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Sneaking a peek: pigeons use peripheral vision (not mirrors) to find hidden food

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Abstract A small number of species are capable of recognizing themselves in the mirror when tested with the mark-and-mirror test. This ability is often seen as evidence of self-recognition and possibly even self-awareness. Strangely, a number of species, for example monkeys, pigs and dogs, are unable to pass the mark test but can locate rewarding objects by using the reflective properties of a mirror. Thus, these species seem to understand how a visual reflection functions but cannot apply it to their own image. We tested this discrepancy in pigeons—a species that does not spontaneously pass the mark test. Indeed, we discovered that pigeons can successfully find a hidden food reward using only the reflection, suggesting that pigeons can also use and potentially understand the reflective properties of mirrors, even in the absence of self-recognition. However, tested under monocular conditions, the pigeons approached and attempted to walk through the mirror rather than approach the physical food, displaying similar behavior to patients with mirror agnosia. These findings clearly show that pigeons do not use the reflection of mirrors to locate reward, but actually see the food peripherally with their near-panoramic vision. A re-evaluation of our current understanding of mirror-mediated behavior might be necessary—especially taking more fully into account species differences in visual field. This study

suggests that use of reflections in a mirrored surface as a tool may be less widespread than currently thought.

Keywords Bird · Mirror-self-recognition · Visual system

Introduction

Human adults understand that the reflections of an object in a mirror represent an actual physical object in space. In contrast, most non-human animals do not easily recognize the identity between an object or agent and its reflection, in particular when seeing themselves (Gallup et al. 2002). Examining behavior in response to mirrored reflections has the potential to provide insight into whether, and to what extent, subjects possess self-recognition, and whether lack of evidence is a result of the lack of capacity to understand the functionality of a mirrored surface itself (Pepperberg et al. 1995).

Gallup (1970) was the first to introduce the mirror-mark test as an objective assessment for mirror self-recognition (MSR). In this procedure, subjects have to respond spontaneously to a mark on their forehead that is only visible in the mirror (see methodology, Gallup 1970). The list of animals that have shown any measure of success at the MSR task is a relatively short one: chimpanzees (Gallup 1970; Suarez and Gallup 1981; Calhoun and Thompson 1988; Povinelli et al. 1993, 1997; Bard et al. 2006), orangutans (Suarez and Gallup 1981), dolphins (*Tursiops truncatus*; Reiss and Marino 2001), Asian elephants (*Elephas maximus*; Plotnik et al. 2006, 2010, but see Povinelli 1989) and two corvid species (Prior et al. 2008; Clary and Kelly 2016, but see Soler et al. 2014). Of these, however, MSR is reported only in two dolphins (Reiss and Marino 2001), and this study and those with magpies (Prior et al. 2008) and Clark's Nutcrackers (Clary and Kelly 2016)

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have yet to be replicated. Macaques' (*Macaca mulatta*) success is highly debated, with evidence both against (Gallup 1970; Gallup et al. 1980; Gallup and Suarez 1991), and for the presence of MSR (Rajala et al. 2010; Chang et al. 2015, but see Anderson and Gallup 2011, 2015, for a critique). Unsuccessful species include numerous monkey species (*Cebus paella*: Roma et al. 2007; *Saguinus oedipus*: Hauser et al. 2001; *Callithrix jacchus*: Heschl and Burkart 2006; *Macaca nemestrina*: Macellini et al. 2010), gibbons (*Hylobates syndactylus*; Heschl and Fuchsichler 2009; Suddendorf and Collie-Baker 2009), gorillas (*Gorilla g. gorilla*; Suarez and Gallup 1981; Ledbetter and Basen 1982; Shillito et al. 1999, but see Posada and Colell 2007; Gallup et al. 2002) and jackdaws (*Corvus monedula*; Soler et al. 2014). In addition to mirror-mark tests, some studies with MSR-like tests that do not involve marks have also indicated a lack of self-recognition in mirrors, such as with rhesus monkeys (Suarez and Gallup 1986; Inoue-Nakamura 1997); capuchin monkeys (Anderson and Roeder 1989); African gray parrots (*Psittacus erithacus*; Pepperberg et al. 1995); gibbons (*Hylobates lar*; Hyatt 1998); and New Caledonian crows (*Corvus moneduloides*; Medina et al. 2011). While there has been some evidence that pigeons show mirror-self-recognition-like responses to the mark test after training (Epstein et al. 1981; Uchino and Watanabe 2014) as well failures to replicate such evidence (Gelhard et al. 1982; Thompson and Contie 1986, 1994), there has been no evidence to date that pigeons display this behavior spontaneously, without multi-phase training or experimental experience.

Although many monkey species do not pass MSR tests, some can use a mirror to locate hidden objects—a mirror-mediated behavior (Anderson 1986; Itakura 1987; Heschl and Burkart 2006; Anderson and Gallup 2011). In a study by Anderson (1986), two of the four monkeys were able to spontaneously track mirror images of their hands or arms to find food otherwise not visible without the reflection of a mirror. In this study, monkeys were placed in a cage that allowed them to see a mirror that was placed outside of the cage. The aim was to manually contact and obtain the food outside of one side wall of the cage. This ability to use a mirror as a tool to find food potentially demonstrates that these subjects have partly understood the reflective properties of a mirror. This ability to find hidden food reflected in a mirror has been shown in many species, such as chimpanzees (Menzel et al. 1985), a gorilla (Nicholson and Gould 1995), Asian elephants (Povinelli 1989), pigs (Broom et al. 2009, but see Gieling et al. 2014) and dogs, although with fairly poor performance in that case (Howell and Bennett 2011; Howell et al. 2013). This task is more complex than it appears at first glance: Subjects must understand first that mirrors provide useful cues to start searching for a hidden target and, second, how to reach this

target based on the correspondence between the location of the target in real space and its reflected information.

In addition to the mammalian studies mentioned above, similar mirror use abilities in respect to finding hidden food have also been shown by African gray parrots (Pepperberg et al. 1995) and New Caledonian crows (Medina et al. 2011). In these two studies, subjects could use the mirror to locate hidden rewards after previous mirror exposure, even in novel locations. Given that the cognitive capabilities of parrots and corvids appear on par with primates in many ways (Pepperberg et al. 1995; Prior et al. 2008; Güntürkün and Bugnyar 2016), such abilities may be expected.

One significant anatomical feature of birds that is of particularly high relevance for these kinds of tasks is that most bird species have very laterally placed eyes in contrast to some mammals (Jahnke 1984). The lateral visual field of one eye extends to 125°, enabling close to panoramic view (220° total) under typical binocular conditions (Jahnke 1984). In a study by Medina et al. (2011), crows had to find hidden food that was fixed in one of the four boxes, in novel locations during each trial. The crows perched directly on top of the compartments. In order to see the reflection of the food bait, each crow had to lean down from the perch and look inside the row of boxes underneath (two for training, four for testing) to see the hidden food reflected in the mirror along the back of the boxes. This experimental design was somewhat similar to that used earlier with parrots in a study by Pepperberg et al. (1995). In this case, parrots had to scrutinize vertically placed mirrors to peek inside three separate sections of a box. In such species, it is potentially the case that the birds used a strategy that involved directly viewing the physical food at some point during the test, simply as a result of their extremely broad peripheral vision. Therefore, we must consider that success at this task in subjects with laterally placed eyes and broad peripheral vision could potentially be explained by direct peripheral visibility of the food object itself after having approached the mirror in order to “retrieve” the reflection. To all appearances, the subject would still apparently successfully use the mirror reflection to find the food, but in reality as a result of direct rather than indirect visual cues. Such false-positive results could appear to support evidence of mirror usage capability in cases where subjects show no other clear evidence of such a capacity. It is important then to develop controls to rule out this type of false positive.

We used pigeons in order to test whether peripheral vision could indeed play a role in food-oriented mirror-mediated behavior. Pigeons have been repeatedly tested for MSR (Epstein et al. 1981; Thompson and Contie 1994; Uchino and Watanabe 2014), but to our knowledge, no research yet exists probing their ability to use mirrors to find hidden food. The current study had two aims: first, to

show whether pigeons are able to use mirror information to locate hidden objects and, second, to discover what strategy, if any, pigeons used during this process.

Methods

Subjects

Six domestic pigeons (*Columba livia domestica*) were used as subjects. They were kept in a cage in a room with the other conspecifics at 80–90% of their free feeding weight. Water was available ad libitum. None of the pigeons had prior experience with mirrors or reflective surfaces, but all were socially housed in an aviary containing eight pigeons. All procedures were in compliance with the National Institutes for the Care and Use of Laboratory Animals and were approved by the National Committee of North Rhine-Westphalia, Germany (84-02.04.2013.A458).

Materials

Experiments were conducted in an experimental setup consisting of a wooden arena, measuring 125 cm in width (W), 100 cm in depth (D) and 32 cm in height (H), with transparent acrylic glass roof (see Fig. 1, the large rectangular area on the left). A smaller box (32 cm W × 30 cm D × 30 cm H) was attached at one end of the experimental arena, with a transparent acrylic glass side dividing it from the experimental area. This area was used as holding box

where pigeons could observe the arena prior to each trial, before being released into the experimental arena (Fig. 1, labeled “holding box”). Two mirrors (measuring 25 cm W × 23 cm H) were placed in the corners of the enclosure at a 45°, on the wall opposite the holding box, as can be seen in Fig. 1. A partition wall was placed between the mirrors, dividing the experimental arena in half, so that both halves were clearly visible from the holding box. Each mirror only reflected the area on one side of the partition. Two boxes (16 cm W × 7 cm D × 7 cm H) were placed in front of each mirror (totaling four boxes), as can be seen in Fig. 1, where boxes A1 and A2 are the left and right boxes farther from the mirror, and boxes B1 and B2 are the left and right boxes closer to the mirror, respectively. In all four of these boxes, the surface facing the mirror was open, such that food placed inside the box was visible to the waiting pigeon only by reflection in the mirror. A feeder was placed at the end of the partition wall for use during the habituation phase (see Fig. 1). A digital video camera recorded all trials.

Procedure

Habituation

Prior to the experiment, all pigeons were habituated to mirrors to reduce fear responses initially caused by mirror reflections. To do this, pigeons were placed in the experimental holding box, with a mirror affixed to one side (see Fig. 1, labeled “holding box”). They were exposed to the mirror in this manner for 30 min per day for four days. On

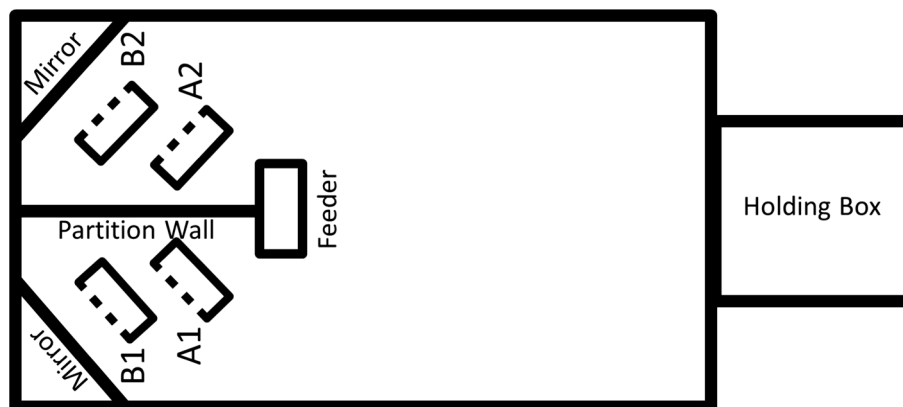


Fig. 1 Schematic view of experimental setup, as seen from above. The holding box on the left is an enclosed area where pigeons were held and could view the arena prior to being released into the arena. The large enclosed area on the left is the experimental arena. The feeder can be seen at the end of the partition wall and was used in habituation trials in order to encourage pigeons to enter the arena from the holding box. The areas on both sides of the partition walls contain identical components: a mirror in each corner and two feeding boxes with only one open side (the dotted lines) facing the mirror.

Boxes B1 and B2 are each closer to the respective mirror, and boxes A1 and A2 are staggered such that they are partially behind the B-boxes, but centrally placed contents are still visible in the mirror. The mirror and boxes are angled such that the pigeon must approach the open side of the boxes by walking close to the outer wall of the arena in both cases, meaning that in every trial, the same eye faces the mirror or the boxes each time for each respective side. (The left eye faces the mirror on the left side of the partition, and the right eye faces the mirror on the right side of the partition.)

the first and fourth day of exposure, we recorded responses of pigeons in front of the mirror, both when the mirror was exposed (30 min) and covered (10 min). During this phase, pigeons were also habituated to the entire experimental arena using the procedure described as follows. Once a day for 5 days, pigeons were placed in the holding box for 1 min and then released and allowed to roam the experimental arena freely and to feed from the feeder at the end of the partition wall for 5 min (see Fig. 1). After the last habituation trial (fifth trial), all pigeons started the experiment. All habituation trials were recorded, and the videos were analyzed by the experimenter (E.Ü). Locomotion, grooming, position in the arena and head orientation with respect to the mirror were analyzed and compared between “mirror-covered” and “mirror-exposed” conditions for the initial 10 min of the first and final sessions. For analysis, interval sampling was done in which those four measures were recorded every 10 s: locomotion (position changed/not changed), grooming (any grooming during the 10-s interval, yes/no), position (front 1/3 or back 2/3) and head orientation (forward/left/right/back).

Testing

After habituation, all six pigeons took part in an experiment consisting of three phases. In each of these phases, subjects had to find food hidden from direct view by using the mirrors. Only one side of the arena (right or left) could be accessed at a time, due to a divider placed in the center (see Fig. 1). In each test trial, one box on one side (of four boxes in total, either A1, A2, B1 or B2 as indicated in the descriptions below) contained food (two corn kernels and two peas), which could only be seen by the reflection in one of the two mirrors. In all three phases, subjects had to wait approximately 1 min in the holding box before being released into the experimental arena. They were allowed to forage for 5 min. During first and second phases, pigeons were tested only under binocular conditions (where both of their eyes were uncovered), and in the third phase, they were tested under monocular conditions (where one eye was covered). For the monocular trials, we used soft eye rings attached around pigeons' eyes and a small, curved eye cap made of cardboard which was attached to the ring.

Binocular A-box phase

In this phase, food was placed in one of the two “A” boxes (the boxes closer to the holding area and farther from the mirror) (see Fig. 1). Only one box contained food in each trial, and food was visible only in one of the two mirrors in the experimental arena. There were 10 experimental trials, with presentation counterbalanced between left and right boxes. There were also five control trials, in which the food

was absent from the boxes. In these control trials there were no food in either feeder. All trials were randomized among pigeons.

Binocular B-box phase

The procedure for this phase was identical to that described for the first phase, except the “B” boxes, farther from the subject, but closer to the mirrors, were used to hide the food (see Fig. 1).

Monocular Phase

In this phase, the “A” boxes, closer to the holding box and farther from the mirrors, were used again. In this phase, no additional control trials were repeated, in order to avoid reducing task engagement. The experimental procedure was identical to the previous two phases, except that pigeons were tested under monocular conditions, where eye caps were used to block vision in one eye (see Fig. 2). In these trials, the pigeons could see the mirror with one eye, while the eye facing the box hiding the food was covered. This prevented possible direct eye contact with the food inside the box. Each day, either the left or the right eye facing the box was consecutively covered in a randomized order.

In this phase, in order to examine exactly how food was found in the monocular condition, the procedure was repeated while being filmed with a top-view camera, in order to document and qualitatively analyze head movements of the pigeons as visible from above. Each pigeon underwent a total of four additional trials, counterbalanced between left and right boxes. Video footage of the head angle was analyzed frame-by-frame, and three time points were identified in each: first visual contact with the mirror reflection of the food reward, first visual contact with the actual physical food reward and consumption of food reward. First visual contact was established by analyzing overhead footage and projecting the angle of the pigeons' visual field to establish overlap with the box containing the food reward. Statistical analysis was conducted using SPSS 22, with Wilcoxon Signed-Rank Tests and Friedman Test used for analysis of group comparisons of two and more than two groups, respectively.

Results

The pigeons that found the hidden food in at least in 80% of the trials in each phase were regarded as successful. Foraging latency was calculated as the duration of time between release of the pigeon from holding box and food consumption. For the analysis, we excluded extreme values

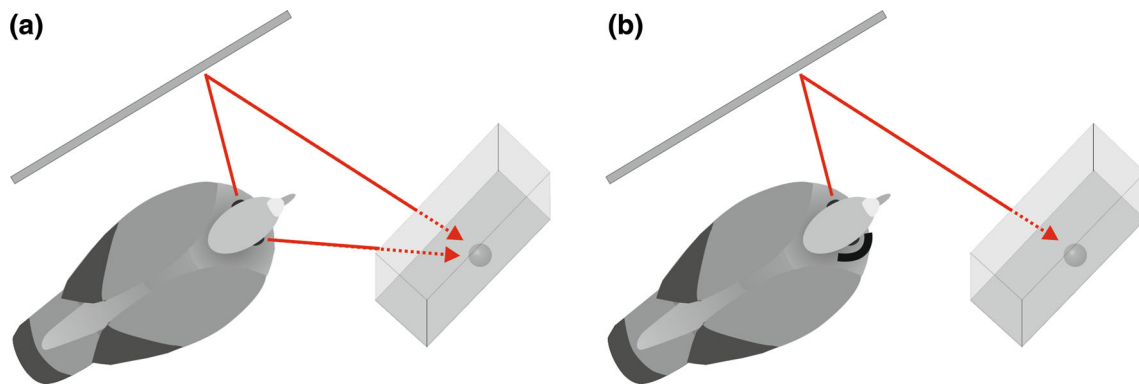


Fig. 2 Schematic overhead view of the two conditions, **a** with unrestricted vision and **b** with monocular vision, only on the side of the head facing the mirror. The *line* in the upper left-hand corner

represents the mirror, and the *small sphere inside the box* represents the exact location of the physical food target inside the box

for each phase based on the *Z*-score, where *Z*-scores greater than 2.0 or less than -2.0 were excluded from the analysis (one run from two pigeons each was excluded).

Habituation

Video analysis of habituation sessions indicated that no pigeons showed especially aversive, aggressive or appetitive behavior toward the mirror (see Fig. 3). Data were compared between first and last (4th) habituation sessions, by taking behavioral measures in 10-s intervals for each 10-min video, for a total of 60 samples for each session.

A Wilcoxon Signed-Rank Test of average latency across every behavioral measure (head direction, grooming, movement, location) indicated there was no overall significant difference between the “mirror-covered” condition and the “mirror-exposed” condition ($Z = -0.659$ $p = 0.510$) when including both sessions.

Looking specifically at a comparison of each behavioral measure across both sessions with a Wilcoxon Signed-Rank Test, two measures initially appear significantly different between the “mirror-covered” and “mirror-exposed” conditions: the time spent with their head facing the back of the arena (without visual contact to the “mirror”

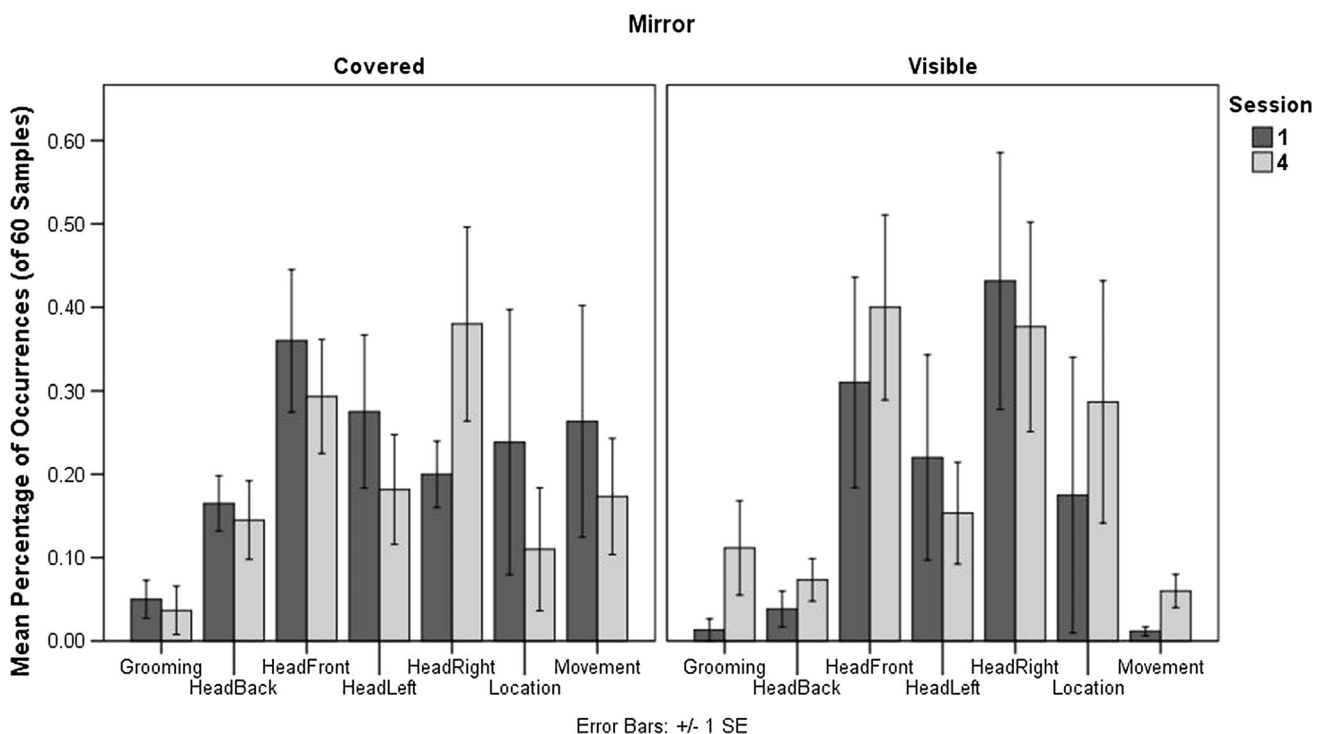


Fig. 3 Observations of behavioral measures documented during habituation to the arena and mirror. Each measure was recorded as being either present or absent in 60 video frame samples, each 10 s apart

side) (mirror 15.42%, no mirror 5.56%, $Z = -0.14$, $p = 0.014$) and movement (mirror 15.42%, no mirror 5.56%, $Z = -2.199$, $p = 0.028$). The time spent facing the mirror (front, left or right), grooming or in the front third of the arena did not significantly differ between mirror and non-mirror habituation conditions. A Bonferroni correction including all seven measures shows no significant differences between mirror and non-mirror conditions in any of the measures.

More specifically, when comparing the first and final sessions for each behavioral measure within each mirror condition (see Fig. 3), a significant difference was only initially apparent in movement (general locomotion) in the mirror visible condition ($Z = -2.032$, $p = 0.042$), where pigeons had made movements on average only 1.11% of the 60 samples in the first session, compared to 6.11% of the final session (see Fig. 3). Again, a Bonferroni correction including all seven of these measures for each of the two sessions (14 conditions) resulted in no significant differences in any behavioral measure during habituation.

Binocular A-box phase

All six pigeons successfully found the food that was otherwise not visible without a mirror in the allowed time for overall 93.3% of trials (56 of 60) in this phase. Pigeon 965 failed to do so in 2 of the 10 trials, and pigeons 964 and 691 failed to do so in 1 of the 10 trials. A binary logistic regression shows that the side of presentation was not a significant factor in success of food retrieval. We excluded extreme outliers (above a Z-score of 2.0 or below -2.0) in our analysis of latency to retrieve food. Across all Binocular A-box Phase trials, the mean was 30.85 s, the median was 14.00 s, and the standard deviation was 33.440. A Wilcoxon Signed-Rank Test showed there was no statistically significant difference in latency depending on side (left or right) ($Z = -0.139$, $p = 0.889$). A Friedman Test

showed there was a statistically significant difference between sessions ($\chi^2(7) = 20.441$, $p = 0.000$), where Session 1 had on average significantly longer latencies than the following sessions (see Table 1 for Wilcoxon Signed-Rank Test results). A Friedman Test also shows there is a statistically significant difference between pigeons ($\chi^2(3) = 12.019$, $p = 0.035$), where pigeons 691 and 964 had on average significantly longer latencies than the other pigeons (see Table 2 for Wilcoxon Signed-Rank Test results). In control trials in the Binocular A-box Phase, none of the boxes contained food, and pigeons did not attempt to approach the mirrors.

Binocular B-box phase

Five of the six pigeons were successful in finding the hidden food in 100% of trials, while the sixth pigeon (691) never retrieved the food. We excluded extreme outliers (above a Z-score of 2.0 or below -2.0). Across all Binocular B-box Phase trials, the mean was 10.09 s, the median was 9.00 s, and the standard deviation was 7.030. A Wilcoxon Signed-Rank Test showed there was no statistically significant difference in latency depending on side (left or right) ($Z = -0.401$, $p = 0.689$). A Friedman Test shows there was no statistically significant difference between sessions in the Binocular B-box Phase ($\chi^2(8) = 2.759$, $p = 0.599$). A Friedman Test shows there was, however, a statistically significant difference in latency between pigeons ($\chi^2(6) = 12.308$, $p = 0.015$) (see Fig. 5b). Pigeons 006 and 997 share the lowest similar latencies (with medians of 4.5 s and 4.0 s, respectively), pigeons 964 and 965 had the highest latencies (with medians of 14.5 s and 12.0 s, respectively), and the latency of pigeon 002 fell in the middle (median 9.0 s), and there are statistically significant differences between those three clusters (see Table 3 for Wilcoxon Signed-Rank Test results comparing individual pigeons). As in the Binocular A-box Phase, in control trials with no food contained in the

Table 1 Wilcoxon Signed-Rank Test results comparing Sessions 1–5 of the Binocular A-box Phase, where pigeons used binocular vision to find food in the boxes farther from the mirrors

	1	2	3	4	5
1		$Z = -2.201$, $p = 0.028^*$	$Z = -2.521$, $p = 0.012^*$	$Z = -2.547$, $p = 0.011^*$	$Z = -2.521$, $p = 0.012^*$
2	$Z = -2.201$, $p = 0.028^*$		$Z = -1.274$, $p = 0.203$	$Z = -2.549$, $p = 0.011^*$	$Z = -2.666$, $p = 0.008^*$
3	$Z = -2.521$, $p = 0.012^*$	$Z = -1.274$, $p = 0.203$		$Z = -2.398$, $p = 0.016^*$	$Z = -2.490$, $p = 0.013^*$
4	$Z = -2.547$, $p = 0.011^*$	$Z = -2.549$, $p = 0.011^*$	$Z = -2.398$, $p = 0.016^*$		$Z = -1.255$, $p = 0.209$
5	$Z = -2.521$, $p = 0.012^*$	$Z = -2.666$, $p = 0.008^*$	$Z = -2.490$, $p = 0.013^*$	$Z = -1.255$, $p = 0.209$	

* $p \leq 0.05$

Table 2 Wilcoxon Signed-Rank Test results comparing the performance of all six pigeons in the Binocular A-box Phase, where pigeons used binocular vision to find food in the boxes farther from the mirrors

	002	006	691	964	965	997
002		$Z = -1.136,$ $p = 0.256$	$Z = -2.521,$ $p = 0.012^*$	$Z = -1.960,$ $p = 0.050^*$	$Z = -1.120,$ $p = 0.263$	$Z = -0.841,$ $p = 0.400$
006	$Z = -1.136,$ $p = 0.256$		$Z = -2.524,$ $p = 0.012^*$	$Z = -2.524,$ $p = 0.012^*$	$Z = -1.893,$ $p = 0.058$	$Z = -0.140,$ $p = 0.889$
691	$Z = -2.521,$ $p = 0.012^*$	$Z = -2.524,$ $p = 0.012^*$		$Z = -1.572,$ $p = 0.116$	$Z = -2.201,$ $p = 0.028^*$	$Z = -2.371,$ $p = 0.018^*$
964	$Z = -1.960,$ $p = 0.050^*$	$Z = -2.524,$ $p = 0.012^*$	$Z = -1.572,$ $p = 0.116$		$Z = -0.509,$ $p = 0.611$	$Z = -2.201,$ $p = 0.028^*$
965	$Z = -1.120,$ $p = 0.263$	$Z = -1.893,$ $p = 0.058$	$Z = -2.201,$ $p = 0.028^*$	$Z = -0.509,$ $p = 0.611$		$Z = -1.521,$ $p = 0.128^*$
997	$Z = -0.841,$ $p = 0.400$	$Z = -0.140,$ $p = 0.889$	$Z = -2.371,$ $p = 0.018^*$	$Z = -2.201,$ $p = 0.028^*$	$Z = -1.521,$ $p = 0.128^*$	

* $p \leq 0.05$

Table 3 Wilcoxon Signed-Rank Test results comparing the performance of all six pigeons in the Binocular B-box Phase, where pigeons used binocular vision to find food in the boxes farther from the mirrors

	p002	p006	p964	p965	p997
p002		$Z = -1.973,$ $p = 0.049^*$	$Z = -2.117,$ $p = 0.034^*$	$Z = -1.752,$ $p = 0.08^*$	$Z = -2.501,$ $p = 0.012^*$
p006	$Z = -1.973,$ $p = 0.049^*$		$Z = -2.384,$ $p = 0.017^*$	$Z = -2.670,$ $p = 0.008^*$	$Z = -1.053,$ $p = 0.292$
p964	$Z = -2.117,$ $p = 0.034^*$	$Z = -2.384,$ $p = 0.017^*$		$Z = -1.051,$ $p = 0.293$	$Z = -2.547,$ $p = 0.011^*$
p965	$Z = -1.752,$ $p = 0.08^*$	$Z = -2.527,$ $p = 0.012^*$	$Z = -1.261,$ $p = 0.207$		$Z = -2.533,$ $p = 0.011^*$
p997	$Z = -2.501,$ $p = 0.012^*$	$Z = -1.053,$ $p = 0.292$	$Z = -2.380,$ $p = 0.017^*$	$Z = -2.384,$ $p = 0.017^*$	

* $p \leq 0.05$

boxes did not elicit a search response from pigeons, and no attempt to approach the mirrors was made.

Monocular Phase

In the Monocular Phase, only three pigeons (6, 964, 997) were successful in finding hidden food in 86.7% of the trials (26 of 30), while the remaining three never found the food (2, 691, 965). A binary logistic regression shows that the side of presentation was not a significant factor in success of food retrieval. We excluded extreme outliers (above a Z-score of 2.0 or below -2.0). Across all Monocular Phase trials, the mean was 37.80 s, the median was 29.00 s, and the standard deviation was 28.331. A Wilcoxon Signed-Rank Test showed there was a statistically significant difference in latency depending on side ($Z = -2.312, p = 0.021$), with the left side showing longer latencies (mean 53.08, median 51.00) than the right (mean 25.67, median 19.00). A Friedman Test shows there was no statistically significant difference between sessions ($\chi^2(2) = 5.200, p = 0.267$) (see Fig. 5a). A Friedman Test

also shows there was no statistically significant difference between pigeons ($\chi^2(6) = 1.000, p = 0.607$).

In addition to the initial 10 trials each bird performed, an additional four (counterbalanced) trials were conducted in order to capture overhead video of each successful pigeon’s specific movements and perform an analysis of head angle relative to foraging success. To this end, we analyzed the position of the head of the pigeon during hold phases. Hold phases are part of the characteristic head bobbing–walking pattern of pigeons. Head bobbing consists of a hold, followed by a thrust phase. Since the head position remains stable during the hold phase, we used them to quantify the behavior of the pigeons in the third experiment. The logic of the analysis is shown in Fig. 4. When the head of a pigeon passed through a line defined by the partition (dotted white line) shown in Fig. 4, we started to count the hold phases of each individual until it successfully pecked the grain. Thus, the number of hold positions was a proxy for passed time. Since pigeons also scrutinize the surrounding during hold, we placed a “visual field circle” on the head, centered on the length axis of the

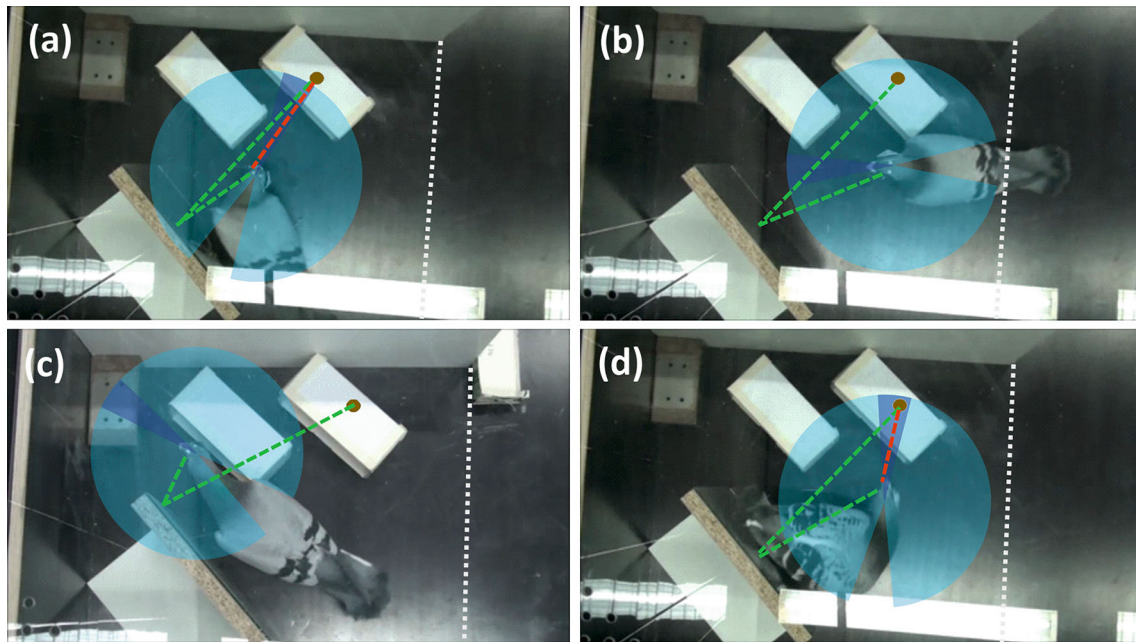


Fig. 4 Example video stills of all three pigeons during trials with the right eye closed (**a, b** pigeon 3, trial 1; **c** pigeon 2, trial 1; **d** pigeon 1, trial 1). The *light gray dotted line* marks the entry of the test zone. The *numbers* of hold positions were counted as soon as the head of the animal had passed this *line*. The *brown spot* shows the position of

the grain within one box. The half-transparent turquoise circle depicts the visual field of the pigeon with the blind area in the *back* and the binocular field in front (*blue*). *Green* and *red* broken lines show the paths of mirror-mediated and direct sightings of the grain, respectively

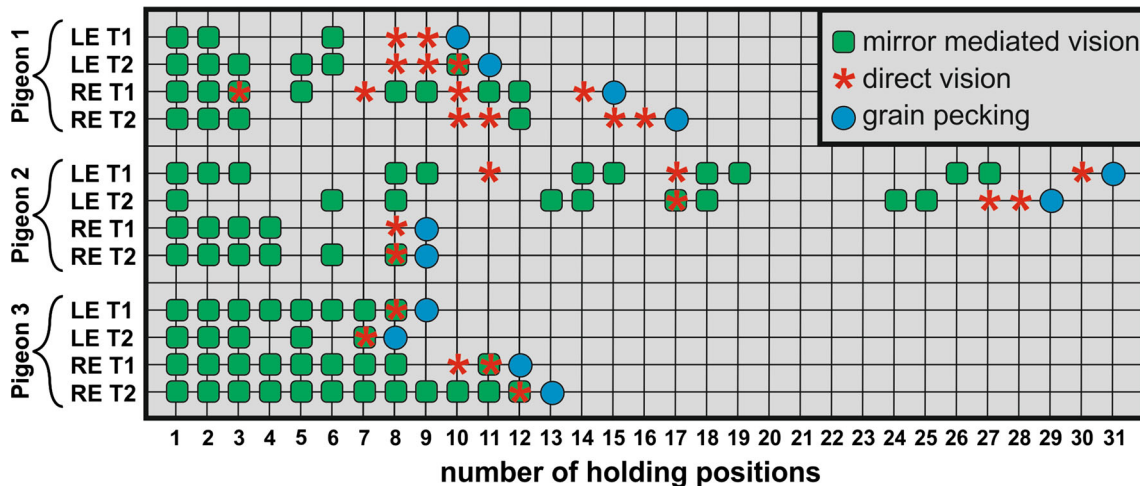


Fig. 5 Schematic depiction of the 12 trials with 3 pigeons and 2 × 2 monocular (LE = left eye seeing; RE = right eye seeing) runs each. X-axis shows number of counted hold positions after entering the test zone. Note that grain pecks always occur after directly seeing the grain

head (Fig. 4). This circle enabled us to estimate whether the animal could see the grain in the box either through the mirror (green dotted lines) or directly with the open eye (red dotted line).

The overall results are shown in Fig. 5 for the three birds and the two trials per testing conditions (left, right eye). Mirror-mediated grain vision is shown as green squares and direct grain vision as red asterisks. As visible, all birds were able to see the grain via the mirror as soon as they entered the critical part of the arena. However, they

needed on average 13.41 hold phases to finally peck the grain. In all 12 observations, the peck on the grain was subsequent to seeing the grain directly. In six of these 12 trials, the grain was in addition visible via the mirror. Thus, not a single time, the grain was pecked after a hold phase in which food was visible by mirror-mediated vision only. On average, the numbers of hold phases with direct grain vision before grain pecking were considerably smaller (P1: 3.25; P2: 2.0; P3: 1.25) than those with vision via the mirror (P1: 5.25; P2: 7.5; P3: 8.50).

We analyzed this pattern nonparametrically. In order to assess whether which form of visual input (direct vision, mirror-mediated vision or a combination of direct and mirror-mediated vision) preceded grain pecking, we used a dependent samples Friedman Test. The test resulted in a significant effect ($\chi^2 = 6.00$; $p = 0.0497$), indicating that mirror-mediated vision (0% of the trials) had a significantly lower chance to precede grain pecking than direct vision (50% of the trials) or a combination of direct and mirror-mediated vision (50% of the trials). To further investigate this effect, we also conducted dependent samples Wilcoxon Signed-Rank Tests for all three possible comparisons of conditions. Both direct vision ($Z = -2.45$; $p = 0.014$) and a combination of direct vision and mirror-mediated vision ($Z = -2.45$; $p = 0.014$) had a significantly higher chance to precede grain pecking than mirror-mediated vision. However, direct vision and a combination of direct vision and mirror-mediated vision did have the same chance to precede grain pecking, as there was no significant effect for this comparison ($Z = 0.00$; $p = 1.00$).

Discussion

In this experiment, we attempted to resolve whether pigeons have the capacity to locate hidden food that is only visible in a mirror. Overall, our results indicate that although pigeons appear initially successful, however, after controlling for peripheral vision they fail to use a mirror reflection to find hidden food. This was not due to an insufficient habituation to mirrors, as visible in the behavioral analyses in the mirror-present or mirror-absent conditions. As such, pigeons appeared habituated to the presence of a mirror, and their performance in our task was unlikely to reflect either particular avoidance of or attraction toward the mirror.

Our experiment consisted of three phases. In the first phase, pigeons had to find hidden food in one of the boxes farther from the mirror (box A in Fig. 1) using binocular vision (both eyes uncovered). In the first trials of this phase, most pigeons approached the mirror first after being released from the holding box, to then turn around (180°) and approach the box containing the food. In subsequent trials, pigeons did not first walk to the mirror but tended to approach the food directly. If pigeons were successful in the Binocular A-box Phase purely due to classical associative conditioning (where the mirror image served as a CS, and the physical food served as a US), then pigeons should have initially displayed significantly delayed latencies for finding food when it was then located in the rear (B) boxes. However, this was not the case and five of the six pigeons were still swiftly able to find the hidden food in B even within the first trial. Thus, the outcome of

the Binocular A-box Phase is unlikely to simply be the result of pure associative conditioning between mirror image (CS) and physical food (US). The mirror image may, however, have served as generic trigger for pigeons to initiate searching for food around the boxes.

In the Monocular Phase, where pigeons searched for food hidden in the front boxes (A1 or A2) under monocular conditions, the results showed stark contrast with the first two phases. In this phase, pigeons needed to demonstrate: 1) the ability to recognize the mirror image of food as a representation and 2) recognition of the real physical location of the food reflected in the mirror. If they were unable to use the mirror to find hidden food, subjects should have only found the food after moving closer toward the box and then directly viewing the food peripherally with the eye facing the food. In this case, they should continue to approach the mirror when the eye facing the food is covered, until they rotate in such a position that the visual field of their uncovered eye overlaps with the food itself.

In this case, only three of six pigeons were successful in finding the food—unsuccessful subjects appeared to try walking “through the mirror” to retrieve the food, reminiscent of the behavior of human patients with parietal lesions, who show visual field “neglect” and reach for the mirror image of objects rather than the object themselves (Ramachandran et al. 1997). Neglect patients do not consciously represent the space ipsilateral to the lesion any more and therefore possibly conclude that the mirrored object has to be real. A similar behavior of our pigeons could indicate that also pigeons do not properly represent the side of the covered eye anymore. However, it is presently premature to discuss in detail whether the mechanisms of the similar behavior of pigeons and neglect patients overlap.

Because half of our subjects were successful and the other half were not, we then more closely analyzed the head angle of the successful pigeons in four additional trials using an overhead camera. We hereby exploited a characteristic head movement while walking of pigeons and many other birds that is called head bobbing (Jiménez et al. 2009). This behavior is characterized by a hold phase followed by a thrust phase. During the hold phase, the head of the bird remains stable in space (Troje and Frost 2000), whereas it is rapidly moved forward during the thrust phase, thus catching up with the constantly moving body. Head bobbing occurs not only during walking but also prior to pecking (Goodale 1983) and when actively observing the environment (Dawkins 2002). Consistently, head bobbing is under visual control since blindfolded birds do not head-bob. It is likely that head bobbing stabilizes the retinal image to facilitate object recognition and to distinguish between self and object motion (Troje and

Frost 2000). This is supported by observations that eye movements exclusively occur during the thrust phase (Wallman and Letelier 1993). However, pigeons are not entirely blind during the thrust phase but are still able to perform basic object vision (Jiménez et al. 2009).

Hold phases are easy to recognize with overhead videos, and we used them to quantify the behavior of the pigeons in the monocular experiment. This analysis showed that in all observations, the peck on the grain was subsequent to seeing the grain directly. In addition, the numbers of hold phases with direct grain vision before grain pecking were considerably smaller than those with vision via the mirror. However, we also observed on 4 of 12 trials that the pigeons were in a position to directly see the grain, but did not immediately approach it. Instead, the birds went on searching for a few more hold phases. It is known that pigeons can miss targets if they do not directly attend to them (Wilkie and Saksida 1994). We consider this to be a likely explanation for these long-search bouts.

Taken together, the results of the first and second phases would typically be interpreted as successful mirror-mediated search behavior. Pigeons' success in finding the hidden food in this context could be interpreted as their successful use of the mirror reflection of food as a simple visual cue, which serves as the learned trigger initiating a search for a physical object (real food) in a specific location, hidden out of direct sight in one of the boxes in the experimental arena. Indeed, in control trials, where none of the boxes contained food during the Binocular A-box and B-box Phases, pigeons did not attempt to approach the mirrors. This interpretation has to be rejected based on our analyses of the monocular trials. These observations make it very likely that finding the grain depended on direct sighting and not on mirror-mediated vision. Thus, the most likely explanation for success in the Binocular A- and B-box Phases is the use of peripheral vision (see Fig. 2). In the Monocular Phase, only pigeons that turned their bodies around, thus allowing direct visual access to the food *after* approaching the image in the mirror, were successful.

It is known that pigeons' total horizontal visual field measures 220° (Jahnke 1984). This wide range of vision allows pigeons to see almost 2/3 of the entire 360° horizontal surrounding environment. Taking this particular anatomy into consideration allows us to account for why most subjects were able to find the hidden food in a significantly shorter time in the first and the second phases than in the third phase.

Previous studies have demonstrated that a number of different species have been able to locate hidden objects by using mirrors (chimpanzees: Menzel et al. 1985; monkeys: Anderson 1986; Itakura 1987; Asian elephants: Povinelli 1989; African gray parrots: Pepperberg et al. 1995; pigs: Broom et al. 2009; New Caledonian crows: Medina et al.

2011; and dogs: Howell et al. 2013), although not all of these have yet been replicated. Each experimental setup was designed in a way that allowed subjects to respond to the mirror image with as little restriction as possible. In doing so, however, very few studies account for the peripheral field of vision in the animal and whether it is broad enough to allow direct visual access to the hidden item after approaching close proximity with the mirror image—something we have revealed in this study as being particularly important for any species with a wide visual field—which includes many bird species. Our results may put into question some of the previous evidence that exists for mirror-mediated search behavior in other species. These potential false positives are one of the central debates in MSR research. Here, in our experiment, results from the Binocular A-box and B-box Phases showed that pigeons seemed as if they had a capacity for locating hidden food. However, the Monocular Phase revealed this was not actually the case and that the results of the Binocular A-box and B-box Phases were likely false positives as a result of using peripheral vision. Studies such as that of Epstein et al. (1981), Pepperberg et al. (1995), Medina et al. (2011) and Uchino and Watanabe (2014), in all of which avian peripheral vision is a very salient feature, may well bear re-examination in light of new findings.

It certainly could be the case that peripheral vision producing a false positive is a less relevant concern for studies focused on some mammals with eyes in a more frontal position and a narrower range of peripheral vision. Our results suggest that species with the laterally placed eyes, and a wide range of vision, have the strong potential to produce false positives in a mirror-mediated spatial location task when this is not controlled for. On the whole, our findings here strongly suggest that experimental controls accounting for visual field and peripheral vision access in mirror-mediated spatial locating tasks are vital in accurately exploring true mirror-mediated behavior.

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