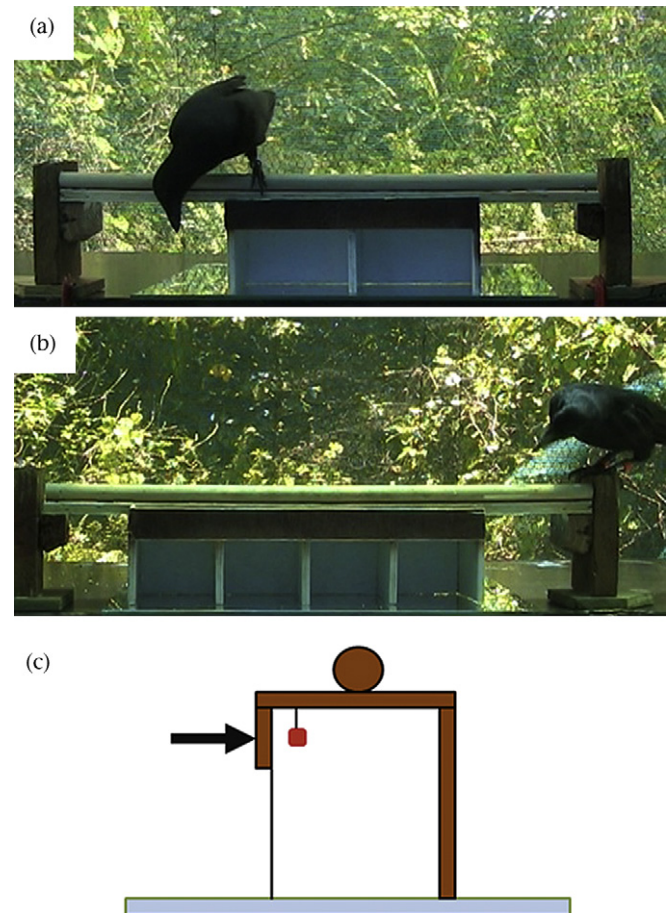


Figure 3. Mirror-mediated spatial location task set-up and apparatus. (a) The two-box training apparatus. (b) The four-box test apparatus. (c) Cross-section of a baited compartment. The black arrow points to the occluding board. The red square indicates the meat bait hanging from a piece of string.

string with meat bait on one end was attached to the roof in the centre of the compartment and just behind the occluding board. A crow was then allowed to retrieve the meat. To encourage birds to locate meat hanging behind the occluding board, we first hung it on a longer piece of string so they could see it without the need to bend their heads into a compartment. The four crows were given a total of 10 habituation trials. However, each bird had a different habituation experience. We had to modify the procedure to suit each bird's level of interest and cooperation. Pelé extracted meat only twice over the 10 habituation trials.

Training

After habituation, the four crows were given three blocks of 10 trials each with the two-box apparatus. The aim of the training was (1) to make crows equally proficient at extracting meat hidden behind the occluding board before testing, and (2) to allow us to determine valid criteria for scoring trials in the four-box condition. As with the habituation phase, the experimenter entered the cage and baited one of the two compartments at random (counter-balanced, see Appendix Fig. A1). With the exception of Pelé, all crows were given trials with completely occluded meat cubes from the start (Appendix Fig. A1). Sessions were terminated once 10 meat cubes had been retrieved or 10 min had elapsed. As before, we sometimes placed a meat cube on the middle of the perch before leaving the cage if a bird was reluctant to come down to the perch.

Reversed mirror control

After the training, three of the four crows were transferred to the four-box spatial location task. The best performing bird (Obo) in training was given a 10 min reversed mirror control before moving to the four-box apparatus. In the control, we reversed the horizontal mirror so that the reflective surface faced downwards. The control was divided into two trials of 5 min each separated by 1 min. One compartment was baited behind the occluding board in each trial: the right compartment in trial 1 and the left one in trial 2. In the first trial, if Obo did not extract the occluded bait by 2 min we placed visible bait on the apparatus every minute for 3 min to keep her interested in it. The first two baits were left on the middle of the perch. The third and final bait was left on the mirror's surface, in front of the separation between the two compartments. In the second trial we did not use any visible meat bait.

Mirror-mediated spatial location task

We used a wooden four-box apparatus (43 × 9 cm and 10 cm high) that differed from the two-box apparatus used in training only in the number and size of compartments (Fig. 1b). Three crows (Español, Sisu and Obo) were given daily sessions of 10 trials. Owing to bad weather conditions, Pelé was tested on the same day, with sessions 3 h apart. In each trial, the experimenter baited pseudorandomly one of the compartments when outside the experimental cage (out of the test crow's view) and made sure that the meat cube could not be seen from the front. The apparatus was then placed in the experimental cage between the mirror and perch as with the two-box apparatus. The experimenter then left the cage and the crow was allowed to retrieve the bait. We did not use any extra meat bait during the testing. A 10-trial session was terminated once 10 meat cubes had been retrieved. At the end of a session, all four compartments had been baited at least twice and no compartment was baited in two consecutive trials.

Data analysis

All trials were recorded on video camera through a small hole in the tarpaulin covering the walls of the experimental cage. We scored mirror-mediated search in a trial if a crow's behaviour met two criteria: (1) it inserted its head only into the baited compartment; and (2) it did not lower an eye below the bottom edge of the 3 cm deep occluding board along the top of an unbaited compartment (or the unseen line of the bottom of the board that projected out either side of the apparatus). Sometimes when a crow clearly moved to insert its head into a baited compartment it violated criterion 2 by partially moving in front of an adjacent unbaited compartment. This behaviour always occurred when a crow was not standing directly above the baited compartment. We still classified these trials as successful if the baited compartment was the first one a crow searched in ($N = 5$ trials). We recorded in which compartment(s) in unsuccessful trials a crow violated criterion 2.

We did not statistically test the crows' performance in the two-box training phase because the compartments were baited in view of the test birds and meat was also sometimes placed on the perch. To test whether crows successfully solved the four-box task, we tested each block of 10 trials for significance using the binomial test ($\alpha = 0.05$); a crow successfully solved the task if they had six or more correct trials out of 10. We terminated testing immediately after a crow met the significance criterion in a block of 10 trials. For each trial, we recorded the approximate position on the perch that a crow initially flew to before it started to inspect the apparatus. We also recorded the time that it took the crow to retrieve the hidden bait from the time it landed on the perch (i.e. latency to food retrieval).

After the present mirror study, the 12 crows used in experiments 1 and 2 participated in further aviary experiments. The research reported in this paper was approved by the University of Auckland Animal Ethics Committee and complies with the laws of New Caledonia.

Results

Training

All four crows readily extracted the occluded meat from the two-box apparatus at the end of training. As Pelé never extracted the occluded bait in his first block unless there was another piece of meat on the mirror's surface (see Appendix Fig. A1), we only used data from the last two blocks for each crow when analysing success rates and latencies to food retrieval. Over the last two blocks (B2 and B3) crows chose to inspect the baited compartment first in 50 of the 79 trials. On the remaining 80th trial (B2 trial 10, Appendix Fig. A1), the crow (Obo) did not visit the apparatus because it was probably satiated. Sisu and Pelé had 10 successful trials out of 20 in the last two blocks, Español 12 out of 20, and Obo 18 out of 19. In two of her 19 trials, Obo chose the previously baited compartment. Sisu did so on nine of the 20 trials, Pelé eight of his 20 trials and Español four of his 20 trials.

We found no evidence that crows had improved their extraction times from block 2 to block 3 (Wilcoxon signed-ranks tests: Español: $W = 22$, $N = 10$, $P = 0.63$; Sisu: $W = 24$, $N = 10$, $P = 0.77$; Pelé: $W = 13$, $N = 10$, $P = 0.16$; Obo: $W = 22$, $N = 10$, $P = 0.63$). However, Obo and Español were faster at getting the meat after landing on the perch (mean \pm SEM = 3.99 ± 0.03 s and 4.02 ± 0.06 s, respectively, $N = 20$ trials) compared to Sisu and Pelé (6.77 ± 0.10 s and 7.60 ± 0.09 s, respectively, $N = 20$ trials).

Reversed mirror control

Obo had no obvious neophobic response to the reversed mirror in the first session. As soon as the experimenter left the cage on the first trial, Obo came down and sat on the far end of the perch and scanned the mirror as she usually did during her training trials. After scanning the mirror, Obo left the apparatus without inspecting any compartment (clip 1 in Supplementary Movie S2). The experimenter then baited the perch and left. Obo came back to the apparatus immediately and ate the extra bait. She slightly lowered her head and scanned the mirror directly below the baited compartment, but again left the apparatus (clip 2 in Supplementary Movie S2). The perch was baited again. This time, after scanning the mirror directly below the unbaited compartment Obo inspected the compartment, and then left the apparatus (clip 3 in Supplementary Movie S2). The last bait was placed on the nonreflective side of the mirror. Obo returned to the perch and reached down and got the bait on the back of the mirror. After taking the meat on the mirror, she immediately extracted the meat behind the occluding board (clip 4 in Supplementary Movie S2).

In the second session, Obo immediately flew down and scanned the mirror from the far end of the perch. She then moved along the perch until she was positioned directly over the wall that separated the two compartments. Obo scanned the mirror again then left the apparatus. She did not return again to the apparatus for the remainder of the session (clip 5 in Supplementary Movie S2).

Mirror-mediated spatial location task

All four crows successfully located hidden meat baits by using the bait's reflection in the horizontal mirror (clip 1 in Supplementary Movie S3). Obo and Pelé reached criterion in

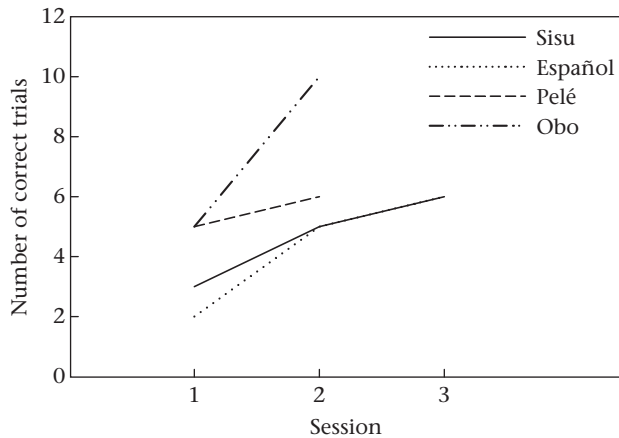


Figure 4. The performance of crows in the mirror-mediated spatial location task. Pelé and Obo reached criterion in session 2, and Español and Sisu did so in session 3. The Y axis shows the number of correct trials per session and the X axis shows the session number.

their second block (Obo scored 10/10 and Pelé 6/10; Figs 4, 5). Both Sisu and Español succeeded in their third block (both scored 6/10). In unsuccessful trials across all blocks (Español: $N = 17$; Sisu: $N = 16$; Pelé: $N = 9$; Obo: $N = 5$), the crows either searched in the compartment that they had last found meat and/or inserted their heads into at least one other empty compartment before choosing the correct one (clip 2 in [Supplementary Movie S3](#)).

On 18 of the 47 unsuccessful trials a crow first potentially inspected a compartment nonadjacent to the baited one before it found the food (Español: $N = 7$; Sisu: $N = 7$; Pelé: $N = 4$) (Fig. 5). On these occasions the crows either (1) inspected the nearest compartment to their landing position on the perch, or (2) inspected the previously baited compartment. Sisu appeared to use the first strategy by default at the start of every block. However, by trial 4 in block 3 she had almost completely switched to using the mirror (Fig. 5). On the other hand, Español used both the above strategies in unsuccessful trials (see his blocks in Fig. 5). Pelé used the second strategy in five of nine unsuccessful trials (Fig. 5). The number of trials ($N = 14$) in which the crows initially searched the compartment where they last found meat tended to decrease over time (Table 5).

The crows other than Español usually landed on the far left end of the perch (when viewing the apparatus from the front as in Fig. 3a) then moved along it to inspect the apparatus. On only six of their 70 trials did these crows land partially or completely on top of one compartment (Sisu: $N = 5/30$; Pelé: $N = 1/20$). On three of Sisu's five trials she inspected the compartment directly below her (Fig. 5). All the six trials were unsuccessful ones. In contrast, Español inspected the compartment directly below his landing position on 17 of his 30 trials. Five of those 17 trials were successful (B1 trials 3 and 5, B2 trials 4 and 8, B3 trial 10).

The time crows took to retrieve the meat after landing on the perch was significantly shorter on successful trials (Español: median = 1.64 s, range 1.08–3.04; Sisu: 1.36 s, 1.04–3.84; Obo: 1.92 s, 1.12–3.2; Pelé: 2.24 s, 1.64–6.0) than on unsuccessful trials (Sisu: 3.24 s, 1.4–7.96; Español: 2.56 s, 1.4–6.0; Obo: 3.56 s, 1.84–6.4; Pelé: 6.6 s, 2.4–18.28; Mann–Whitney U test; Español: $U = 37.5$, $N_1 = 11$, $N_2 = 19$, $P = 0.003$; Sisu: $U = 21.5$, $N_1 = 13$, $N_2 = 17$, $P < 0.001$; Obo: $U = 12.5$, $N_1 = 14$, $N_2 = 6$, $P = 0.012$; Pelé: $U = 13$, $N_1 = N_2 = 10$, $P = 0.004$).

Discussion

All four wild-caught NC crows successfully learnt to use a horizontal mirror to locate hidden food in the four-box spatial location task, doing so in either 20 or 30 trials. The four crows did not seem to be using olfaction to find the meat baits. First, Obo's poor performance in the reversed mirror control suggested that she at least was not using olfaction to find hidden baits. Without a meat bait on the mirror's surface, Obo's behaviour gave no indication that she knew one of the compartments was baited. Second, if crows were using olfaction and not the mirror to locate meat we would have expected little difference in latency to food retrieval between trials. However, Obo, Pelé and Sisu took significantly less time to retrieve the meat in successful trials than in unsuccessful ones. Last, if crows depended on olfaction alone we would also have expected them to search consistently the previously baited compartment on unsuccessful trials where meat had recently been hanging. Obo, Pelé and Sisu had 30 unsuccessful trials in total. On only 10 of those 30 trials did these crows search in the previously baited compartment (five trials each for Pelé and Sisu; see Fig. 5). As the meat bait was never in direct contact with the walls of a compartment but hung from string, any residual odour once the bait was removed should have been very weak compared to that coming from the baited compartment.

Our study crows may have had some experience with horizontal reflections of themselves in the wild (e.g. when drinking from pools of rain water). Therefore, it was possible that they had used this past experience to solve the spatial location task. However, given that only one of the four crows solved the two-box training phase in the last two blocks this possibility seems highly unlikely.

Although Español met the statistical criterion for solving the problem, he may not have used the mirror to locate food in five of his 13 successful trials. In these five trials, he found the bait in the compartment directly below his landing position, which he immediately inspected after landing (see Fig. 5). On the remaining eight successful trials he did not look in the compartment directly below his landing position. On 11 of 17 unsuccessful trials, Español immediately looked in the compartment directly below his landing position. Similar behaviour was reported for one of two African grey parrots (Kyaaro, juvenile) in a study by [Pepperberg et al. \(1995\)](#) which used a three-box apparatus. Kyaaro appeared to have used the mirror to locate hidden pasta in 44 of 60 trials. However, the authors argued that Kyaaro developed a position preference and inspected the compartments in consecutive order, starting with the same compartment on one side of the apparatus ([Pepperberg et al. 1995](#)).

The two juveniles that had no vertical mirror experience (Obo and Pelé) solved the four-box spatial location task faster than Sisu and Español who had had experience with vertical mirrors in experiment 1. In fact, Obo's performance was by far the most impressive. In the two-box training phase she chose correctly nine of 10 times in each of her three blocks, and she scored a perfect 10 out of 10 in the final block of the four-box task.

Obo's poor performance in the reversed mirror control ([Movie S2](#)) suggests that she had used the mirror in the training and the second block of the four-box condition to decide which compartment to inspect first. However, her performance in the last six trials in the first block of the four-box task was surprisingly very poor (unsuccessful in trials 5–8 and 10; Fig. 5). We conservatively scored trials 5–8 and 10 as unsuccessful, but it was unclear whether Obo had first inspected a nonbaited compartment. It was possible that she had lowered her head in front of an unbaited compartment (violation of criterion 2) in the process of moving it to extract the

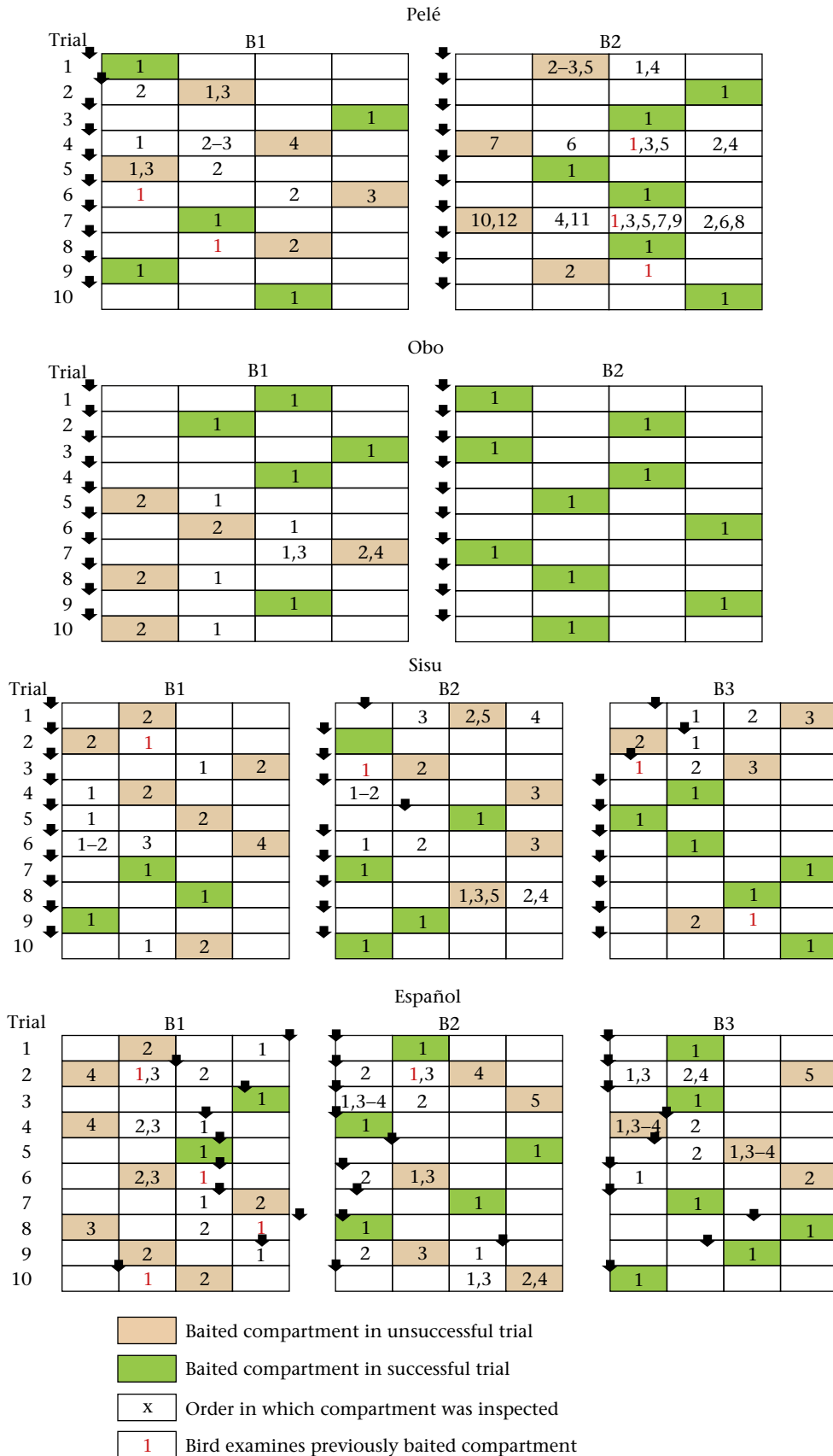


Figure 5. Trial-by-trial performance in the mirror-mediated spatial location task. A row of squares in each block indicates one trial. The four rectangles in a row that make up a trial represent the four compartments from left to right as seen in Fig. 3b. The black arrows represent a crow's approximate landing position.

Table 5
Number of searches in the last baited compartment

Subject	Session 1	Session 2	Session 3
Sisu	1/10 trials	1/10 trials	2/10 trials
Español	4/10 trials	1/10 trials	0/10 trials
Pelé	2/10 trials	3/10 trials	–
Obo	0/10 trials	0/10 trials	–

meat in the baited one. Such a false violation of criterion 2 could occur because of two related factors: a bird not standing directly over the meat and the relatively narrower compartments of the four-box apparatus.

How were Obo and Pelé using the mirror to solve the four-box task? It seems unlikely that Obo and Pelé relied on mirror-triggered search because their performance met our criterion for significance in block 2. That is, they went directly to the baited compartment more times than would have been predicted by chance. It also seems unlikely that they had developed a full understanding of mirror correspondence before starting the four-box task because both birds made errors in their first block of trials. Povinelli (1989, page 129) argued that an animal capable of mirror-mediated spatial location must 'understand the correspondence between the object's relative position in a mirror and the real world counterpart to the position'. He also speculated animals could use mirrors to estimate and move towards the approximate location of the food. Once close enough, they would then use other proprioceptive means to find the exact location of the food (Povinelli 1989).

In our study crows, this type of mirror use would not require the mental representation that the food reflected in the mirror was the same as that in the real world behind the occluding board. Rather, it would only require learning to expect to find food (visible in the mirror) when moving towards the food's mirror image. Therefore, Obo and Pelé were more likely to have been exploiting the correlation between the location of objects and their mirror images. In other words, they learnt to associate the mirror image of the meat with finding the bait in the compartment at that location. However, we cannot exclude the possibility that crows like Obo could use this correlation to develop heuristically over time an understanding of mirror correspondence based on mental representations of visually displaced objects.

CONCLUSION

Our study is the first to investigate the mirror-induced behaviour of captured corvids that had become independent in the wild. In agreement with the jungle crow study (Kusayama et al. 2000), NC crows did not habituate to vertical mirrors. Instead, they consistently engaged in agonistic behaviour in response to their mirror reflection. However, unlike the jungle crows, which could not look behind the mirror, NC crows made exploratory behaviours similar to those seen in primates. Our study suggests that mirror-directed behaviour and exploration in birds as well as primates is facilitated by free access to the back of the mirror.

We also found that NC crows could successfully use a mirror to locate food, probably by exploiting the correlation between the location of objects and their mirror images. Not only did all four crows reach criterion within three sessions (30 trials), the crows without vertical mirror experience (Obo and Pelé) did so in fewer trials than the two crows with experience. These findings suggest that neither self-contingent responses to mirror reflections nor prolonged exposure to mirrors is necessary for some species to

exploit the basic correspondence between mirrored objects and their location in the real world.

The performance of three crows (Español, Pelé and Sisu) in the training and test conditions indicated that they had to learn by experience how to exploit the correspondence between the mirror image and the actual location of the meat. In contrast to these three crows, Obo's performance suggested that she had learnt the correspondence during the very first trial of training. Individual differences in mirror use performance might reflect each individual's cognitive abilities (e.g. brain capacity to process visual and spatial information) and/or the amount of experience with mirrors. Obo's relatively error-free performance tends to suggest that the speed at which NC crows learn to use mirrors depends on their cognitive abilities rather than the amount of mirror experience given. She was also the fastest of three crows in solving the trap tube problem (Taylor et al. 2009). Therefore, Obo's performance with mirrors may be associated with a superior ability to solve visuospatial problems. Additional studies will help determine whether there are any significant age or sex effects on mirror use in NC crows.

Previous mirror studies have not been designed to provide cross-species data in birds (Pepperberg et al. 1995; Kusayama et al. 2000; Prior et al. 2008). Also, most avian mirror studies have exclusively focused on using mirrors and the mark test to look for evidence of complex social cognition (for a complete list of species that have failed the mark test, see Pepperberg et al. 1995). Rigorous cross-species comparisons about birds' understanding of how mirrors work will require careful attention to the design of mirror tasks. For example, the use of large or vertical mirrors may trigger social responses that inhibit learning about how mirrors work. The design of mirror-guided reaching tasks also needs to take into account the absence of manipulatory limbs. Birds have yet to be tested in mirror-guided reaching tasks, although one design involving string pulling has been proposed (Pepperberg et al. 1995). In an unrelated visually restricted string-pulling study, the string-pulling efficiency of naïve NC crows increased when visual feedback was available in a nearby mirror (Taylor et al. 2010b). This suggests that with the appropriate experimental design NC crows might be able to learn how to use mirrors in synchrony with their body movements.

Along with the African grey parrot study (Pepperberg et al. 1995), our findings show that birds are suitable for investigating a range of cognitive abilities using mirrors. Although we do not know whether NC crows can pass the mark test after extended mirror exposure, their ability to succeed at a mirror-mediated spatial location task demonstrates that *Corvus* species are capable of primate-like processing of mirror information. NC crows are an appropriate model because they react to mirrors and can use them to find visually displaced objects. More importantly, they help to fill the large gap in mirror studies on corvids, a group of birds considered to be the primate equivalents of the avian world (Emery & Clayton 2004).

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2011.07.033.

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APPENDIX

Table A1
Responses to vertical reflective (R) mirror sessions: Group 1

Responses	Español			Angel			Boxer			Sisu			Cuba		
	R ₁	R ₃	R ₅	R ₁	R ₃	R ₅	R ₁	R ₃	R ₅	R ₁	R ₃	R ₅	R ₁	R ₃	R ₅
Social															
Vocalization	21	7	12	0	0	0	0	0	0	2	0	0	22	2	3
RHM	2	1	1	21	12	10	1	0	3	1	2	0	0	1	0
Tail-up	19	5	8	38	27	14	5	2	2	6	11	5	3	5	3
Attack	2	0	0	41	37	28	0	0	0	2	16	23	3	8	8
Exploratory															
Peck	1	0	0	38	20	1	2	0	0	0	7	89	2	1	6
Peekaboo	3	0	0	3	17	2	0	0	0	0	9	6	0	0	0
Search															
LUT	2	3	0	15	4	0	4	0	3	7	0	0	2	1	0
LBM	5	3	0	38	20	7	2	0	1	3	22	54	1	7	11
Other															
Startle	2	0	3	0	0	1	4	1	1	1	0	3	0	0	2

RHM: rapid head movement; LUT: look under table; LBM: look behind mirror.

Table A2
Responses to vertical reflective (R) mirror sessions: Group 2

Responses	Robin			Egg			Slevin			Ronja			Tiga		
	R ₂	R ₄	R ₆	R ₂	R ₄	R ₆	R ₂	R ₄	R ₆	R ₂	R ₄	R ₆	R ₂	R ₄	R ₆
Social															
Vocalization	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RHM	3	5	5	3	0	0	0	0	0	1	3	2	4	4	1
Tail-up	3	5	8	6	0	0	2	0	0	3	5	4	7	11	0
Attack	0	0	0	0	0	0	0	0	0	1	0	0	0	9	0
Exploratory															
Peck	0	4	4	2	0	0	0	0	1	0	1	0	2	46	0
Peekaboo	0	1	1	0	0	0	0	0	0	0	0	0	3	16	0
Search															
LUT	1	3	0	1	4	2	0	1	1	0	2	2	0	0	0
LBM	1	5	1	2	0	0	0	0	0	0	4	2	0	8	0
Other															
Startle	4	6	10	4	2	0	1	0	1	2	3	0	1	1	0

RHM: rapid head movement; LUT: look under table; LBM: look behind mirror.

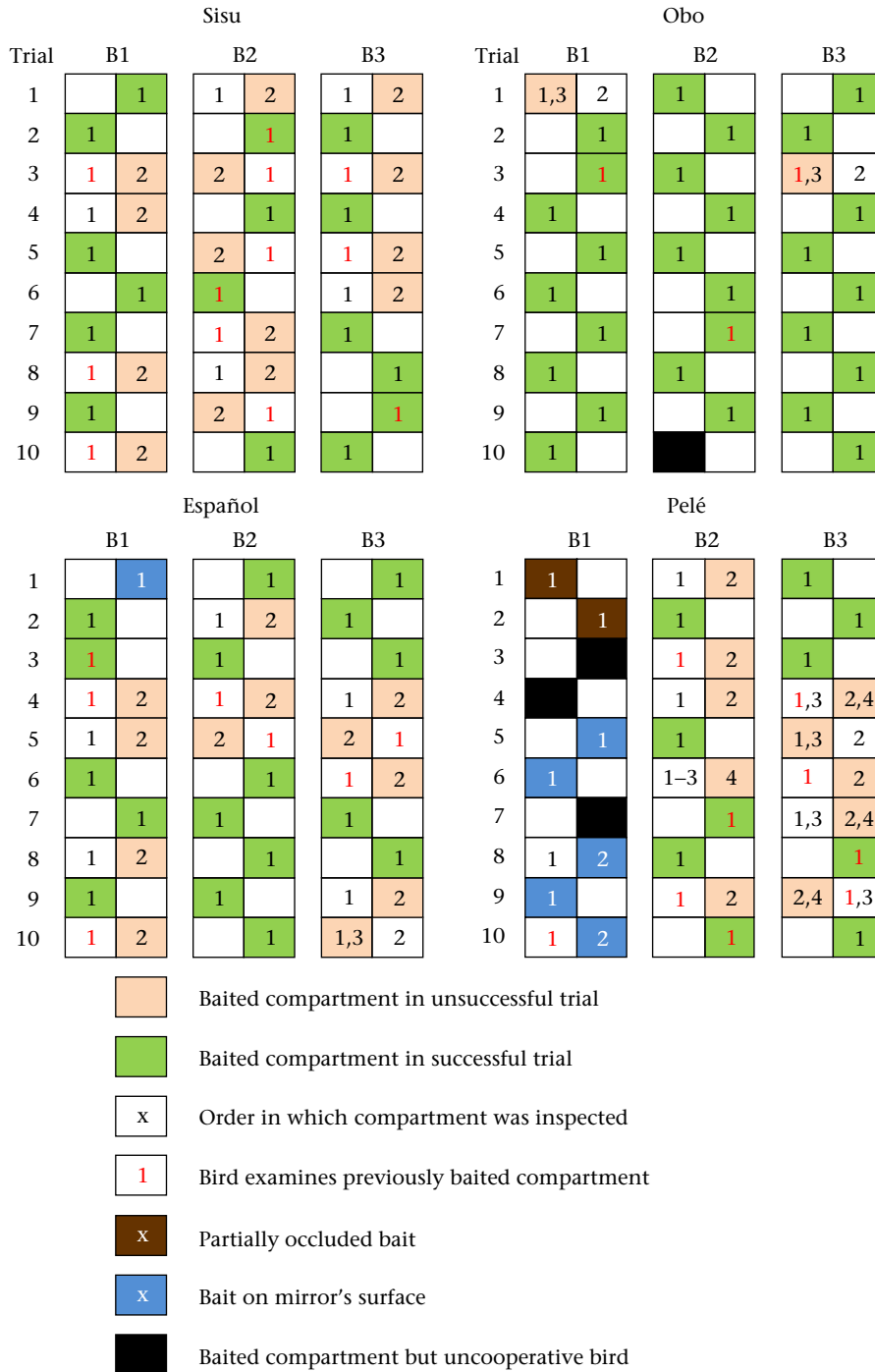


Figure A1. Trial-by-trial performance in the two-box training task. A row of squares in each block indicates one trial. The two squares in a row that make up a trial represent the two compartments from left to right as seen in Fig. 3a.