When pigeons in motion lose sight of their food: behaviour on visible displacement tasks revisited

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Abstract: In traditional visible displacement tasks, animals view an object as it is moved out of their sight, but either the object moves behind an occluder or an occluder moves in front of it. Here we present a more ecologically realistic visible displacement task for pigeons (Columba livia (Gmelin, 1789)) in which it was the animal that occluded the object, a food dish in this case, by virtue of its own motion. In a branched maze, pigeons had visual access to food, which they would lose from view as they moved through the maze. A within-subject design was used whereby the task was presented first in descending order of difficulty (i.e., decreasing memory load owing to the opening of (i) gaps and (ii) windows in the walls of the maze), and followed 10 months later by an ascending order. When the food was visible at all times through windows and gaps, pigeons would make turns in the maze that would bring them closer to the food (i.e., they chose the shortest route above chance levels). In general, they failed to do so when the food was lost from view, but there was one exception at the end of the study (the second time that there were gaps but no windows): there was a significant tendency for the last two turns that brought the bird out of the maze to be the shortest route to the food. The pigeons may have learned to take advantage of opportunities to lighten their memory load.

Résumé: Dans une tâche standard de déplacement visible, les animaux regardent un objet qui est déplacé hors de leur champ visuel; cet objet peut être déplacé derrière un panneau opaque ou le panneau, lui-même, peut être déplacé pour cacher l’objet. Dans notre étude sur les pigeons (Columba livia (Gmelin, 1789)), nous avons développé une tâche plus réaliste du point de vue écologique dans laquelle l’animal lui-même cause la disparition de l’objet, un bol de nourriture dans ce cas, par son propre déplacement. Les pigeons avaient un accès visuel à la nourriture dans un labyrinthe à bifurcations et, ensuite, la perdaient de vue en se promenant dans le labyrinthe. Nous nous sommes servis d’un plan expérimental intrasujets dans lequel la tâche fut d’abord présentée dans un ordre de difficulté décroissant (car (i) des fentes et (ii) des fenêtres étaient ouvertes dans les panneaux du labyrinthe, entraînant une réduction de la charge mnésique) et, 10 mois plus tard, dans un ordre de difficulté croissant. Lorsque la nourriture était visible en tout temps, à travers les fenêtres et les fentes, les pigeons firent des virages dans le labyrinthe qui les rapprochaient de la nourriture et choisirent le trajet le plus court avec une fréquence d’occurrence plus élevée que le hasard. En général, ce n’était pas le cas lorsqu’ils perdaient de vue la nourriture, mais une exception fut observée : à la fin de l’expérience (lors de la deuxième présentation des fentes, sans fenêtres) les pigeons prenaient, dans les deux derniers virages, le chemin le plus court pour atteindre la nourriture. Ce dernier résultat donne à penser que les pigeons ont pu mettre en œuvre une stratégie pour alléger leur charge mnésique.

Introduction

In the everyday lives of animals, objects such as food, shelter, predators, prey, and young move in and out of view all the time. For some species, such as the adult human, memories bridge the disappearance and reappearance of these objects so fluidly and effortlessly that the disappearance is barely noticed. If it were not so, routine tasks such as driving would be impossible. Packs of hunting dogs (Canis familiaris L., 1758) might not be able to coordinate hunting behaviour and anticipate the reappearance of moving prey that had been lost from sight (Gagnon and Doré 1994). Whereas an anthropomorphic view would be that cueing interpretations have been ruled out. This latter category is seen in a variety of primate species including orangutans (Pongo pygmaeus (L., 1760); de Blois et al. 1998), an object have been delineated by Etienne (1984). (1) Unlearned motor reactions such as the stereotypic behaviour manifested by dragonfly (Aeshna cyanea (Müller, 1764) = Aeshna cyanea (Müller, 1764)) larvae in response to the disappearance of prey (Etienne 1972). (2) Associative learning of the relation between the disappearance of an object and the delayed response, such as progressive learning by young chicks (Gallus gallus (L., 1758)) to locate a mealworm behind one of two screens (Etienne 1973). Other examples in this category include bumble bees (Bombus impatiens Cresson, 1863) learning to find a nest entrance using landmarks (Plowright et al. 1995) and swimming rats (genus Rattus G. Fischer, 1803) learning to find a platform hidden underwater in the Morris water maze (Morris 1981). (3) Spontaneous search behaviour in both novel and familiar situations for which cueing interpretations have been ruled out. This latter category is seen in a variety of primate species including orangutans (Pongo pygmaeus (L., 1760); de Blois et al. 1998),...
gorillas (*Gorilla gorilla* (Savage and Wyman, 1847); Natale et al. 1986), brown capuchin monkeys (*Cebus apella* L., 1758; Dumas and Brunet 1994), chimpanzees (*Pan troglodytes* (Blumenbach, 1775); Call 2001), cotton-top tamarins (*Saguinus oedipus* L., 1758; Neiworth et al. 2003), and white-tufted-ear marmosets (*Callithrix jacchus* (L., 1758); Mendes and Huber 2004).

Little is known about how birds solve the problem of locating objects that have disappeared from view. Ultimately, one aim of research in this area is to make species comparisons, and indeed some such comparisons have already begun to surface in the literature. For instance, when a piece of food is dropped down one of four clear chutes into an opaque compartment, common pigeons (*Columba livia* Gmelin, 1789) fail to choose the correct compartment at a level above chance, whereas common hill mynahs (*Gracula religiosa* L., 1758) succeed (Plowright et al. 1998). When food in a cart disappears through a tunnel, crows (genus *Corvus* L., 1758) will spontaneously dart to the point of emergence (Krushinskii 1960). In contrast, pigeons fail to spontaneously follow the path of the cart (Krushinskii 1960); however, by explicit training or trial-and-error experience they can learn a practical rule such as “go to the end of the tunnel to receive food” (Plowright et al. 1998) and so the second of Etienne’s (1984) categories captures their behaviour. When food is hidden behind one of two screens as the subject watches, both pigeons (Plowright et al. 1998) and ringed turtle-doves (*Streptopelia risoria* (L., 1758); Dumas and Wilkie 1995) fail to choose the correct screen at levels above chance. Psittacine birds such as yellow-crowned parakeets (*Cyanoramphus auriceps* (Kuhl. 1820); Funk 1996), and grey parrots (*Psittacus erithacus* L., 1758; Pepperberg and Funk 1990; Pepperberg and Kozak 1986; Pepperberg et al. 1997) are particularly skilled at finding hidden objects, as are the only species of passerines studied, the food-storing black-billed magpies (*Pica pica* (L., 1758); Pollok et al. 2000).

In our work on pigeons described above, we used a visible displacement task, which consists of occluding the object while it is being viewed by an animal and then recording the viewer’s search behaviour. The term “visible displacement” is taken from Piagetian psychology (for a description of Piagetian tasks see Doré and Dumas 1987). Although behaviour on such tasks is often cast in a Piagetian framework of development, Shettleworth (1998) noted that the focus of our research in this area is not so much on whether pigeons “pass a test” or on what they “believe about a hidden object”, such as whether it continues to exist, what it is, whether it remains attractive or not, and where it is. Instead, the main interest is in what animals do (i.e., how they behave) when their food disappears from view.

In the visible displacement tasks described above, either (i) food was moved behind an occluder (food was moved through an opaque tunnel; food was dropped down a clear chute into a compartment covered with an opaque lid) or (ii) an occluder was moved in front of the food (a screen was dropped in front of the food). The latter procedure is more ecologically relevant (Dumas and Wilkie 1995), because in nature pigeons and ringed turtle-doves do not contend with moving food. While foraging in a field, a bird’s view of food could conceivably become occluded by moving objects (e.g., by another bird landing in front of the food). In this paper, we take the ecological argument one step further: in nature, if food does become occluded, it might also be a result of the bird’s own movement. From a physics point of view, what moves is immaterial: the relative motion can be the same if a bird moves behind an occluder, food moves behind an occluder, or an occluder moves in front of food. From a psychological point of view, however, such detail may well be important.

We designed a new maze for this task. It consists of a T maze with a Y-shaped branch at each end of the horizontal crossbar (Fig. 1). Pigeons entering the maze were attracted to a dish with a few grains of food (a “ lure”). By eating the food in the dish, the birds gained visual access to a group of three bowls of food (the “target”) clustered outside the maze, and we gained an operational definition of attention to food and motivation that has often been lacking in previous research on visible displacement tasks — eating from the lure was intended to be analogous to a peck to a centre key prior to choice in an operant task. To attain the target, the birds had to move through the maze, thereby losing visual access to the target. Because the birds themselves occluded their own view of the target, we eliminated the experimenter intervention present in previous research. Because there were four direct paths to exit the maze (two possible first turns × two possible second turns), the one leading directly to the target would be taken by chance one time in four. Deviations from a chance value of 0.25 are easier to detect than deviations from a chance value of 0.50 (because the variance is necessarily lower) in the more traditional T maze. We began with a difficult version of the task and progressively made it easier by introducing gaps in between the panels of the maze and (or) introducing windows in the panels to afford additional viewing of the target, thereby reducing the memory load for the birds. The task was then made progressively more difficult again. On each test we examined whether the birds made turns in the maze that brought them closer to or farther from the target.

In summary, our aim was to determine whether pigeons in this new visible displacement task would approach the food when it was hidden from view just as when it was visible. If, as in previous work, the visible displacement task proved to be too great a challenge for the pigeons, the gradual change in task difficulty would help to determine at what point performance broke down.

**Materials and methods**

**Subjects**

The animals were treated in accordance with the guidelines of the Canadian Council on Animal Care and the research was approved by the Animal Care Committee of the University of Ottawa. The study began with 13 female pigeons being housed in individual cages where water and grit were continuously available. Lighting was on a 12 h light : 12 h dark cycle. Prior to the study they had been group-housed in the flight cage used in this experiment (described below). The use of the home flight cage where the birds had been fed daily may have led to an expectation of food and may have served to maintain motivation to search
for food. The pigeons were purchased between 1998 and 2000 from the Palmetto Pigeon Plant in South Carolina. One was naïve at the time of this experiment, one had previous experience in an experiment on foraging behaviour, and the rest had been used in operant studies of pattern recognition. Food was restricted so that the birds would maintain 90% ± 5% of ad libitum body mass. In between conditions 4 and 5 (which were replications of each other, see Design section below), 10 months elapsed during which time four of the birds died (not of contagious disease).

**Experimental setup**

The experiment took place in a flight cage (2.56 m high × 3.33 m long × 1.94 m wide). A maze, described below, was constructed for this study. The door of the flight cage opened directly onto the entry of the maze where a pigeon is diagrammed in Fig. 1. The floor of the flight cage was covered with wood chips.

The maze consisted of wood panels painted white. Each panel was 1 cm thick, 40 cm long, and 50 cm high. L brackets on a wooden base held each panel in a vertical position. The panels were arranged to form the six corridors shown in Fig. 1, each 40 cm wide, through which the pigeon would navigate. The corridors were arranged so that when a pigeon entered the maze and walked forward, it arrived at a T junction. After turning left or right, the pigeon would arrive at a Y junction where it could again turn left or right. So that the birds would not attempt to jump or fly out of the maze, after pretraining the corridors were covered with white crinoline that was secured to the tops of the panels with thumbtacks.

Four white ceramic dishes (6.5 cm in diameter and 4 cm deep) containing mixed grain were placed in the maze. These white dishes were not new to the animals, as they had been fed from them outside of the experiment. One dish will be referred to as the “lure” and the cluster of three remaining dishes as the “target”. The purpose of the lure was twofold: (1) to attract the pigeon’s attention to the location of the target — if the bird could attain the lure, then the target was within full view for the animal; (2) to have an operational measure of attention and motivation by food. The position of the lure depended on placement of the target. If the target was at position A or B, then the lure was at x; if the target was at position C, then the lure was at y; and if the target was at position D, then the lure was at z.

**Procedure**

**Pretraining**

Before the experiment began, the birds were first trained to eat from the lure, were then given the opportunity to familiarize themselves with the spatial layout of the maze without any food present, and finally were given additional experience eating from the lure.

Each bird was given 15 trials (1 per day) in which they ate food from the lure five times at each of the three positions x, y, and z (Fig. 1a). Order of position of the lure was counterbalanced across subjects. The exits were blocked off so that the birds could not run out of the maze without noticing the lure.

After 12 of the 15 trials, the birds were given 4–5 days to become more accustomed to the layout of the maze without any food present. The birds were allowed to wander in and out of the maze and even to fly above it (11 of the 13 birds flew around the maze during pretraining at least once, and 8
did so at least twice). Occasionally a bird would confine itself to one side of the maze, in which case that side would be temporarily blocked off to ensure that the bird had been through the entire maze.

After 4–5 days of becoming accustomed to the maze, the birds were then given the remaining 3 of the 15 trials to again eat from the lure, once at each of the positions x, y, and z. These trials served to refresh the birds’ memory of the lure and its three possible locations in the maze.

**General experimental procedure**

Subjects were tested individually and were each given one trial per day or two trials per day (one in the morning and one in the afternoon). Daily feeding to maintain body mass was carried out after all the testing of all the birds was completed for the day. At the beginning of each trial, the pigeon was placed at the entrance to the maze. The trial began when the pigeon had advanced to the position of the lure and lowered its head to eat from the dish. If a pigeon did not eat from the dish, then the trial was re-administered on another day, up to a maximum of three re-takes on 3 different days. The trial was not counted in the analysis unless the pigeon eventually ate from the dish on a re-taken trial. If the pigeon ate from the dish but then just wandered around the maze without exiting, then the trial was counted as an instance of the pigeon not having taken the shortest route to the target. The experimenter recorded the entire sequence of turns at each juncture in the maze (e.g., turned left at T junction, returned to centre, went to the right, turned left at Y junction, exited maze). The trial ended when the pigeon exited the maze and came to within approximately 5 cm of the target or until 8 min had expired, which ever came first. The objective of this study was not to train birds to find food; therefore, to avoid reinforcing behavioural sequences with food, as soon as the bird approached the target the room light was turned off, which plunged the room into complete darkness so that the pigeon could not see the food, and the subject was removed from the flight cage before it had a chance to eat the food. Very occasionally, quick birds managed to consume a grain or two, but this happened after the shortest route trials, as well as others; therefore, any reinforcement was likely non-differential.

**Design**

A within-subject design was used. The experiment consisted of two phases separated by 10 months. The first phase was a series of four conditions (conditions 1–4) of descending difficulty (i.e., reducing memory load), while the second phase was a series of three conditions (conditions 5–7) of ascending difficulty. In condition 1 (Fig. 1a), the birds were tested for their ability to attain the target by the shortest route when there was no opportunity to see the food in between the time of eating the food in the lure and the time of exiting the maze. In keeping with Pollok et al. (2000), to determine whether the birds could detect the food by odour, two types of trials (four of each, see Table 1) were run in condition 1: the dishes at the target position were either filled with mixed grain or left empty. In both cases, they were slightly tilted away from the birds so that they could not see whether the dishes were full or empty. Each bird received four of each type of trial presented in random order over 8 days. The target dishes were located once at each of positions A, B, C, and D for each type of trial. The remaining conditions 2–7 were run for four trials each, once for each target position A, B, C, or D, and there was food in the dishes in all trials. In those conditions, the target dishes were slightly tilted towards the birds so that the food was visible to them. Order of presentation of the target position was counterbalanced across subjects.

In condition 2, the memory load was reduced by allowing the birds the opportunity to see the target a second time at the Y junction of the maze: gaps approximately 6 cm wide were inserted between the panels at the junctions (Fig. 1b). The gaps were wide enough for a pigeon’s head to fit through, but not its body. In condition 3 (Fig. 1c), the memory load was further reduced by cutting windows (16 cm high and 30 cm long) into the panels, affording the pigeons an uninterrupted view of the target as they navigated through the maze. In this condition, however, to attain the food, it was still necessary for the bird to walk past the target as it moved through the last corridor to exit the maze. Distancing oneself is likely an unprepared response for pigeons to the sight of food. Moreover, as birds moved past the food, it would likely be lost briefly from view. For these reasons, in condition 4 (Fig. 1d), the position of the target was moved to the extremity of the last corridor so that the pigeons would have truly continuous visual access to the target and would never need to move farther away from it to attain it.

For the second phase, which began 10 months after the end of the first phase, the target was kept at the end of the Y junction. The second phase was undertaken to determine whether any change in performance in the first phase was due to experience or was due to the ease or difficulty of the tasks themselves. Given the time delay between the two phases of the experiment, condition 5 was a replicate of condition 4. In condition 6, the windows were shut by covering the openings with cardboard (Fig. 1e), and in condition 7 (Fig. 1f), the gaps were also closed.

**Scoring**

The data are scored in binary fashion (see Statistics section below): in a sequence of two turns (one at the T junction and the other at the Y junction) that brought the bird out of the maze, the shortest route was either adopted or not. In other words, we scored trials as to whether each of two turns in the maze brought the animal closer to or farther from the target. The chance value is 0.25 (0.5 for the first turn × 0.5 for the second turn). The data are reported in two ways as described below. In both cases, the two turns referred to are the two turns that brought the pigeon out of the maze. If the first two turns brought the bird out of the maze, then these two turns were the only ones made. If it was the last two turns that brought the bird out of the maze, then the bird made any number of turns prior to them.

**First (and only) two turns**

A restrictive scoring system was to only consider trials in which the bird took a direct route to exit the maze, i.e., one turn at the T junction followed by a turn at the Y junction where the pigeon would exit the maze. If and only if both turns brought the bird closer to the target, the trial was
which individuals had choice proportions that differed from chance. To specify individual contributions to goodness-of-fit tests, we used generalized linear interactive modeling (GLIM; Francis et al. 1993) to fit a logistic model, which specifies a binomial error term, to the data.

Results

Table 1 shows the number of trials that could be retained under the two scoring systems. The proportions of trials in which the shortest route to the target was taken, shown in Fig. 2, are based on these totals. The time to attain the target varied from 5 to 470 s.

First (and only) two turns

In condition 1, the ratio of shortest routes taken versus not taken on the 4 days in which food was present in the bowl was 13:15, whereas it was 9:26 on the four trials when the bowls were empty. The difference between the two conditions was not significant ($\chi^2_{11} = 2.57, p < 0.11$), showing that the pigeons could not locate the food dish by any possible odour from the grains.

Figure 2a shows the proportions of trials on which the shortest route was taken for each condition. Table 2 gives the results of the $G$ tests for each condition. Only in conditions 4 and 5, which were repeats of the same situation where the birds had unbroken visual access to the target, did the group choice proportions differ significantly from chance. Individual differences were not significant except in condition 5. Examination of the individual $G$ values revealed that five pigeons showed individual proportions that were significantly greater than chance, whereas three pigeons showed no significant $G$ values, and so the overall tendency to take the shortest route was not uniform in magnitude.

One possible explanation for the apparent jump in performance (from 0.53 to 0.75) between conditions 4 and 5, although the stimulus conditions were identical, is subject selection: in between the two conditions, four birds died. This explanation is unlikely, however, because if we look only at the nine birds that went on to participate in condition 5, their mean proportion of shortest route trials in condition 4 did not differ significantly from the group as a whole (0.50 vs. 0.53, respectively). Alternative explanations are re-
lease from pro-active inhibition or increased motivation after a long period without foiled attempts to eat food. The median time to attain the food dropped slightly from 26.5 s (range 6–457 s) in condition 4 to 22 s (range 6–385 s) in condition 5, which is consistent with both possibilities. The main comparisons in this study, however, were not between conditions 4 and 5 and so it does not matter much which, if any, of our suggested scenarios are correct. More important were the comparisons, reported below, between condition 4 and the preceding ones, and between condition 5 and the subsequent ones.

If the procedure of preventing the pigeons from eating the food once it was attained had led to an overall decline in motivation, a steady increase would have been expected in the number of trials excluded from analysis as a result of a failure to engage in the task (i.e., a failure to respond to the lure). Table 1 shows that the proportion of trials coded fluctuated but did not decline systematically with experience in the maze.

**Last two turns**

**Food versus no food**

The ratio of shortest routes taken versus not taken on the 4 days in which food was present in the bowl was 16:26, whereas it was 11:32 on the four trials when the bowls were empty. The difference between the two conditions was not significant ($\chi^2_{1} = 1.54, p < 0.22$), again showing that the pigeons could not locate the food dish by any possible odour from the grains.

**Comparison of proportions with chance**

Figure 2b shows the proportion of trials on which the shortest route to the target was taken on the last two turns. Not only were the proportions in conditions 4 and 5 significantly higher than chance, as with the previous scoring system, but the proportions in conditions 3 and 6 were also high. Individual differences were significant only in conditions 5 and 6. Partitioning the total $G$ value into individual components revealed that six of the eight birds in condition 5, and four of the eight in condition 6, showed proportions that were significantly greater than chance, with proportions between 0.75 and 1.0 (compared with a chance value of 0.25) — the overall tendency to take the shortest route was not uniform in magnitude. In the conditions with the highest memory demands (conditions 1, 2, and 7), the group proportions did not differ significantly from chance (Table 2).

The surprisingly good performance in condition 6 compared with condition 2 raised the possibility that over the course of the experiment the nine birds in condition 6 might have learned to return to the centre of the maze to take another look at the food if its location had been forgotten. This may have been true for one bird that, over four trials, returned more frequently to the centre of the maze in condition 6 (nine times versus just three times, respectively), but another bird showed just the opposite pattern, returning to the centre less frequently (only once instead of six times, respectively). Two other birds did not return to the centre at all in condition 2, but did so once over four trials in condition 6. The five remaining birds

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Note: Either the first (and only) two turns or the last two turns that brought the bird out of the maze were examined. The $G_{pooled}$ value tests for a deviation of the group proportion of trials on which the shortest route was taken from a value of chance (0.25). The $G_{heterogeneity}$ value tests for individual differences. The $G$ test statistic is compared with a $\chi^2$ value. *, $p < 0.05$; **, $p < 0.005$; ***, $p < 0.001$. 

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showed no change between conditions 2 and 6. In short, the behaviour of returning to the centre of the maze — and so seeing the target more than once from the position of the lure — was comparable in both conditions.

**Comparisons among conditions**

The analysis above showed that adding windows improved performance to a level that was significantly higher than chance. Using a logistic model, a comparison between conditions 5 and 6 further revealed that removing the windows had a deleterious effect (Fig. 2b). Although both conditions showed above chance performance, the proportion of trials on which the shortest route was taken in condition 6 was significantly lower than in condition 5 ($\chi^2_{11} = 4.28, p < 0.04$). The comparison between conditions 3 and 4 showed that, given the above chance performance seen in condition 3, the further improvement associated with a new food placement was not significant ($\chi^2_{11} = 1.13, p < 0.29$).

As mentioned previously, when the birds ate from the lure the target was in full, clear view for them. Nonetheless, to address the possibility that the target was not seen by the birds from the position of the lure in the first and last conditions, we examined just the first turn to determine whether there was a tendency to move toward the target. There were no individual differences ($G_{\text{heterogeneity}} = 8.38, df = 11, p < 0.68$). The proportion of turns towards the target was 0.60, which was significantly higher than chance ($G_{\text{pooled}} = 4.35, df = 1, p < 0.04$).

**Discussion**

Regardless of how the data were examined (restrictive or less restrictive scoring), the pigeons failed to attain the target by the shortest route when the maze lacked both windows and gaps. The fact that they failed twice, both at the beginning of the experiment (condition 1) and at the end (condition 7), even though they had succeeded in some intervening conditions, shows that the failure was attributable to the difficulty of the test itself and not to any time-related factor. The failure to take the shortest route to the target in both conditions cannot be due to the birds’ not having seen the target because their first move tended to be a turn towards the target. Also using both scoring systems, the birds unequivocally succeeded in conditions 4 and 5, in which they had unbroken visual access to the food. Odour cannot have been used as a cue, as there was no difference between the four trials in condition 1 where the target bowls contained food and the four trials where they did not. Pigeons will approach the target in this apparatus when they have uninterrupted visual access: the maze is not too complicated and the response of direct approach to food is not too taxing (i.e., moving towards food is part of the animals’ basic behavioural repertoire).

The direct approach to food seen in conditions 4 and 5 and the absence of it in conditions 1 and 7 was observed in both scoring systems (Figs. 2a, 2b), leaving little doubt as to the outer bounds of the birds’ abilities. For the remaining intermediate conditions, however, the two scoring systems yielded different results and so there is room for debate. In the “first and only two turns” system, the birds failed in all conditions except for the identical conditions 4 and 5 in which the target was always in view. The skeptical approach is to conclude that the pigeons failed all the visible displacement tasks, just as they did in our previous work using three other tasks (Plowright et al. 1998). Given that pigeons do not even spontaneously complete partially occluded objects (Sekuler et al. 1996), although recognition improves with training (DiPietro et al. 2002), it should come as no surprise that “out of sight, out of mind” describes the data reasonably well.

A more nuanced view, however, is supported by the data scored by examining the last two turns. Instead of picturing a two-state (can or cannot) situation, it revealed some gradations. One possible reason for the differing results in Figs. 2a and 2b is that the less restrictive scoring system included trials in which the birds returned repeatedly to the centre and looked through the gap, thus enabling better encoding of the position of the food. Another nonexclusive possibility is that it is a statistical issue: only using the less restrictive scoring system, in which all sequences were included, was the number of observations large enough to detect small differences among the conditions.

The less restrictive scoring system revealed two effects that went undetected by the restrictive system. (1) There was a consistent effect of opening or closing the windows: not only did removing windows have a deleterious effect in condition 6, but adding them earlier in the experiment in condition 3 had a beneficial effect. The inverted U pattern again argues against a time-related factor as an explanation: it is the occlusion of the food that hinders performance. (2) The birds could solve the visible displacement task (i.e., above chance performance was observed) when there were no windows but when there were gaps. This was only true, however, at the end of the experiment (condition 6) but not at the beginning of the experiment (condition 2). The difference may have to do with the different food placements, as the new food placement led to an improvement between conditions 3 and 4. The effect, however, was not significant. The frequency of sequences in which the birds returned to the centre was comparable in both conditions, and so it seems unlikely that birds had learned to “zig-zag” close to the lure to look through the gap in the maze and better encode the position of the target, which would become subsequently occluded as the bird moved through the maze. One post hoc explanation is that the birds had simply not taken advantage of the gaps as a “memory booster” until they had had some experience with them. If so, the present design does not allow us to determine which of the intervening experiences with gaps between conditions 2 and 6 were responsible for the improvement. In summary, the less restrictive scoring system revealed that the birds seem capable of solving visible displacement tasks, but only under minimal memory strain, and that they may possibly learn to benefit from experience in a way that improves their own memories.

Notwithstanding the different interpretations offered here as to whether pigeons simply cannot solve visible displacement tasks or whether they can do so under restricted conditions, the salient fact remains that when pigeons traveled about 80 cm (the length of two 40 cm panels in the maze), during which time they lost sight of their food, they failed to take the shortest route to the food at frequencies greater than
chance, although they succeeded when the food was visible at all times. Before this study, we had tested pigeons in a visible displacement task that required no search behaviour (Plowright et al. 1998). We had also used stationary food and moving occluders, as well as moving food and stationary occluders. To this list we now add a fourth version that included the ecologically realistic aspect of the animal’s own motion being the cause of the disappearance of food from view (stationary food, stationary occluders, moving bird). Pigeons in motion that momentarily lost sight of food through their own search behaviour did not solve the visible displacement task in the sense that they lost their tendency to directly approach food. We would be hard-pressed to find a yet more ecologically justifiable or “user friendly” visible displacement task for pigeons, although it may well exist. The development of such a task would be facilitated by research, along the lines developed here, on what factors might possibly facilitate or hinder performance. Future research might also turn its sights to the pigeons themselves and examine the performance of pigeons foraging in their natural environments. An ecological approach lends itself to bridging the gap between the laboratory and the wild (Shettleworth 1989).

Although the focus of this study was on what pigeons do in the face of a particular problem, the data raise the question of process. On the surface, pigeons would seem to have what it takes to solve visible displacement tasks: they have good visual acuity as evidenced by their ability to detect cryptic prey (Reid and Shettleworth 1992), well-developed navigational skills (Prior et al. 2002), good working memory (Spercht and Edwards 1986; Spercht and Honig 1988), the ability to encode spatial position (Cheng and Sherry 1992), and the ability to bridge gaps of up to 25 s in an operant spatial non-matching to sample task (Olson 1991). According to Neiworth and Rilling (1987), pigeons can even mentally represent the trajectory of a moving object as it disappears from view, i.e., they are capable of mental imagery. Either the pigeons are missing some key perceptual or cognitive process or they are failing to use the ones they have. In this light, further progress awaits some theoretical emphasis in the area of animal cognition on ecology (Dukas 1998) with all the promise of psychology to the understanding of behaviour.

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