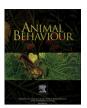
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New Caledonian crows' responses to mirrors

F. S. Medina*, A. H. Taylor, G. R. Hunt, R. D. Gray*

Department of Psychology, University of Auckland

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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 ages 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

^{*} Correspondence: F. S. Medina and R. D. Gray, Department of Psychology, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand.

E-mail addresses: fmedinaro@gmail.com (F. S. Medina), rd.gray@auckland.ac.nz (R. D. Gray).

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 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 ($60 \times 100 \text{ cm}$) 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 problemsolving 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

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