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„Mirror image stimulation: An investigation of mirror self-
recognition in carrion crows
(*Corvus corone corone, corvus corone cornix*)“

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ABSTRACT

In 1970, Gordon G. Gallup showed for the first time that non-human animals are able to recognize themselves in mirrors. Since this experiment in which 4 chimpanzees succeeded to pass the then newly designed “mark test”, many other species were subjected to the same paradigm, but only few of these species passed this test. The ability to recognize oneself in a mirror and to pass the Mark Test has been used as an indicator of the possession of self-awareness which is a prerequisite for Theory of Mind related cognitive abilities like the expression of empathy and sympathy. The success of several great apes and the continuous failing of monkeys revealed an evolutionary gap for mirror self-recognition (MSR) in the primate order. However recent studies showing that dolphins (*Tursiops truncatus*), Asian elephants (*Elephas maximus*) and magpies (*Pica pica*) pass the mark test suggest convergent evolution of this trait. The emergence of this specific ability might be connected to the possession of common cognitive abilities, considering that all the species that have passed the mark test are social animals, with complex social cognition and advanced abilities in theory of mind related tasks.

The present study is the first exploration of mirror self-recognition in carrion and hooded crows and aims to provide additional information on the evolution of MSR and its link to other cognitive abilities. I investigated how crows respond to mirrors with a special focus on mirror self-recognition, which was tested using a classical mark test paradigm. The crows showed a preference for the mirror and exhibited the expected sequence of behaviours during their individual exposure sessions – starting by social behaviours, over inspective behaviour up to contingency testing, but failed to show self-directed behaviours. In the subsequent Mark Test, the crows did not exhibit any self- and mark-directed behaviour, rendering the results inconclusive and refraining conclusions about the ability of MSR in the case of the carrion crow.

ZUSAMMENFASSUNG

Im Jahre 1970, bewies Gordon G. Gallup erstmals, dass Spiegelselbsterkennung keine ausschließlich menschliche Eigenschaft ist. Seit diesem Experiment, in dem 4 Schimpansen, den damals entstandenen Spiegeltest, erfolgreich bestanden, wurden zahlreiche anderen Tierarten dem gleichen Paradigma unterzogen, doch nur wenige dieser Arten bestanden den Test. Die Fähigkeit sich selbst in einem Spiegel zu erkennen und den sogenannten Spiegeltest zu bestehen, wird als Indikator des Selbstbewusstseins eines Individuums gesehen, welches eine Grundvoraussetzung für bestimmte kognitive Fähigkeiten, die mit der Theory of Mind in Verbindung gebracht werden, wie zB. dem Ausdruck von Empathie und Sympathie. Der Erfolg mehrerer Menschenaffenarten und das stetige Scheitern von Affen in dieser Aufgabe, offenbart eine evolutionäre Kluft innerhalb der Ordnung der Primaten. Jüngste Studien zeigten jedoch, dass auch Delfine (*Tursiops truncatus*), Asiatische Elefanten (*Elephas maximus*) und Elstern (*Pica pica*) den Spiegeltest erfolgreich absolvieren können. Diese rezenten Ergebnisse lassen ebenfalls auf eine konvergente Evolution dieser Eigenschaft schließen. Es wurde vorgeschlagen, dass die Entwicklung dieser Fähigkeit im Zusammenhang mit bestimmten kognitiven Fähigkeiten stehe, die die erfolgreichen Arten miteinander teilen. All diese Arten leben in sozial komplexen Verbänden, besitzen fortgeschrittene soziale Kognition und erzielen meist gute Ergebnisse in Theory of Mind Aufgaben. Die vorliegende Arbeit ergründet erstmals Spiegelselbsterkennung bei Aaskrähen und trägt somit zur wachsenden Literatur über Spiegelversuchen an Corviden, und der Erkundung der möglichen Ursachen für die beobachteten Unterschiede zwischen den Corvidenarten bei. Es wurde untersucht wie sich Krähen vor einem Spiegel verhalten, mit Fokus auf Spiegelselbsterkennung, die durch Anwendung des klassischen Spiegeltest nachgewiesen werden soll. Die getesteten Krähen offenbarten eine eindeutige Präferenz für den Spiegel und wiesen die vorhergesehenen Abfolge der Verhaltensweisen vor, beginnend mit sozialem Verhalten ihrem Spiegelbild gegenüber, über die Erkundung des Spiegels bis zu Kontingenztestendes Verhalten. Das im Spiegeltest dargelegt Verhalten erlaubt aufgrund der ausgeblieben selbstbezogenen bzw. markierungsbezogenen Verhaltensweisen keine Schlüsse über die Fähigkeit der Selbsterkennung bei diesen Individuen zu fällen.

INTRODUCTION

Mirror self-recognition (MSR) develops between the ages of 18-24 months in human children (Amsterdam, Carolina, Hill, & Carolina, 1972; Lacan, 1949; Zazzo, 1969, 1979) at which point they are thought to possess a concept of self that goes along with the development of e.g. pretend play and imitation (Nielsen & Dissanayake, 2004). Mirror guided self-directed behaviours are the result of experience and maturation. Past research shows that the ability to recognize oneself in a mirror is not only subject to cultural variation (Broesch, Callaghan, Henrich, Murphy, & Rochat, 2011) but can be altered in a certain number of psychological disorders like autism (Mckissiek, 1984), schizophrenia (Platek & Gallup, 2002) or Alzheimer's disease (Biringer & Anderson, 1992). Due to the link between mirror self-recognition and the ability of self-representation, the study of the ability of MSR in patients with various psychological disorders could allow to determine the relationship MSR has with self-awareness and to pinpoint the neurological origin of self-awareness in humans and possibly by the same means in animals.

MSR is seen as an indication that an animal has a concept of its own body image (Nielsen, Suddendorf, & Slaughter, 2006), and has been interpreted as an index for the possession of a concept of self and self-awareness and therefore connected to autonoetic consciousness (Gallup, Jr, 1982, 1998; Gallup, Platek, & Spauling, 2014; Gallup & Povinelli, 1993; Keenan, Wheeler, Gallup, & Pascual-Leone, 2000). Mirror self-recognition has additionally been linked to Theory of mind related cognitive traits like the ability to express sympathy and empathy.

Investigations about MSR in non-human animals have shown that MSR is a scarcely spread ability in the animal kingdom. In a seminal experiment (Gallup, Jr, 1970), chimpanzees, stumptail macaques, long-tailed macaques and rhesus monkeys were confronted with their own reflection. The chimpanzees engaged in contingent and self-directed behaviour when facing the mirror and explored parts of their body they would not be able to see otherwise (e.g. the inner of their mouth, teeth and genitals) whereas the monkeys uttered none of these behaviours. Furthermore, to enforce these observations all were subjected to a mark test i.e. the animals were anesthetized then marked with a dye on a part of their body they would not be able to see without looking in the mirror (e.g. ears or forehead). Subsequently, their reactions were observed and compared when they were allowed access to a mirror or when not. The chimpanzees showed mirror guided self-directed behaviours like touching the spot with their

fingers while looking in the mirror, rubbing it and even looking at their fingers afterward. None of those behaviours were observed when the chimpanzees were denied access to the mirror. This data suggests that the chimpanzees recognized themselves. In contrast, the tested monkeys failed the mark test.

When confronted with a mirror, animals seem to go through a similar succession of up to four behavioural stages (Reiss & Marino, 2001). Yet not all species go through all of these stages. At first, they exhibit social behaviours (i.e. aggressive or submissive behaviours) acting upon their reflection as if confronted with an unknown conspecific. In a second stage, the animal inspects the mirror and in a third stage, it investigates its function and tests contingencies by for example looking behind the mirror or moving back and forth in front of it. Most species will continue to manifest behaviours indicative of the first and second stages throughout their mirror exposure, however long it might be. In the fourth and final stage, that only few species achieve, the individuals manifest self-directed mirror-mediated behaviour like investigating body parts that would not be visible to them otherwise. If an individual reaches this stage, it is assumed that, it understands the physical properties and function of a mirror and was able to make the connection between its reflection and its own body, which should be reflected in them passing the Mark Test.

Conversely, failing the mark test does not preclude the ability of self-recognition nor self-awareness, since numerous other factors like the motivation to attend to marks, the understanding of a mirror's function and the interest for the own body image can influence the outcome of the mark test. Therefore, the interpretation of the results of the Mark Test as well as the relation between MSR and self-awareness remain controversial (Heyes, 1994, 1995, 1996; Suddendorf & Butler, 2013, 2014; Swartz, 1997). Multiple models propose other interpretations of the results emanating from the Mark Test involving different mechanisms to reach the same results; these include cognitive (Bard, Todd, Bernier, Love, & Leavens, 2006), affective or dual route model approaches (Butler, 2015). The cognitive models incorporate interpretative approaches ranging from associative learning to rich interpretations like self-awareness and "the ability to become the object of one's own attention (Gallup, Jr, 1970, 1982, 1998). The cognitively less demanding interpretations of associative learning (Epstein et al., 1981) exclude the involvement of mental models, seeing MSR as "a by-product of the ability to distinguish between sensory information originating from within our body and sensory information from external sources" (Heyes, 1994, 1998) or as a result of contingency checking behaviour like Mitchell's theory, who tries to explain self-recognition via

kinesthetic visual matching (Mitchell, 1993a, b, 1997). In contrast, the affective models base themselves on studies showing that MSR can be affected by emotional states and might be related to attachment styles and the regulation of emotions (Butler, 2015). However, none of the numerous approaches can account for all the phenomena associated with mirror self-recognition and how humans and other animals react to mirrors.

For a long time, studies on MSR focused on primates revealing a dichotomy between apes and monkey and possibly even between apes and great apes (Suddendorf & Collier-Baker, 2009) in the ability to show MSR when given enough exposure time. Only chimpanzees (Gallup, Jr, 1970; Povinelli et al., 1997; Povinelli, Rulf, Landau, & Bierschwale, 1993; Veer, Gallup, Theall, Bos, & Povinelli, 2003), bonobos (Walraven, van Elsacker, & Verheyen, 1995), Orang-Utans (Lethmate & Dücker, 1973; Suarez & Gallup, 1981) and gorillas (Patterson & Cohn, 1981; Posada & Colell, 2007) but not gibbons (Hyatt, 1998; Suddendorf & Collier-Baker, 2009; Ujhelyi, Buk, Merker & Geissmann, 2000) were shown to pass the mark test, while monkeys systematically failed it and exhibited social behaviours towards the mirror indicative of stage 1 (stumptail macaques: Anderson, 1983; Garnett's greater bush baby: Becker, Watson, & Ward, 1999; pygmy marmosets: Eglash & Snowdon, 1983; Long tailed macaque: Gallup, 1977; Lemurs: Fornaseri, Roeder & Anderson, 1991; Cotton-top tamarins: Hauser, Miller, Liu & Gupta, 2000; Capuchin monkeys: Anderson & Roeder, 1989; Paukner, Anderson, & Fujita, 2004; Roma et al., 2007; Talapoin: Posada & Colell, 2005) even when the exposure time was prolonged (Gallup, 1977) or the motivation enhanced (Suddendorf & Collier-Baker, 2009). This indicates an evolutionary gap in MSR among primates. However, this idea has recently been challenged by a study on Rhesus macaques (Chang, Fang, Zhang, Poo, & Gong, 2015) in which the authors showed that Rhesus macaques are able to acquire the ability to pass the mark test with a high amount of visual-somatosensory training and then generate the behaviour spontaneously in a different setting, Hereby supporting an observation that showed Rhesus macaques with head implants inspected themselves in front of a mirror (Rajala, Reininger, Lancaster, & Populin, 2010).

Apart from primates, many other species have been tested in similar settings (e.g. seals: Delfour & Marten, 2001; dogs: Zazzo, 1979; pandas: Ma, Jin, Luo, & Zhang, 2015; cheetas: Wielebnowski, 1999; Fish: Desjardins & Fernald, 2010) but most exhibited no signs of mirror self-recognition. However, apes are not the only animals capable of MSR. Dolphins (Reiss & Marino, 2001), elephants (Plotnik, de Waal, & Reiss, 2006), magpies (Prior, Schwarz & Gürtürkün, 2008), ants (Cammaerts & Cammaerts, 2015) and cleaner wrasses (Hotta,

Takeyama, Asai, Tanaka, & Jordan, 2016 in rev) tested positive, while others like orcas and pseudoorcas (Delfour & Marten, 2001), manta rays (Ari & D'Agostino, 2016) and jackdaws (Soler, Pérez-Contreras, & Peralta-Sánchez, 2014) showed striking contingency checking behaviour. Although most self-recognizing species so far shared common ecological and cognitive characteristics that had been related to MSR, i.e. living in socially complex structures, possessing advanced abilities in Theory of Mind related task and being endowed with complex cognitive abilities; the results above testify of a convergent evolution as well as showing that this ability might not be as scarcely spread in the animal kingdom and as highly cognitively demanding as initially assumed.

Birds show a similar heterogeneous picture in their ability to pass the mark test as primates. While Epstein and colleagues showed in 1981 that with extensive training, pigeons trained to peck on marks, could react to marks on their own body and pass the mark test, Thompson and Contie (1994) were not able to replicate these results. Past studies on mirror image stimulation in birds proved the interest birds have in mirrors and their mirror reflection. Finches and budgerigars exposed to mirrors, showed an increasing preference for their own reflection compared to the exposure to a conspecific, food, or cardboard (Gallup Jr. & Capper, 1970). The interest seems to be particularly strong in naturally social bird-species that were socially deprived (Andrews, 1966; Diamond & Bond, 1989). However, most avian species, similar to monkeys, maintain a social reaction towards their reflection. Mirrors were therefore used to study social responses of bird species as they reliably elicited behaviours that were repeatable over time (blue grouse: Stirling, 1968; glaucous-winged gulls: Stout, Wilcox, & Creitz, 1969) and as potential “social substitutes” for laboratory birds, by giving them a sort of social stimulation, which in turn could have a stress-reducing effect on singly housed birds (Henry, Cars, Mathelier, Bruderer, & Hausberger, 2008). None of these studies reported the birds behaving any differently over time. Interestingly however, more recent studies on African grey parrots (Pepperberg et al. 1995) and New Caledonian crows (Medina, Taylor, Hunt, & Gray, 2011) showed that these two species were successful in a mirror mediated spatial location task. Thus proving that, even though the ability of self-recognition in these species is unclear¹, some birds do learn to utilize a mirror to locate food. This corroborates findings in Japanese monkeys that were able to retrieve a piece of apple by using a mirror

¹ The grey parrots were observed tapping the mirror with an open beak which was interpreted by the authors as being either beak wrestling (a social behaviour that would have been exhibited towards a conspecific) or a self-directed behaviour (Pepperberg et al., 1995). The New Caledonian crows (Medina et al., 2011) were given a relatively short amount of mirror image stimulation during which they exhibited social and investigative behaviours towards the mirror, that did not decrease in frequency during that time.

(Itakura, 1987) and pygmy marmosets that were given a mirror to observe conspecifics and directed their social responses not to the mirror but to the actual location of the conspecific (Egash & Snowden, 1983) even though neither one of these species pass the mark test. However, the ability to use a mirror and to understand its physical properties is not correlated to an animal's ability to recognize itself in a mirror though does appear to be a prerequisite for it.

Recent experiments on several corvid species reported contrasting results about the corvids' reaction to mirrors. Despite being relatively closely related (all members of the Corvinae sub family) (Ericson, Jansén, Johansson, & Ekman, 2005), some like magpies showed contingent and self-directed behaviour and even passed the mark test (Prior, Schwarz & Gürtürkün, 2008), whereas jackdaws (Soler et al., 2014), New Caledonian crows (Medina et al., 2011) and jungle crows (Kusayama, Bischof, & Watanabe, 2000) did not display any evidence of self-recognition, although the jackdaws did exhibit contingency checking behaviours when facing the mirror. The magpies thus remain the only avian species to have successfully passed the mark test.

There are however several methodological differences which might explain the observed discrepancies. The jungle crows in Kusayama and colleagues study (2000) were not given the possibility to look behind the mirror as it was placed against a wall. That might have hindered them to overcome the “social behaviour”-stage as they could not investigate the back of the mirror. The New Caledonian crows (Medina et al., 2011) in turn were given a much shorter exposure time to the vertical mirror than it was the case in Prior and colleagues study on magpies (2008). Finally, the study on jackdaws (Soler et al., 2014) questioned the efficiency of their marking method using stickers, that might have resulted in sensory cueing of the mark's location. Consequently, additional investigations into this interesting lineage are necessary. They will allow us to further the understanding of the evolution of mirror self-recognition by contributing to a comparative approach of the subject as well as possibly finding links between mirror self-recognition and other cognitive attributes.

Here I aimed to investigate MSR in carrion and hooded crow hybrids (*Corvus corones* and *corvus cornix*) further on referred to as “crows”. Given their high encephalization index (Iwaniuk, Dean, & Nelson, 2005; Emery, 2004), individual recognition abilities (Marzluff, Walls, Cornell, Withey, & Craig, 2010), social structure of seasonally variable fission-fusion societies (Uhl, 2016) and complex social and physical cognitive skills (Bagotskaya, Smirnova, & Zorina, 2012, 2013; Smirnova, Lazareva, & Zorina, 2003; Smirnova, Zorina,

Obozova, & Wasserman, 2015; Vonk, 2015) crows appear to be prime subjects for mirror self-recognition investigations. Food-storing birds, like crows, with complex social understanding may be particularly prone to empathic behaviour and perspective taking, which may coevolve with mirror self-recognition (Prior, Schwarz & Gürtürkün, 2008).

Therefore, the present experiment examines how crows behave when facing a mirror and whether crows show evidence of self-recognition when confronted to their own reflection following a classical MSR paradigm with a subsequent mark test. Based on the observations of other species, we predict the crows to overcome their neophobia toward the mirror, to develop a preference for the mirror and to undergo the usual behavioural steps of reactions to mirrors. We anticipate the crow's initial reaction to be similar to the one exhibited by other birds, namely social behaviour (e.g. aggressive behaviours toward the mirror) but also for this behaviour to fade in time, in order to be replaced by displays of investigative behaviour and possibly by exhibitions of contingent and self-directed behaviours while in front of the mirror. We furthermore investigated whether crows could pass the mark test. Successfully passing the mark test presupposes an interest on the animal's part to attend to a mark and the motivation to remove it. If these conditions are met, crows like magpies would be expected to pass the mark-test and should try to remove the mark placed on them only when facing a mirror.

METHODS AND MATERIAL

Subjects and Housing

A total of 8 hand-raised hooded and carrion crow hybrids native to Europe's hybridization belt (5 females and 3 males) between the ages of 2 and 4 years participated in this experiment (Appendix Table A1). Four of these subject (3F, 1M) were group living (in a group of six individuals²) and housed in an outdoor aviary (9,6x10x5m) at the Haidlhof research facility in Bad Vöslau, Austria. The aviary consisted of 4 compartments that were freely accessible to all the birds. (Figure 1a). The other 4 subjects were kept in pairs in 2 separate outdoor aviaries (3x6x4m each) at the same facility (Figure 1b). Due to medical reasons or the formation of pair bonds within the group, the group constellation and living arrangements of some of the birds changed over the course of the experiment (Appendix Table A1 and A2). Every aviary was accommodated with branches, perches, trees and different surface structures. The crows were fed twice a day with a mixed diet of meat, fruits, vegetables, milk products, cereals, eggs etc. and had ad libitum access to water.

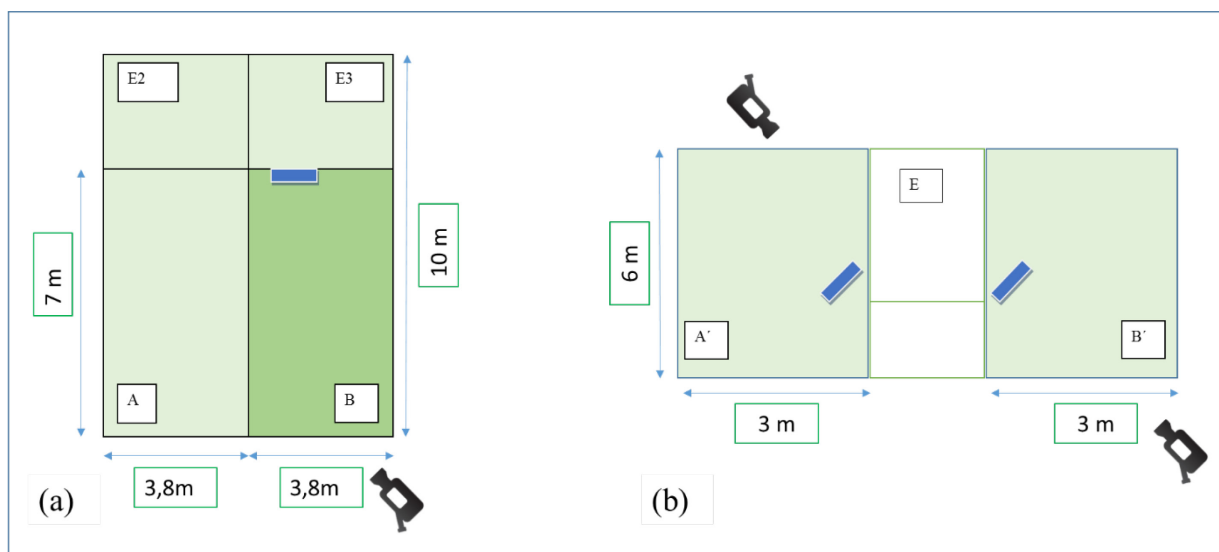


Figure 1 Setup in the group aviary (a): divided into 4 compartments, B is the testing compartment (3,8x7x4m) (dark green). The mirror (blue rectangle) is installed on the back wall of the testing compartment. The crows are granted free access to E2, E3, A and B (except during the experimental sessions). Setup for the paired birds (b): A' and B' (3x6x3m) are both the home range and testing compartment of respectively one pair. An apparatus (blue rectangle) was installed in each one of the aviaries.

² The two other birds of the group had to be excluded from the experiment as they never habituated to the experimental procedure (showing signs of distress when separated alone in the experimental compartment with the mirror).

Apparatus

For the group living subjects, a frame with interchangeable plates was suspended in the testing compartment of the aviary at 1m50cm off the ground and at 30cm from the wall, allowing the crows to comfortably get behind the apparatus (Figure 1a and Figure 2). A branch allowed the crows to sit in front of the apparatus. The frame could contain a board covered with a silver foil (Figure 2a), a 50x50cm mirror (Figure 2d) or a wooden board (Figure 2c) of the same dimensions. For the paired subjects, the frame was placed on a table (Surface:70x80cm), 1m off the ground, allowing the birds to easily walk around the mirror (Figure 2b).

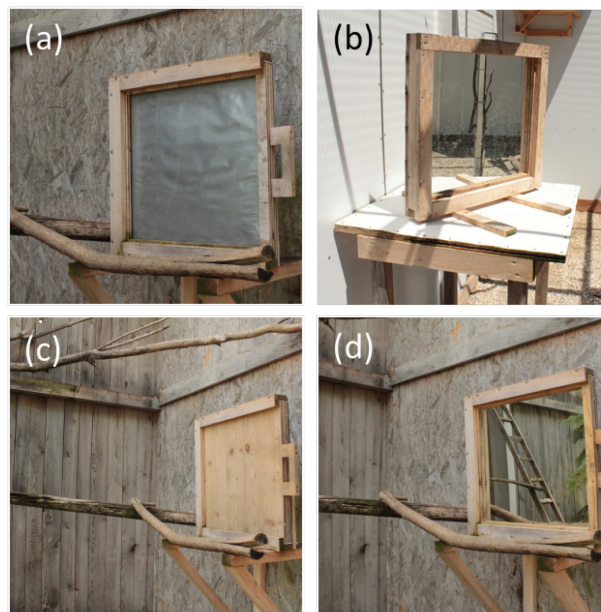


Figure 2: Apparatus installed in compartment B containing the silver foil used for habituation and in between testing sessions (a) and the apparatus containing the 50x50cm mirror (d) or the wooden board of the same size (c) and apparatus as installed in compartment A' and B' (on a table) (b).

Procedure

The study was carried out between May 2015 and March 2016. All subjects were naïve to mirrors at the beginning of the experiment.

For the group living birds, the experiment took place in one of the home range compartments of the aviary (compartment B) familiar to the subjects (Figure 1a). For the paired individuals, the test was conducted in their home-range compartment (A' and B' respectively) while the partner was separated in an adjacent compartment (E). During the experiment the testing compartment was only accessible to the test subject (with the exception of one pair – see Addendum 2).

Habituation. All the subjects were first given one month to habituate to the apparatus and to being separated from the group in the testing compartment for up to 20min. The birds entered the testing compartment voluntarily, none of the separations from the group (during habituation and the subsequent exposure and test session) included capturing the bird. In case the bird exhibited signs of distress the session was aborted and the bird was released back into the group. During this habituation phase the apparatus contained a board covered with a non-reflective silver foil (Figure 2a) in order to minimize the neophobic reaction to the mirror during trials, while avoiding habituation to the mirror itself.

Group Exposure. As sub-adult crows show social facilitation and increased interaction with objects when conspecifics are present (Miller et al., 2015), once habituated, the 6 out of the 8 tested crows received 3 group exposure sessions consisting of a period of free exploration in a group setting with ad libitum access to the testing compartment with the mirror (for a total of 190min) or the wood (for a total of 130min), intended to dampen the neophobic reaction and to quicken the individuals approach to the mirror and the wooden board during individual exposure. 2 birds (Corbie and Rainer) were already pair-bonded at the beginning of the experiment and received 3 paired exposures of the same duration.

Individual Exposure. During the individual exposure sessions, the test subject was separated from the group in the testing compartment. The birds were given at least 5 sets of sessions, one set consisting of two 20-minute sessions in the mirror condition and one 20-minute session in the wooden control condition. In the first stage (2 sets) of the individual exposure sessions, the apparatus got baited by the experimenter twice per session, once at the beginning of the session and once 10min into the session. In the second stage (3 sets) the apparatus was only baited once at the start of the session. The apparatus was always baited with 7 pieces of cheese, that could all be taken within one visit at the apparatus by the test subjects.

Each bird had to meet 2 criteria before being entered in the test phase of the experiment: complete 10 mirror and 5 control sessions (corresponding to a total of 200 min of individual exposure to the mirror) and spend at least a cumulative time of 10min in front of the mirror. These 2 criteria resulted in some birds receiving additional sessions of mirror exposure until they met the criteria (either because they spend a shorter amount of time in front of the mirror in each session than the other birds on average or because they did not approach the mirror

during their first sessions). For an overview of the amount of sessions and times spent at the apparatus refer to Table A3 of the Appendix.

Due to the transfer into another aviary 3 of the birds (Juno, Corbie and Rainer) received 4 mirror and 4 control sessions as a baseline for the new aviary and the slightly different setup before entering the mark test.

Marking Training. Before the start of each individual exposure session, the bird received a training session in which it was stepwise habituated to the marking procedure. The application of the mark to the subject's throats in this study was not unobtrusive but controlled for with a sham mark. The subjects were trained to approach the fence voluntarily, stretch to reach a bait offered by the experimenter thus exposing their throat and to allow a touch with a brush in this spot, without using any actual dye but regularly involving a dyed brush i.e. the tip of the brush was dyed with red or blue paint and dried out before using it with the birds, so that it would not leave any mark on the birds while allowing habituation to the different aspects of the brush. For 2 individuals (Corbie and Rainer) the marking took place whilst the bird was sitting on the experimenter's arm, while the crows were stretching to reach a bait in the experimenter's hand. They were habituated to this marking process over the course of their individual sessions, rendering the marking a routine procedure, which was subsequently enforced during the mark test.

Mark Test. The mark test consisted of two 20-minute sessions per individual in each of the following four conditions: open-mirror/mark, open-mirror/sham mark, wood/mark and wood/sham mark. The crows were marked on their throats with glycerine in its pure form (sham mark) or mixed with blue or red food colouring. The throat is supposed to be a part of the body crows are not able to see without the help of a mirror (Prior, Schwarz & Gürtürkün, 2008). The sham mark aimed to counterbalance for the somesthetic cueing of the location of the mark. Glycerine is water-soluble, odourless and almost colourless in its pure form. It is nontoxic and non-irritating (American cleaning institute, The Soap and Detergent Association- Glycerine and Oleochemical Division, 1990) with a refractive index between $n=1,47$ and $n=1,67$, an extinction coefficient of $k=0$ and an absorption coefficient of $\alpha=0,0000\text{cm}^{-1}$ for wavelength between $0,2\mu\text{m}$ and $0,6\mu\text{m}$ (Birkhoff et al., 1978) (Appendix Figure A1). Glycerine is absorbing light the strongest around $0,1\mu\text{m}$. Carrion crows as other corvids are tetrachromatic and possess "a short-wavelength sensitivity biased towards violet"

(wavelength inferior to 0,4 μm) (Ödeen & Håstad, 2003). Therefore, the glycerine in its pure form should appear colourless to them as well and should not be more noticeable than a drop of olive oil.

Motivation Control. A motivational control was performed with each crow after it had completed all its test trials, in order to test the crow's inclination to remove marks placed on its body. For this purpose, each individual was marked on visible parts of its body (belly, wing or foot) with a coloured and sham mark.

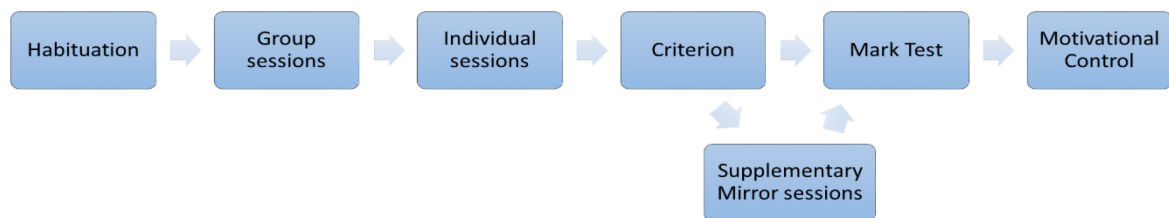


Figure 3. Schematic summary of the experiments procedural steps

Measurements

During all the sessions we measured the amount of time spent in front of and in close proximity to the apparatus as well as the amount of time facing the apparatus and the latency to approach the apparatus. We also coded for a suit of behaviours exhibited when in close proximity or in front of the apparatus (for the ethogram see Table 1) and for the location of the bird in the testing compartment during the session. In the mark test sessions, we additionally coded for any mark-directed behaviour. (e.g. scratching, pecking, bathing, autopreening the throat region etc.).

For the analysis the behaviours were pooled in 4 main categories: Social behavior (including SAD, Vocalizations, Attacks of the mirror or the wood), Inspective behaviours (Pecking of the surface or frame of the apparatus, looking behind, looking under the apparatus), Contingent behaviours (Peekaboo, Stretching, Object manipulation), self-directed behaviours (Scratching, Autopreening) and mark-directed behaviours (Scratching and preening directed towards the mark) (Table1).

Analysis

Each experimental session was recorded from the outside of the testing compartment by two cameras (Canon Legria HFG25 CMOS Pro) and coded for study-relevant behaviours (Table 2) with Solomon Coder Version beta (András Péter). The data was then analysed using Wilcoxon's Test in IBM SPSS Statistics 23 to compare the crows' performances in the mirror and in the control condition during the exposure sessions. I expected the crows to spend more time in front of the mirror than in front of the wooden control plate and to perform behaviours more frequently when facing the mirror. Furthermore, a change point analysis was performed on the data to examine the fluctuations in durations and behavioural frequencies over the course of the session by using Change Point Analyzer (Taylor, 2000). The results of the Mark Test were analysed with a Friedman's Test in IBM SPSS Statistics 23 comparing the four experimental conditions (Mirror Mark, Mirror Sham, Wood Mark and Wood Sham). I predicted the crows to spend the most time and perform more self- as well as mark-directed behaviours in the Mirror Mark condition. The crows should not perform mark-directed behaviours in the other 3 conditions.

Table 1. Ethogram used for behavioural coding

Behaviour	Definition
Social behaviour:	
Attack	Jumping at the mirror
Vocalizations	Vocalizing in front of the apparatus (all types of calls)
SAD (self-assertive displays)	Erecting of lower feathers (display of dominance), tufted ears feathers, thick head display due to erected head feathers
Inspection behaviour:	
Mirror or plate Peck	Pecking at the mirrors or the wooden plates surface
Frame peck	Pecking at the frame surrounding the mirror
Looks behind the mirror (LBM) under the mirror (LUM)	Search response
Contingent behaviour	
	Systematic moving in front of the mirror, often rhythmically, while looking at the mirror
Peekaboo	Staring at mirror image and then quickly moving its head out of view and then back within 3s
Leg stretching	Stretching of the leg away from body
Yawning	Opening of the beak while facing the mirror
Object manipulation	Manipulating a brought object in front of the mirror
Self-directed behaviour:	
Scratching	Scratching own body while in front of the mirror: autpreening using their feet
Autopreening	Crows preens itself while in front of the mirror: cleans feathers by using its beak
Mark directed behaviour	
Location and Orientation	
Next to	The crow is in standing next to the apparatus
On top	The crow is perched on the apparatus
In front	Sitting on the branch in front of the apparatus
Behind	The crow is behind the apparatus
Other	
Startle	Backjump or flight after having been in close proximity to the apparatus
Bristling	Bristling of feathers in front of the apparatus
Shaking	Shaking of plumage in front of the apparatus
Beak wipe	Moving of the beak along a surface in one or both directions
Tail fan	Lifting of the tail feathers
Wing flapping	Flapping of the wings in front of the apparatus
Visit	Approach of the apparatus
Close Inspection	Crow is sitting or standing in front of the apparatus in a calm manner, staying on the same spot and only moving the head (tilting of the head)

RESULTS

In this study I tested the reaction of carrion crow hybrids during mirror image stimulation. In a first stage, the crows were allowed access to the mirror and to the wooden control plate in a group setting to facilitate the approach to the apparatus and the overcoming of their natural neophobia. In a second stage, the birds received a series of individual exposure sessions in both conditions during which the individuals could gain experience with the mirror and were habituated to the marking procedure needed for the mark test. Finally, the birds participated in a classical mark test in order to determine their ability of mirror self-recognition by testing them in four conditions (Mirror/Mark, Mirror/Sham, Wood/Mark and Wood/Sham).

1. Group Exposure

During the group exposure sessions, the subjects did not spend significantly more time around the apparatus when it contained a mirror than when it contained the wooden control plate ($n=8$, $p=0,237$, $T^+=21$; time next to the apparatus ($n=8$, $p=0,686$, $T^+=9$); time behind the plate ($n=8$, $p=0,180$, $T^+=3$); time on top ($n=8$, $p=0,600$, $T^+=8$)), nor did they visit the apparatus more often when it contained the mirror ($n=8$, $p=0,612$, $T^+=17$). The crows spent however more time specifically in front of the mirror than in front of the control ($n=8$, $p=0,075$, $T^+=19$) (Figure 4). The same is true for the time they spent in close inspection of the apparatus ($n=8$, $p=0,068$, $T^+=10$). Although all 8 birds entered and stayed in the experimental compartment, three individuals never visited the mirror in these sessions and two of them even refused to approach the apparatus when it contained the wooden plate. When excluding these 3 birds from the statistical analysis, the results do show a significant preference for the mirror ($n=5$, $p=0,043$, $T^+=13$) in these birds (Figure 4).

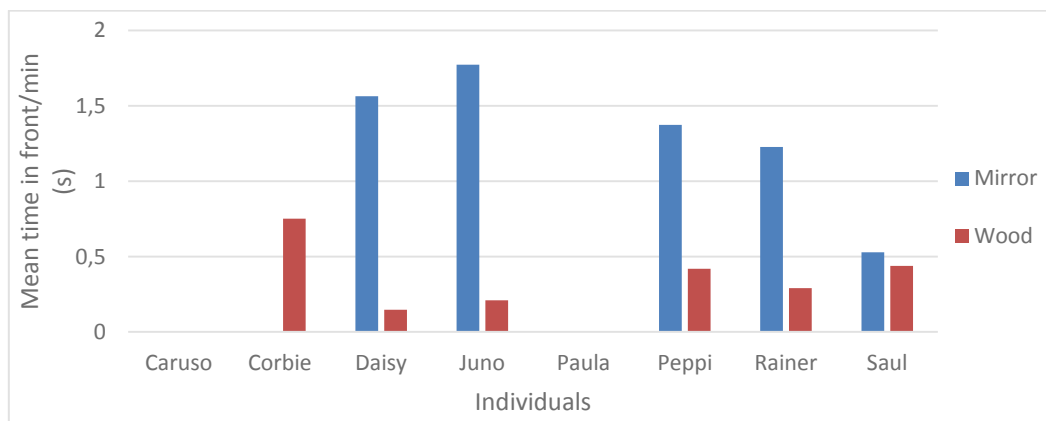


Figure 4. Proportion of time spent in front of the mirror and the wooden control plate by the subjects during the group exposure sessions (after correction for the duration of the sessions)

During the group exposure sessions none of the following behaviours and behavioural categories were performed significantly more in the test condition than in the control condition: Vocalizations ($n=8$, $p=0,317$, $T^+=1$), Beak Wipes ($n=8$, $p=1,000$, $T^+=3$), Looks Behind ($n=8$, $p=1$, $T^+=3$), Social Behaviours ($n=8$, $p=0,180$, $T^+=3$), Contingent behaviour ($n=8$, $p=0,317$, $T^+=1$), Self-directed behaviours ($n=8$, $p=1,000$, $T^+=0$), Shakes ($n=8$, $p=0,317$, $T^+=1$). However, the crows tended to perform more tail fanings ($n=8$, $p=0,068$, $T^+=10$) and inspective behaviour i.e. pecking ($n=8$, $p=0,068$, $T^+=10$) in the mirror condition than in the control condition during the group exposure sessions.

2. Individual exposure

During the individual exposure sessions, the crows ($n=8$) visited the apparatus significantly more often in the mirror condition (Wilcoxon signed rank, $n=8$, $p=0,036$, $T^+=33$) and spent significantly more time around the apparatus when it contained a mirror than when it contained the control board (Wilcoxon signed rank, $n=8$, $p=0,012$, $T^+=36$). They continued to spend significantly more time in front (Figure 5 and 6) of the apparatus when it contained the mirror than when it contained the wooden control plate (Wilcoxon signed rank, $n=8$, $p=0,012$, $T^+=36$) while not spending more time behind ($n=8$, $p=0,273$, $T^+=8$), on top ($n=8$, $p=0,069$, $T^+=31$) or next to ($n=8$, $p=0,575$, $T^+=22$) the apparatus when it contained the mirror.

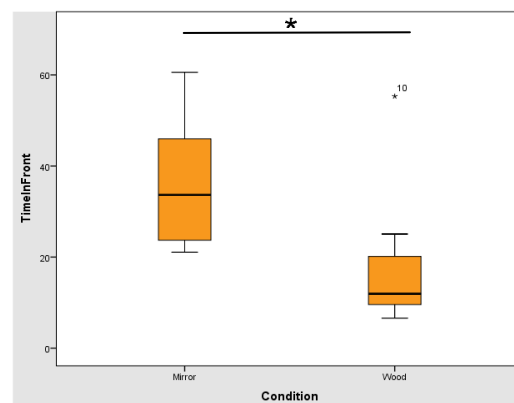


Figure 5. Mean amount of time spent in front of the mirror and the wooden control during individual exposure sessions

The crows spent an average of 36,46s in front of the mirror and 20,58s in front of the control per session. The average time spent in front of the mirror on a group level in each mirror session did not show any significant fluctuations. Some changes could be found in certain individuals, either linked to an increase (Caruso, Juno, Paula) or in some cases a decrease (Peppi, Rainer) in time spent in front of the mirror. None of the subjects showed any change in the time spent in front of the apparatus in the control condition (Table 2).

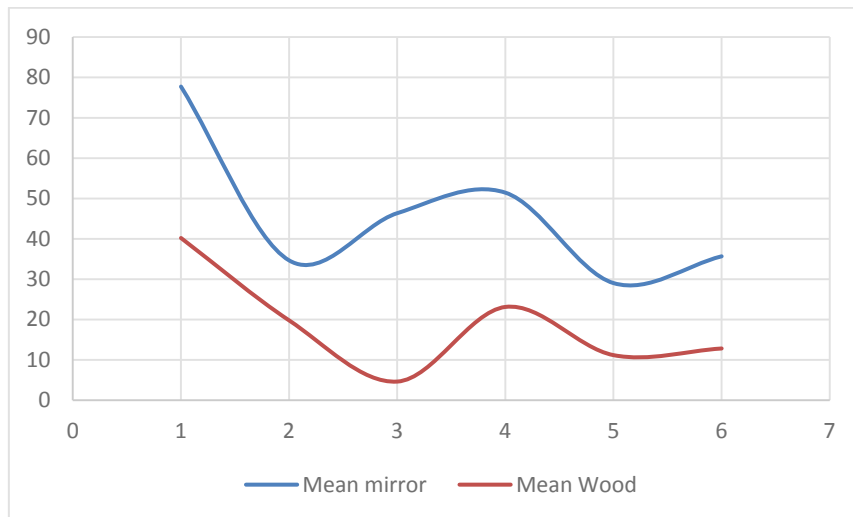


Figure 6. Running average of time spent in front of the mirror and the wooden control during the first 6 sessions of each condition

The crows spent significantly more time performing close inspection (i.e. the crow is calmly sitting or standing in front of the apparatus, staring in its direction, staying on the same spot and only tilting the head) (Wilcoxon signed rank, $n=8$; $p=0,012$; $T^+=36$) when facing the mirror, a behaviour that was almost non-existent during the control sessions (Figure 7).

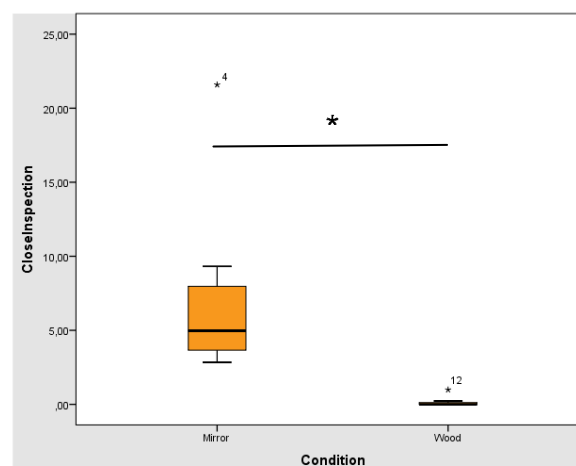


Figure 7. Mean amount of time spent in Close inspection in both exposure conditions during individual exposure

The behaviours exhibited during the individual exposure sessions were pooled into 4 behavioural categories for each tested individual and were analysed on a group level (results presented below). Details on the behaviours of each individual can be found in Appendix Figure A2 a-h.

Table 2. Changes on a group and individual level during the individual mirror exposure sessions (excluding baseline sessions) indicating the number of changes, the session in which the change occurred (row), the confidence level in percent and the level (an indication on the importance of the change)

Individual	Time in front mirror	Time in front wood	Social behaviours	Social behaviours + vocalizations	Inspective behaviours	Contingent behaviours	Self-directed behaviours
Caruso	1 (Row 8, 97%, level 2) ²	0	0	0	1 (Row 13, 98%, Level 1) ¹	0	0
Corbie	0	0	0	0	0	0	0
Daisy	0	0	0	0	0	0	0
Juno	1 (Row 8, 98%, level 1) ²	0	0	0	1 (row 8, 99%, level 1) ^{**2}	0	0
Paula	1 (Row 9, 100%, level 1) ²	0	0	0	0*	1 (row 10, 91%, level 1) ^{**2}	0
Peppi	1 (Row 7, 95%, level 1) ¹	0	0	0	0	0	0
Rainer	1 (Row 4, 96%, level 1) ¹	0	0	0	0*	0	0
Saul	0	0	0	0	0	0	0
Group	0	0	0	0	1 (Row 13, 96%, level 1)¹	0	1 (Row 16, 91%, level 1)²

*: Detection of outlier, **: Dependent Error Structure Detected: Violation of the independent error assumption, possibly affecting the confidence intervals and confidence levels, ¹: decrease, ²: increase

a. Social Behaviours

When restricted to aggressive, dominant and submissive displays there was no significant difference between the two experimental conditions (Wilcoxon signed rank, n=8, p=0,109, T⁺=6), in fact these kind of behaviours were very rare and happened only on 3 occasions in 3 different birds (2 of which were coded as being attacks). When vocalizations were included into the category of social behaviours the difference between the two conditions remains non-significant (Wilcoxon signed rank, n=8, p=0,091, T⁺=24) but indicates a trend towards social behaviours being performed more often in front of the mirror than in front of the wood.

Social behaviours (mainly vocalizations) occurred mostly between the 1st and 9th individual session (Figure 9). A change of setting (transfer to another aviary) caused some of the birds to vocalize more in front of the mirror once again (in the baseline sessions for the new aviary), a behaviour that extinguished within 2 sessions (Figure 8). However, on a group level no significant changes in the frequency of social behaviours derived from Taylor's change point analysis in either one of the conditions (Table 2).

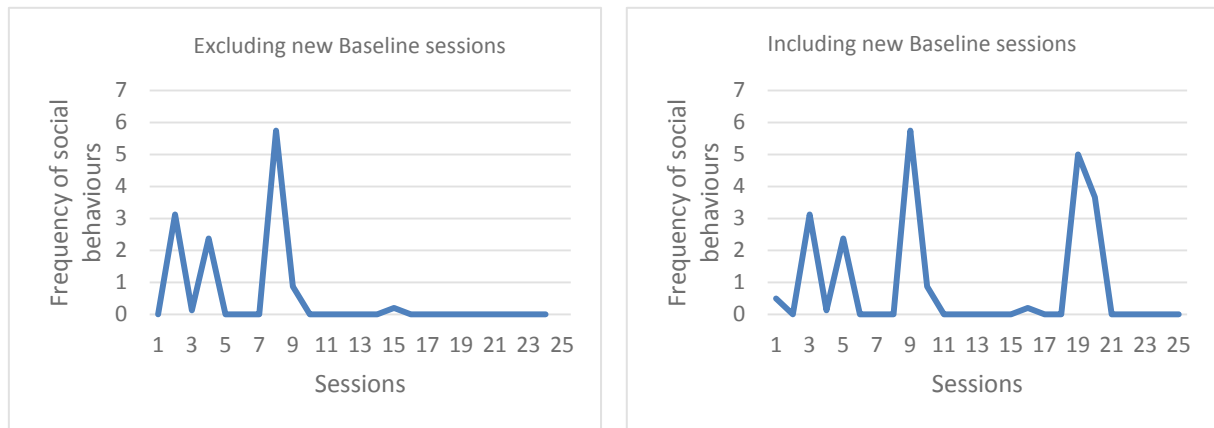


Figure 8. Mean amount of social behaviours including vocalizations of all the experimental subjects over the course of the mirror session (excluding the baselines in the new aviary of 3 of the birds in graph (a) and including these sessions for the calculation of the mean in graph (b))

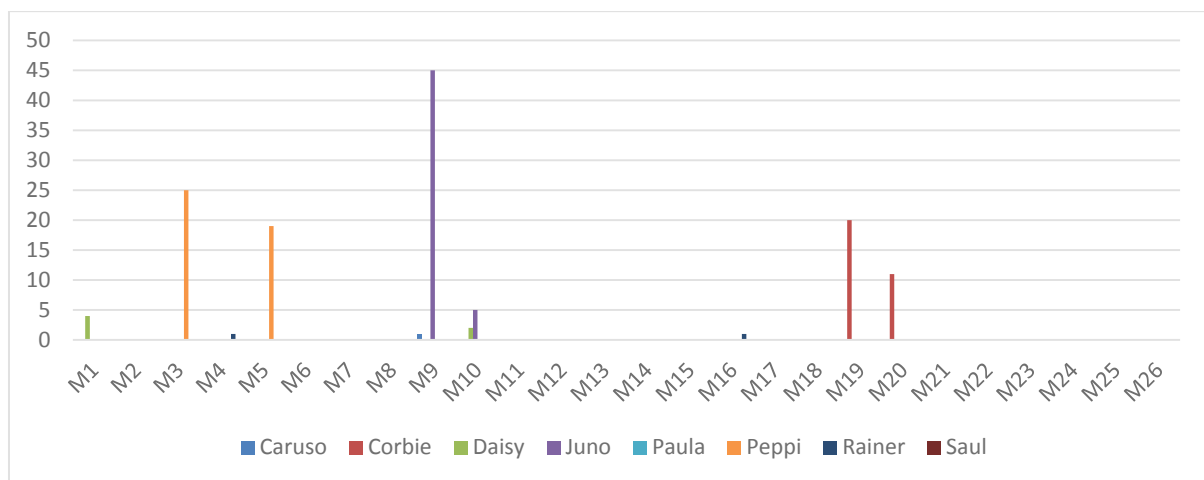


Figure 9. Number of social behaviours including vocalizations performed by each individual in front of the mirror over the course of the individual exposure sessions (including baseline sessions)

b. Investigative Behaviours

Pooled together investigative behaviours were not more frequent in front of the mirror than in front of the control (Wilcoxon signed rank, $n=8$, $p=0,123$, $T^+=29$), but some of the single behaviours of this category showed a significant difference between the two conditions: e.g. Pecking the surface of the apparatus (mirror or wood) happened significantly more towards the mirror than towards the wooden plate (Wilcoxon signed rank, $n=8$, $p=0,018$, $T^+=28$), while looking behind (Wilcoxon signed rank, $n=8$, $p=0,463$, $T^+=7$) and looking under (Wilcoxon signed rank, $n=8$, $p=0,655$, $T^+=1,5$) did not.

Investigative behaviours almost exclusively occurred between session M1 and M10 for every bird, with the exception of 2 birds (Corbie and Rainer) that resumed these behaviours shortly after being transferred to a new aviary which was associated to a slight modification to the apparatus (as displayed on Figure 2) in the first 2 of the 4 baseline sessions (M19 and M20) (see Figure 10 below). Taylor's change point analysis determined a change of investigative behaviour on the group level in mirror session 13 (96%, level 1) at which point the amount of investigative behaviours decreased, while no change was detected in the control condition (Table 2).

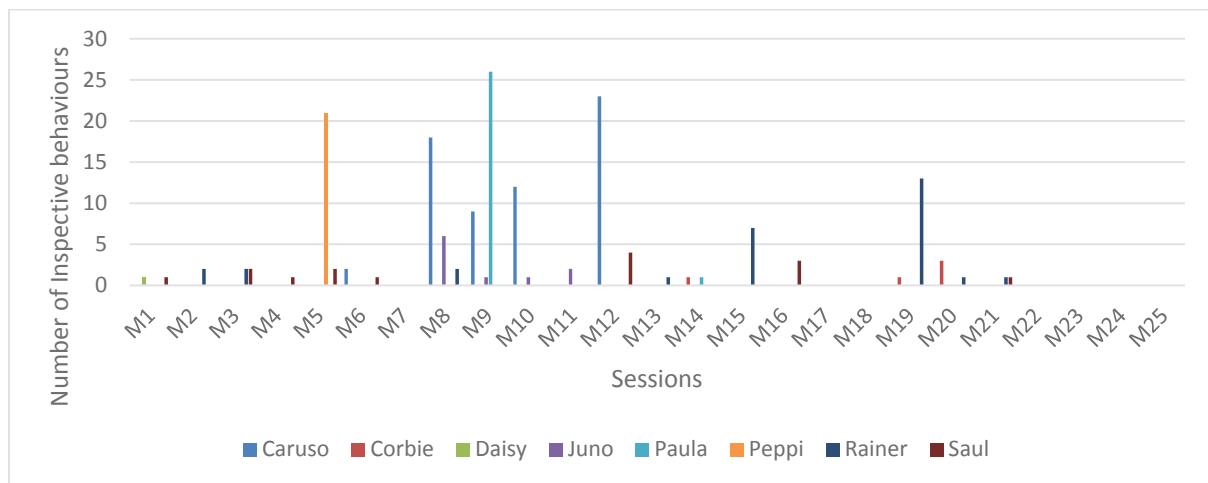


Figure 10. Number of inspective behaviours performed by each individual in front of the mirror over the course of the individual exposure sessions

c. Contingency Checking behaviours

When including Object manipulations, Stretching and peekaboo behaviours, then the behavioural category of “contingency checking” did not differ significantly across conditions ($n=8$, $p=0,116$, $T^+=18$), as none of the crows stretched in front of either the mirror nor the

wood and object manipulations rarely occurred. The crows performed significantly more peekaboo behaviours (i.e. Staring at mirror image and then quickly moving its head in and out of view within 3s) in the mirror than in the control condition (Wilcoxon signed rank, $n=8$, $p=0,043$, $T^+=15$). These behaviours were also not performed by all the birds and were never exhibited during the first 5 mirror sessions by any of the 8 birds but mostly occurred between session M6 and M15 (Figure 11), but no significant changes in contingency checking behaviours were detected by the change point analysis in the mirror nor in the wood exposure sessions (Table 2).

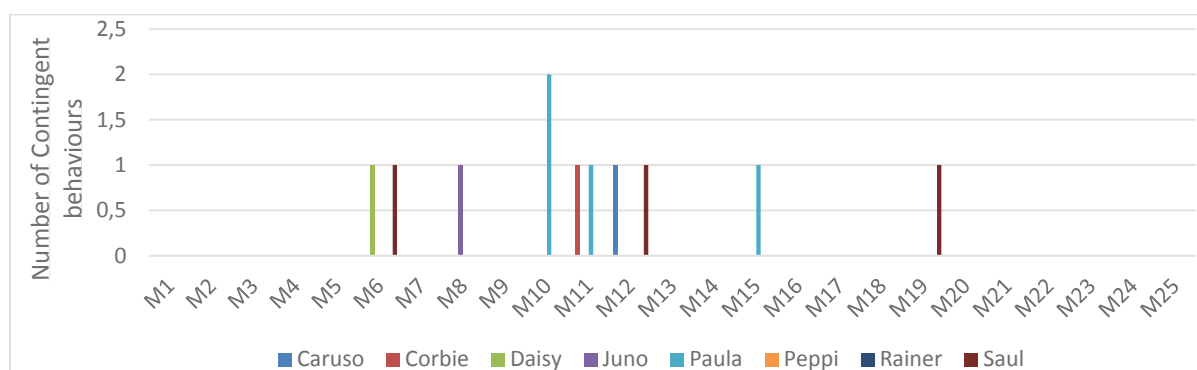


Figure 11. Contingent behaviours over the course of the mirror sessions for every individual.

d. Self-directed behaviours

No significant difference in self-directed behaviours was detected between the two conditions (Wilcoxon signed rank, $n=8$, $p=0,180$, $T^+=3$) as only two events of autopreening were coded during the individual exposure sessions on session M16 and M17 (Figure 12) leading to a significant increase in self-directed behaviours (91%, level 1) according to the change point analysis whereas no changes were detected in the control condition (Table 2).

e. Other behaviours

Some of the non-categorized behaviours were performed significantly more often when in the presence of the mirror e.g. Tail fanning ($n=8$, $p=0,018$, $T^+=28$) and Beak wiping ($n=8$, $p=0,5$, $T^+=10$), whilst most of these behaviours were as likely performed in both experimental conditions: Head shake ($n=8$, $p=0,285$, $T^+=5$), Shake in front of the apparatus ($n=8$, $p=0,273$, $T^+=8$), Shakes in close proximity of the apparatus ($n=8$, $p=0,063$, $T^+=25$), Bristle ($n=8$, $p=0,317$, $T^+=1$).

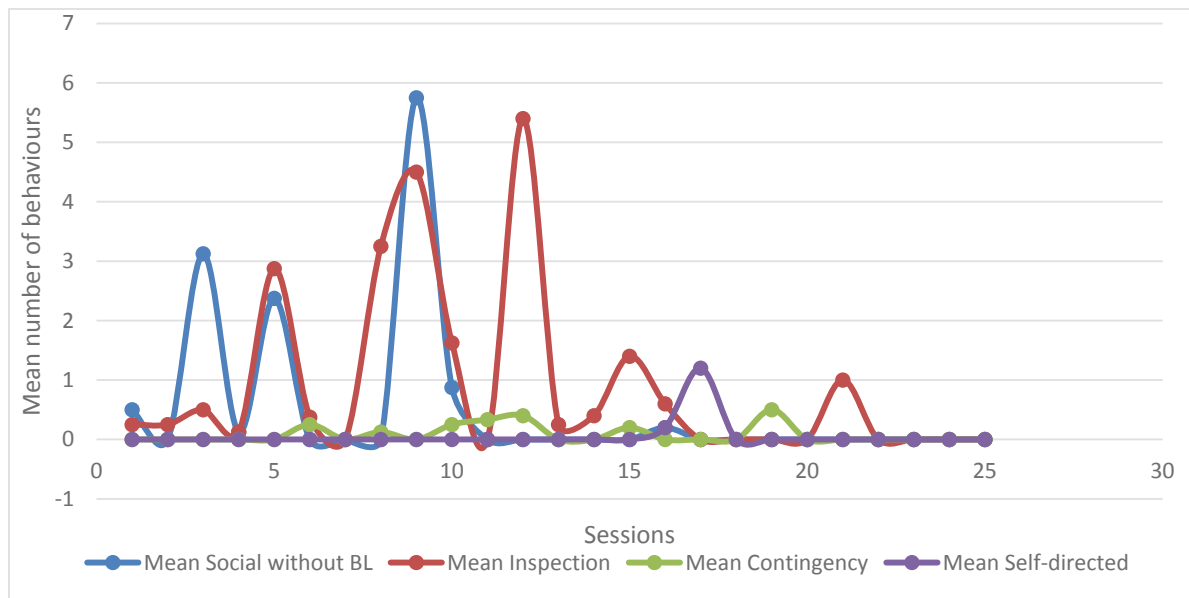


Figure 12. Number of social, inspective, contingent and self-directed behaviours performed in front of the mirror on a group level over the course of the sessions, excluding the baseline sessions (BL) in the new aviaries for the birds Corbie, Rainer and Juno (see Figure 8).

3. Mark Test

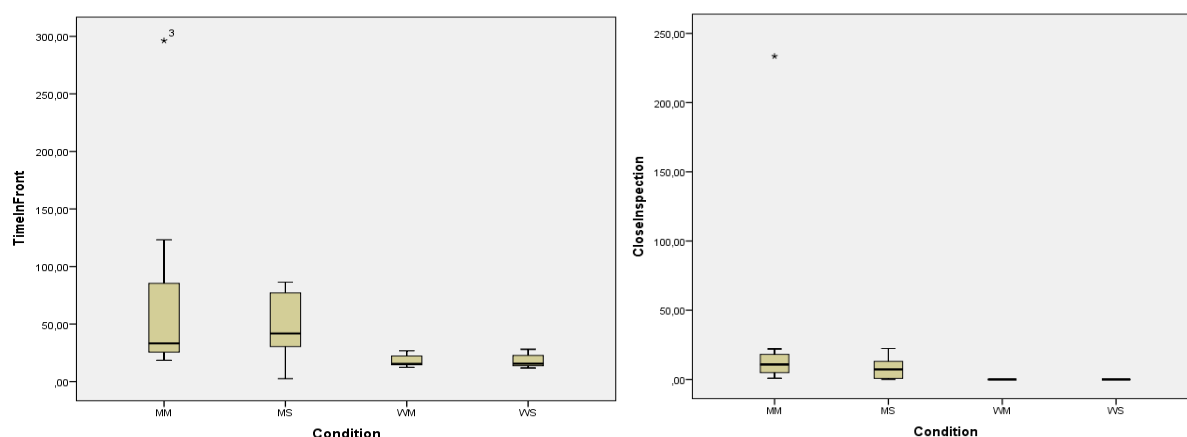
Motivation Control. When the applied marks were visible, each subject reacted to the coloured mark within a minute after marking and in almost every case within 30 seconds of applying the mark by trying to remove the mark by preening the area until the mark was removed whereas none of the subjects had a similar reaction to sham mark. Therefore, validating the method employed in the mark test using glycerine and colour pigments.

Only 6 of the 8 crows completed all the sessions of the Mark test. One of the birds (Paula) never habituated to the marking procedure and was therefore excluded from the test and a second bird (Daisy) completed 6 out of the 8 test sessions and refused to be marked for the last two test sessions. The results beneath are presented in exclusion and inclusion of this individual (n=6 and n=7).

In the Mark Test, the number of visits of the apparatus (Friedman Test, n=6, p=0,109, $\chi^2=6,053$; n=7, p=101, $\chi^2=6,231$) nor the time spent at the apparatus (Friedman Test, n=6, p=0,145, $\chi^2=5,4$; n=7, p=0,134, $\chi^2=5,571$) differed between the 4 conditions. There was

however a significant difference in the time spent in front of the apparatus (Friedman Test, $n=6$, $p=0,006$, $\chi^2=12,6$; $n=7$, $p=0,013$, $\chi^2=10,714$): i.e. a difference between the mirror and the wood conditions (WM-MM: post-hoc test, $n=7$, $p=0,018$, $T^+=28$; $n=6$, $p=0,028$, $T^+=21$). But no significant difference was found between the mirror mark (MM) and mirror sham (MS) conditions (Post hoc test, $n=7$, $p=0,612$, $T^+=17$; $n=6$, $p=0,917$, $T^+=10$), nor between the wood mark (WM) and wood sham (WS) condition (Post hoc test, $n=7$, $p=0,735$, $T^+=12$; $n=6$, $p=0,463$, $T^+=14$) (Figure 13a).

The duration of close inspection varied significantly across the four experimental sessions (Friedman Test, $n=6$, $p=0,002$, $\chi^2=14,761$; $n=7$, $p=0,001$, $\chi^2=16,474$). As there was no significant difference between the MM and MS ($n=6$, $p=0,345$, $T^+=15$; $n=7$, $p=0,310$, $T^+=20$) nor between the WM and WS condition ($n=6$, $p=0,317$, $T^+=1$; $n=7$, $p=1,000$, $T^+=0$), this significant difference indicates once more the tendency of the crows sit longer in front of the mirror than in front of the wooden plate (MM-WM: $n=6$, $p=0,028$, $T^+=21$; $n=7$, $p=0,018$, $T^+=28$) (Figure 13b)



(a) (b)

Figure 13. Time the crows ($n=7$) spent in front of the mirror (a) and performing close inspection (b) in the 4 experimental conditions of the mark test: mirror/mark (MM), mirror/sham (MS), wood/mark (WM) and wood/sham (WS).

a. Self-/Mark-directed behaviours

No significant difference in crows' self-directed behaviours was found between the conditions when the bird was facing the apparatus (Friedman Test, $n=6$, $p=0,572$, $\chi^2=2,0$; $n=7$, $p=0,572$,

$\chi^2=2,0$). Only one event of mark-directed behaviour was recorded throughout the experiment, in which the bird (Rainer) attempted to remove the red mark on her throat with its beak while standing in front of the mirror. This behaviour was not repeated in a latter session of this condition.

The behaviour in the four experimental conditions though did not vary significantly in the amount of inspective behaviours ($n=6$, $p=0,284$, $\chi^2=3,8$; $n=7$, $p=0,284$, $\chi^2=3,8$) but a tendency to continue to exhibit contingency checking behaviours ($n=6$, $p=0,066$, $\chi^2=7,2$; $n=7$, $p=0,019$, $\chi^2=9,923$) was noticeable.

b. Differences between blue and red markings

There were no significant differences in the behaviour of the crows when facing the mirror with a blue or red mark on their throat: Time at apparatus ($n=6$, $p=0,345$, $T^+=6$), Time in front of the mirror ($n=6$, $p=0,249$, $T^+=5$), Autopreening ($n=6$, $p=0,317$, $T^+=1$), Close inspection ($n=6$, $p=0,345$, $T^+=15$).

DISCUSSION

The present study aimed to investigate the abilities of mirror self-recognition in a further corvid species, the carrion and hooded crow hybrid. Contrarily to most species, the crows did not exhibit significantly more social behaviours towards their reflection than towards the wooden plate. Furthermore, the tested crows failed to show self-directed behaviours during the exposure sessions and subsequently also failed the mark test. They did however exhibit behaviours indicative of contingency testing (e.g. peekaboo) during the individual exposure sessions.

Most crows, as expected, overcame their neophobic reaction towards the mirror during the group exposure sessions (with the exception of 3 birds: Caruso, Corbie and Paula, that did not approach during group sessions), and as most bird species e.g. weaver finches, zebra finches, budgerigars (Gallup Jr. & Capper, 1970; Ryan, 1978; Watanabe, 2002), showed a clear preference for the mirror and spent considerably more time in front of it right from the start of the group sessions, as well as in the individual exposure sessions and the subsequent Mark Test. Although the time spent in front of the mirror did not fluctuate on a group level, several individual showed a change during the individual sessions. The changes in 3 of the birds (Caruso, Juno and Paula) indicate an increase of the time spent in front of the mirror, caused by their lack of visits (and therefore lack of time spent in front of the apparatus) during their first sessions. The change is thus indicating the moment the birds overcame their neophobia. As for the 2 other individuals (Rainer and Peppi) the change consists of a decrease in the time spent in front of the mirror, possibly indicating a habituation effect that did not occur in the other birds.

One of the explanations for a preference for mirrors is that the mirror represents a “supranormal social stimulus” (Gallup Jr. & Capper, 1970). Individuals facing the mirror behave socially (often aggressive and territorial behaviour) towards their own reflection, while the reflection can only mimic the behaviour without being able to mimic the produced sounds. The mirrored reflection is therefore an incomplete and in some ways unnatural imitation of the exhibited social behaviour in front of the mirror. However, in our case, the crows did not exhibit any form of *aggressive or submissive display* towards the mirror. On 2 out of 3 occasions of social displays, “attacks” towards the mirror were coded, but as these were neither preceded nor followed by any form of social display, it is probable that these behaviours were in fact attempts to fly through the mirror. The crows did however show a tendency to vocalize more in the presence of the mirror during the individual sessions. Crows

use *Vocalizations* in a variety of social contexts e.g. affiliative and agonistic behaviour and are a relevant part of the behavioural repertoire of corvids, but were rarely taken into account in past MSR studies. Despite not being a purely social behaviour, vocalization do play an important role in the social interaction of crows (Thompson, 1982; Wascher, Szipl, Boeckle, & Wilkinson, 2012). Likely some vocalization produced in proximity of the mirror were not directed towards the mirror and influenced by external event (e.g. wild birds flying over the aviary etc.).

Contrary to our initial hypothesis, the crows seemed to investigate the mirror as much as the wooden plate. The crows showed however already a tendency to perform some behavioural components of this category, i.e. *pecking of the surface* more towards the mirror during the group session and significantly more in the individual sessions. Contrarily, the crows did not seem to “search for the crow in the mirror” as they lacked to show a difference in “*looking behind*” and “*looking under*” behaviours. They were as curious about investigating behind the wooden plates as behind the mirror. In spite of being commonly interpreted as a searching behaviour for the conspecific observed in the mirror and assumed to be the second level of mirror interaction, it is possible that the “looking behind” and “looking under” behaviours rather conveyed the crows’ curiosity to investigate a location that was out of their sight as it was blocked by an obstacle then a search for the “individual in the mirror”, which would result in them looking as much behind the mirror and the wooden plate.

Maybe due to their restricted mobility in front of the mirror (Figure 2), in front of which they only had a branch to perch on, the crows did not show much *repetitive behaviours*. Nonetheless, behaviours like “*peekaboos*” were performed significantly more in the mirror condition and do indicate a form of contingency checking, even though they did not exhibit the typical contingency checking behaviours that were observed in other species e.g. checking the inner mouth. It is furthermore noteworthy that these behaviours were not exhibited in the 5 first individual sessions, but only after a total of 260 minutes of exposure to the mirror and only performed by one of the birds (Daisy) during group exposure, unlike the magpies tested by Prior and colleagues in 2008, that started exhibiting contingency checking behaviours already after 150 minutes of exposure.

The behaviour of tail fanning, that could not indubitably be assigned to one of the four behavioural categories, was also exhibited more in front of the mirror than in front of the wooden plate in the group exposure as well as in the individual exposure sessions, possibly signalling increased arousal levels when facing the mirror.

As to the expected substitution of one displayed behavioural category for another over time (from social behaviours to self-directed behaviours), we were able to observe a tendency towards such a fluctuation that was however not detected by Taylor's change point analysis (Table 2).

Although the displays of *self-directed behaviours* during the exposure sessions were scarce, the crows did perform contingency testing behaviours and therefore performed comparably to the tested jackdaws (Soler et al., 2014) and magpies (Prior et al., 2008) during the exposure sessions.

But contrarily to the jackdaws and the magpies, the crows although they spent more time in front of the mirror, did – with one exception - not show any self- or mark-directed behaviour during the mark test. While they did remove the coloured marks when they were applied to a visible body part (like the chest, wing or foot), presumably indicating the animals' motivation to remove marks.

Unlike in the present study, the marking method used in both previous mark test studies on corvids (Prior, Schwarz & Gürtürkün, 2008; Soler, Pérez-Contreras, & Peralta-Sánchez, 2014) made use of coloured stickers to mark their study subjects and black stickers as a control, which, as mentioned by Soler and colleagues, might have provoked somatosensory cueing, causing the birds to feel the stickers on their plumage and react to this sensation. Furthermore, none of these studies reported the subjects' reaction to the stickers on a visible part of their body. In contrast, the crows' in this study were marked by different means. Their reaction to the coloured mark on a visible part of its body and its lack thereof when the sham mark was applied, as well as the fact that we did not find any difference in behaviour between the Mirror/Mark (MM) and Mirror/Sham (MS) nor the Wood/Mark (WM) and Wood/Sham (WS) conditions proves the effectiveness of the method employed to mark the animals in this study.

Possible reasons for failing the mark test

The above mentioned findings show that despite their close phylogenetic relatedness the performances in the mark test of magpies, jackdaws, jungle crows and carrion crows vary substantially. The origin of these differences remains unknown but could be found on an individual or a species level. Factors influencing the ontogeny of an animal (e.g. rearing conditions) (Broesch et al., 2011), personality and even genetics (Mahovetz, Young & Hopkins, 2016) could influence the individuals' performance in the test. Whilst the effect of

different evolutionary constraints, social structures, breeding types could affect the species abilities of MSR.

In children, for instance, the behaviour exhibited in front of mirrors has been proven to be subject to culture and upbringing (Broesch et al., 2011). Children that were not raised in western cultures, e.g. Kenya, mostly did not pass the Mark Test by the age of 24 months in contrast to children raised in western societies, some even continue to fail the mark test by the age of six. These children are not lacking empathy nor do they differ in their performances in Theory of mind related tasks. One of the attempts to explain these differences refers to the influence of independent or interdependent raising styles (Keller, Ka, Borke, Yovsi, & Kleis, 2005). Furthermore, children with secure attachments to their mothers, are, by the age of 2 years (age at which also the ability of mirror self-recognition develops), able to solve more complex symbolic games (Matas, Arend, 2015), showing that upbringing and the resulting attachment styles have an influence on the cognitive development of children as well as on, for example, their perseverance in a problem solving task. As rearing conditions of test subjects from different studies may vary substantially, it is conceivable that alike humans, rearing conditions might have a similar influence on the cognitive development in other species.

The observed differences between the tested species could also derive from methodological discrepancies in housing, handling, experimental setups or exposure time. While, the magpies (Prior et al., 2008) received a maximum of 250 min of mirror exposure before the mark test consisting of five 30-minute sessions of open mirror exploration in a 4x4m room and five 20-minute sessions in two 60x100x60cm compartments in which only one contained a mirror and between which the magpies could roam freely, the jackdaws (Soler et al., 2014) received three 50-minute sessions in a 160x100x80cm compartment followed by six 20-minute sessions in which they could choose to be exposed to the mirror or not, amounting to a maximal exposure time to the mirror of 280 minutes. On the other hand, all crows in this study got a minimum of 360 minutes of exposure time (excluding the mark test) in the test compartment containing a mirror and spent at least 10 minutes in front of the mirror during that time -it is however likely that the subjects could see their reflections from other locations in the aviary as well. The crows experimental compartment (dimensions depending on the compartment: 3,8x5x7m or 1,5x5x10m or 3x3x6m: width x height x length) was on the one hand considerably larger than the compartments in which the magpies and jackdaws were tested and was furthermore supplied with branches and perches offering the crows locations out of sight of the mirror,

while the magpies and jackdaws were forced to stay on the ground at the level of the mirror (Prior, Schwarz & Gürtürkün, 2008; Soler, Pérez-Contreras, & Peralta-Sánchez, 2014). It is conceivable that the crows would have required an even longer period of mirror exposure due to these methodological differences, a theory partly substantiated by the appearance of self-directed behaviours in the terminal sessions of some birds and the arising of contingency checking behaviours around 260 min in crows whereas it emerged after 150min in magpies.

As previously mentioned, the crows were not successful in passing the mark test. Yet failing the mark test does not necessarily imply a lacking ability of self-recognition. Developmental psychologists differentiate 4 levels of mirror-understanding, ranging from level 0 (mirror-other confusion) to level 3, that if reached consists in mirror self-recognition. Individuals reaching level 1 are able to differentiate between their reflection and the environment whereas at level 2 the individuals explore contingencies. These levels are reflected in the 4 behavioural steps (social, investigative, contingency checking, self-directed behaviours) commonly observed in animals.

Several factors need to be combined in order for the subject facing the mirror to successfully pass the mark test. A fundamental condition for success is that the tested individual needs to show interest in the mirror but even more importantly the subject needs to show interest in its own body image. Indeed, mirror self-recognition and the interest in the own body image surface at the same time in children (Nielson, 2004). Second, the subject needs to be able to perceive the mark, i.e. the mark needs to be salient enough (Hauser, Kralik, Botto-Mahan, Garrett, & Oser, 1995) and be motivated to remove this coloured mark from its body when it sees it (Plotnik, de Waal, & Reiss, 2006; Suddendorf & Collier-Baker, 2009). The third and fourth pre-requisites for passing the mark test are the understanding of the virtual image the mirror reflects (and through this its workings) and the ability to connect this image to the own body image.

In this study we were able to show that crows are indeed interested in the mirror as an object and possibly in their reflection, as well as showing that they are motivated to remove coloured marks from their body and that this mark is salient enough to be perceived and to incite a response (i.e. preening behaviour). While ultimately failing the mark test, the crows' contingency checking behaviours seem to indicate that at least some individuals understood the physical properties of the mirror comparably to the New Caledonian crows (Medina et al.,

2011) and the African grey parrots (Pepperberg et al., 1995). However, further testing is required to provide evidence for this hypothesis.

Problems connected to the Mark Test

Despite being the recognized way of studying self-recognition and, by the same mean, of assessing self-awareness in children and animals, the Mark Test conceals some problems linked to the performance of individuals in the test and the categorisation and therefore interpretation of some of the behaviours exhibited by the test subject during trials. The performances of subjects within this test reveal a high level of inter-individual variation in a species, with only few individuals passing the test in each cohort e.g. only about $\frac{1}{4}$ of all tested chimpanzees, one out of three elephants and two out of five magpies successfully passed the mark test. The origin of these variations are still mostly unknown. Recent findings in chimpanzees showed however that the performance in MSR is influenced by genetic factors like the possession of a certain morph of a vasopressin receptor gene (AVPR1A) (Mahovetz, Young & Hopkins, 2016).

Initially designed for primates and first and foremost applied with children apes and monkey, it was considered that the Mark Test could be better suited to reveal an “anthropoid-like sense of self” (Hart & Whitlow, 1995). The sense and concept of self of primates and corvids could underlie different psychological functioning’s driven by different evolutionary constraints. It was furthermore originally conceived to enforce the observations made of animals seemingly recognizing themselves in mirrors, which manifested through the inspection of otherwise not visible body parts like the inner mouth and the genital region. This poses difficulties in avian species, as birds are known to be able to see most of their body (Jahnke, 1984) and causes problems in the definition of behaviours possibly indicating self-recognition previous to the mark test.

It is moreover imaginable that different species react in distinctive ways to a mirror. Broesch and colleagues hypothesized that children from non-western countries, that did not pass the mark test at the expected age, might display other behaviours indicative of MSR when facing a mirror e.g. freezing behaviour (Broesch et al., 2011). If the behavioural range in the human

species is as widespread as varying between active self-inspection and freezing, then the behaviours between species could fluctuate significantly as well.

Finally, according to Gallup Jr.'s self-awareness theory, a successfully passed Mark Test is an indication for the individual's ability "to become the object of your own attention" (Gallup Jr., 1982), which is assumed to be an indication for the individual and the species to be self-aware. This direct link between MSR and self-awareness is challenged by findings in patients with psychiatric or neurodegenerative diseases like Alzheimer's disease, who often do not recognize themselves in mirrors anymore (Biringer & Anderson, 1992) while still possessing a sense of self (Fazio & Mitchell, 2009), or are able to use a mirror e.g. for shaving, but do not identify their reflection as being their own when asked.

Possible further investigation

Due to the inconclusive results emanating from the Mark Test performed on crows in this study, further investigations into the questions of mirror self-recognition and self-awareness in crows are indispensable to draw definitive conclusions on the level of understanding crows have of reflective surfaces. Such investigations could include tests on the crows understanding of a mirror's properties e.g. a mirror mediated location task, similar to the ones performed with the New Caledonian crows (Medina et al. 2011) and Grey parrots (Pepperberg et al., 1995).

The self is not only expressed in an individual's visual aspect but also in other sensory modalities i.e. own voice recognition. Crows are known to be very skilled in visual and auditory individual recognition (Izawa and Watanabe, 2008; Kondo et al., 2012), therefore future investigations should further be expanded to experimental designs providing supplementary cues, beyond the visual reflection from the mirror. These type of designs could thus incorporate multimodal or cross-modal conditions, assessing if the presentation of additional cues during mirror-exposure (e.g. auditory cue by playbacks) could facilitate MSR and the passing of the mark test by facilitating the understanding of the contingency between mirror reflection and own body (Platek et al., 2003). Several strategies can be devised to build or enhance the correspondence made between reflection and body. A paired exposure with a familiar and affiliated individual for instance might allow the tested subjects to make the connection between the image and the individual next to them and transfer this relation to

their own reflection and their own body (Gallup, 1983) or the subjects could be given access to a mirror while wearing a mark on a visible part of their body.

Finally, self-awareness does not only translate through MSR. For example, in their study Moore and colleagues (2007) tested 16-21 month old childrens' ability of mirror self-recognition and body self-awareness. They assessed the MSR with a mark test and the body self-awareness by asking the toddlers to push a toy shopping cart towards their mothers. In the "self condition" of this test, a mat, on which the child had to step on in order reach the handle of the cart, was attached to the back of the cart, causing the child's own body weight to prevent the motion. Therefore, in order to move the cart, the kids had to either step off the mat, indicative of the child's awareness of its own body. They showed that in children body self-awareness develops around the same time as mirror self-recognition during the second year and that it translates the development of "an objective awareness of self" (Moore, Mealiea, Garon, & Povinelli, 2007). The same kind of testing used in this study could be applied to animals to get a notion of their body self-awareness i.e. the awareness of their own weight or height. In order to further the investigations on animal self-awareness in its integrality, we will be required to go beyond mirror self-recognition and the mark test, and start exploring other facets of what could be considered "animal self-awareness".

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APPENDIX

Table A1. Characteristics of the study subjects, and their living and testing situation over the course of the entire experiment: Due to medical reasons or the formation of pair bonds some birds were not tested in the compartments (and aviaries) in which they had gotten their exposure sessions. Following table gives an overview of the changes in group constellations and living arrangements of the test subjects over the course of the experiment (Table 1 and 2).

Subject	Sexe	Birth year	Exposure (M1-2+W1)	Exposure sessions	Test session	New baseline (after transfer in new aviary)
Daisy	F	2012	In group	Group living-Individual sessions	Group living-Individual session	Not necessary (no transfer)
Saul	M	2012	In group	Group living-Individual sessions	Group living-Individual session	Not necessary (no transfer)
Peppi	F	2012	In group	Group living-Individual sessions	Group living-Individual session	Not necessary (no transfer)
Paula	F	2014	In group	Group living-Individual sessions	Not tested – no habituation to marking procedure	Not necessary (no transfer)
Caruso	M	2013	In group	Group living-Individual sessions	Group living-Individual session	Not necessary (transferred after the end of the test)
Juno	F	2012	In group	Group living Individual sessions	Paired - Individual session	4 mirror and 4 wood individual exposures
Corbie	M	2012	In pair	Living in pair Sessions in pair	Paired-Individual session	4 mirror and 4 wood individual exposures
Rainer	F	2012	In pair	Living in pair Sessions in pair	Paired - Individual session	4 mirror and 4 wood individual exposures

Table A2. Life history of test subjects during the experiment

Daisy	Group living over the course of the entire experiment.
Saul	Group living over the course of the entire experiment.
Peppi	Group living over the course of the entire experiment.
Paula	Group living over the course of the entire experiment.
Caruso	Group living d. Paired with a female (Juno) and transferred to a new aviary in December 2015.
Juno	Group living during the exposure sessions. Paired with a male (Caruso) and transferred to a new aviary between exposure sessions and mark test
Corbie + Rainer	Paired since the beginning of the experiment. Exposure sessions M1 and M2 together in compartment B (3,8x7x5m); Birds were not available for testing between mid-Mai 2015 and August 2015 due to a transfer to another facility for medical reasons. Back to the Haidlhof research station in August where they got the exposure sessions together (compartment size: 1,5x10x5m) as a separation of the birds was not possible (M3-M17+W2-6). In December 2015 transferred to a new aviary (3x6x3m), in which they got individual baseline sessions (4 mirror and 4 wood exposure session in the new aviary) and in which they were tested individually

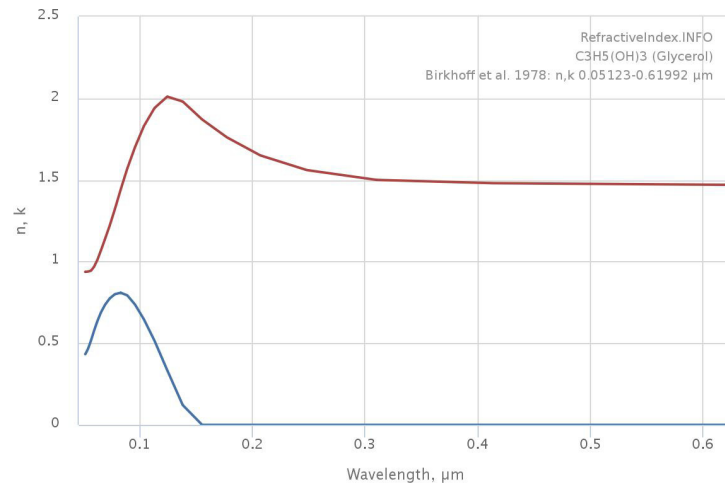


Figure A1. Refractive Index (n, red line) and Extinction coefficient (k, blue line) of glycerol for wavelengths between 0,05 and 0,6μm according to Birkoff et al. 1978.

Table A3. Amount of sessions each bird received in each of the conditions and amount of time the bird spent at the apparatus and in front of the apparatus in each condition during the individual exposure sessions and in total including the group exposure sessions and the visits to the mirror that occasionally happened in between the sessions while the next bird was getting separated.

Individual	Caruso		Corbie		Daisy		Juno		Paula		Peppi		Rainer		Saul	
Condition	Mirror	Control	Mirror	Control	Mirror	Control	Mirror	Control	Mirror	Control	Mirror	Control	Mirror	Control	Mirror	Control
Number of individual sessions	19	6	21	9	10	6	14	9	18	6	12	7	21	9	29	7
Time at apparatus during individual sessions (s)	1052,8	136,1	1521,7	533,4	467,9	131,8	943,1	312,5	1009,3	121	462,4	125	1034,1	291,6	1027,1	143,8
Time in front during individual sessions (s)	661,6	39,5	1272,6	497,7	214,7	77,4	781,5	121,7	520	53,5	311,3	61,5	758,3	225,6	547,8	54,8
Total time at apparatus (s)	1113,3	150,8	1521,7	631	1281,6	809,2	2170,9	448,8	1586,7	126,6	1636,6	263	1267,9	329,4	1686,6	621,6
Total time in front (s)	676,4	39,5	1272,6	595,3	696,9	134	1774,8	149	814,7	53,5	1208,9	131,1	954,7	263,4	787,5	125,8

Figure A2 a-h: Evolution of the 4 behavioural categories for each individual during the individual sessions (excluding the baseline sessions for the new aviaries): social behaviours with vocalization in dark blue, social behaviors without vocalization in dark red, Inspective behaviours in light green, contingency checking behaviours in violet, self-directed behaviours in light blue.

