

Internal Sense of Direction and Landmark Use in Pigeons (*Columba livia*)

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The relative importance of an internal sense of direction based on inertial cues and landmark piloting for small-scale navigation by White King pigeons (*Columba livia*) was investigated in an arena search task. Two groups of pigeons differed in whether they had access to visual cues outside the arena. In Experiment 1, pigeons were given experience with 2 different entrances and all pigeons transferred accurate searching to novel entrances. Explicit disorientation before entering did not affect accuracy. In Experiments 2–4, landmarks and inertial cues were put in conflict or tested 1 at a time. Pigeons tended to follow the landmarks in a conflict situation but could use an internal sense of direction to search when landmarks were unavailable.

Orientation based on a sense of direction, often called *inertial navigation*, *dead reckoning*, or *path integration* (Etienne & Jeffery, 2004; Gallistel, 1990), allows an animal to update a representation of its position on the basis of internal cues derived from self-motion (*idiothetic cues*). In mammals, these include cues from the vestibular system (Wallace, Hines, Pellis, & Whishaw, 2002). Some researchers (e.g., Gallistel & Cramer, 1996; McNaughton et al., 1996; review in Etienne & Jeffrey, 2004) have proposed that idiothetic cues establish a spatial reference frame onto which information from visually perceived landmarks is added. Evidence that landmark learning is impaired in the absence of a stable reference frame (Biegler & Morris, 1996; Knierim, Kudrimoti, & McNaughton, 1995) is consistent with this proposal. Whether it is the basis for landmark learning, a stable relationship between an animal's internal position sense and a goal could be learned and combined with information from predictive landmarks to improve orientation. While a good deal is known about how idiothetic cues affect landmark use in small mammals (Etienne, 2003), almost nothing is known about whether comparable effects exist in birds.

Recent research with rats suggests that sense of direction derived outside an apparatus plays an important role in navigation tasks in the laboratory (e.g., Dudchenko & Davidson, 2002; Dudchenko, Goodridge, Seiterle, & Taube, 1997; Huxter, Thorpe, Martin, & Harley, 2001; Stackman & Herbert, 2002). The most common manipulation of sense of direction in rats is to disorient the animal by rotating it before placing it in the apparatus, thus eliminating any vestibular cues to direction relative to the wider world. For example, Dudchenko et al. compared landmark use on a radial maze in groups of rats that received identical training on

the maze but different experiences outside the enclosure around the maze before and after each trial. One group was transported in a transparent carrier and had full access to visual cues in the room outside the maze, and one group was transported in an opaque carrier and disoriented before being placed on the maze. During acquisition, more rats with access to visual cues reached a learning criterion than did rats in the disoriented group. The rats that reached criterion were then tested with the landmark, a white sheet on one side of the enclosed maze, rotated or removed. On landmark rotation trials, all rats rotated their arm choice to correspond with the new landmark information, indicating that a strong reliance on the landmark had developed even in disoriented subjects. When the landmark was removed, however, the oriented rats were much more successful at locating the correct arm, presumably because they had also learned the position of the correct arm relative to the extramaze environment and could use their position sense to locate it. A similar pattern of results was shown for a water maze task (Martin, Harley, Smith, Hoyles, & Hynes, 1997; but see Gibson, Shettleworth, & McDonald, 2001).

There was additional evidence in Dudchenko et al.'s (1997) study that restricting visual cues alone was sufficient to disrupt learning the goal's location relative to the extramaze environment. Another group of rats was transported in an opaque container like the explicitly disoriented rats but not rotated before being placed on the maze. These rats behaved like the disoriented rats, displaying an inability to fall back on a sense of direction when the landmark was removed. However, in a number of other studies, rats transported in opaque containers but not explicitly disoriented have retained their sense of direction. For example, rats trained to perform delayed alternation on a T maze in a featureless square enclosure still alternate significantly when successive trials are on identical mazes in neighboring rooms, but only if the mazes are in the same orientation in absolute space (Dudchenko & Davidson, 2002). Thus, T maze alternation seems to be based on a sense of direction relative to a larger spatial frame. Similarly, in their study of the effects of vestibular lesions on spatial learning, Stackman and Herbert (2002) kept rats between trials in a cardboard box. Sham-lesioned rats were able to locate the rewarded corner of a square arena in the absence of landmarks in the arena, whereas lesioned rats needed landmarks to do so. In addition, intact rats rotated at a rate below the threshold for vestibular stimulation were

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systematically disoriented in this task by the amount of the rotation (Golob, Stackman, Wong, & Taube, 2001, Experiment 2). The latter finding provides further evidence that orientation within an experimental enclosure is based to some extent on an animal's sense of its direction in global space. With hamsters, too, passive transport in the dark is integrated into the animal's sense of its position (Etienne, Maurer, Saucy, & Teroni, 1986).

Little is known about whether birds also encode the location of a goal in a search task relative to the larger spatial reference frame provided by their knowledge of the extra-apparatus surroundings. There is a large body of work on landmark use by pigeons in laboratory arenas (e.g., Cheng, 1989, 1994; Spetch et al., 1997; Sutton, 2002) and food-storing birds such as Clark's nutcrackers (Gould-Beierle & Kamil, 1999; Kamil & Jones, 2000). However, although varying the point of entry is typical in studies of landmark use with rats (e.g., Huxter et al., 2001; Morris, 1981), in most examples with birds of which we are aware, the animals always entered the experimental space from the same direction. Thus, they need not have used any sense of direction in the wider world to find a goal. Rather, if the goal and landmarks were in a fixed location in the experimental enclosure, the local view of the landmarks from the entrance and/or an egocentric strategy of moving in a certain way from the entrance would suffice. Rats use each of these strategies under some conditions (Arolfo, Nerad, Schenk, & Bures, 1994; Moghaddam & Bures, 1996). Even if a landmark array is moved from trial to trial, as long as it remains in the same orientation, animals can get their bearings within the apparatus from the fixed entrance point (as in Kamil & Jones, 2000). In one notable exception to the use of fixed entrances for birds in a spatial search task (Gibson & Kamil, 2001), Clark's nutcrackers walked through a room in different directions to enter a semienclosed space where they searched for seeds that were buried in a fixed location relative to the room. Despite the availability of global visual cues and cues from self-motion, at first the birds were most influenced by unreliable landmarks close to the goal. Later, however, they did learn to use cues from the room outside the search space.

Because disorientation is necessary for revealing control by environmental geometry in rats (Margules & Gallistel, 1988), disorientation has been used in tests of geometry learning in pigeons (e.g., Kelly & Spetch, 2001; Kelly, Spetch, & Heth, 1998) and chickens (e.g., Tommasi & Polli, 2004; Tommasi & Vallortigara, 2000). However, it is not clear that rotating the birds before training trials and introducing them into the testing enclosure in different places or orientations were actually necessary in these studies. In any case, because much of what we know about landmark use in pigeons and other birds in laboratory tests comes from experiments in which sense of direction is kept constant, it is important to know if such a sense contributes to landmark use at all. Furthermore, if it does, what are the roles of visual, vestibular, or other cues such as feedback from self-motion in establishing a sense of direction?

An experiment by von St. Paul (1982) suggests that access to visual cues may be a crucial component of sense of direction in birds. Greylag goslings were placed in a cart and transported up to 1,500 m away from home, via an indirect route, to a release point. If the goslings were given visual access to the surroundings during the outward journey, they departed in a homeward direction, a direction different from the way they arrived at the release site

(i.e., they were not retracing the outward path). If the surrounding visual cues were blocked on the outward journey, however, the geese oriented randomly when departing and sometimes failed to depart the release point at all. In a further experiment, goslings and adult domestic geese were carried on a two-leg journey. During the first leg, the transport cage was uncovered. It was then covered for the second leg and the geese proceeded on to the release location. The question of interest was whether the geese integrated the uncovered and covered legs of the journey to orient accurately toward home from the release point. Instead of doing so, they oriented toward home as if they had been released at the end of the first leg of the journey, indicating a failure to continue updating an internal representation of their position during the covered leg. It is important to note that the geese and goslings in these experiments were not disoriented through repeated rotation but were merely passively transported to the release sites with or without visual cues along the way. Depriving them of visual cues apparently deprived them of the means to update information about their distance and direction from home. The fact that at the end of the trip they headed in a direction appropriate to the end of the uncovered leg suggests they may have been referring their heading to an external referent such as the sun compass. When visual access to the surrounding environment was unrestricted, the geese may have obtained information about distance and direction along the outward path from visual flow. Optic flow is an important cue to self-movement in honeybees (Srinivasan, Zhang, Altwein, & Tautz, 2000), and neurobiological studies show that bird brains are sensitive to optic flow and integrate signals from the visual and vestibular systems (reviewed by Wallman & Letelier, 1993).

The experiments reported in this article were designed to discover whether landmark use by pigeons is affected, as it is in small mammals, by the animal's internal sense of its location in the environment surrounding a laboratory enclosure. Furthermore, to test whether any such effect exhibited by the pigeons requires visual cues or could be based on vestibular cues alone, access to visual cues outside the arena was manipulated. Two groups of pigeons were trained to find buried food in a constant location within an enclosed arena that contained three fixed, cylindrical, brightly colored landmarks. Pigeons in the transparent carrier group were kept between trials and transported to the entrance in a transparent carrier; for the opaque carrier group, the carrier was opaque. In Experiment 1, search accuracy was measured when novel arena entrance locations were used; the opaque carrier group was also rotated before some tests. In Experiments 2, 3, and 4, the relative weighting of landmark cues and cues based on an internal sense of direction in the larger environment was more directly investigated by rotating the landmarks within the arena and by removing the most informative landmarks.

Experiment 1

Experiment 1 investigated whether visual cues outside an enclosed arena were necessary for accurate landmark-based searching within the arena when pigeons approached the landmarks from a novel direction. Pigeons were moved from a fixed start platform to the various entrances during training and testing by using either a transparent carrier (transparent carrier group) or an opaque carrier (opaque carrier group). Birds in both groups learned to find buried seeds first from a single entrance and then from either of

two entrances on opposite sides of the arena. Once they were performing equally accurately from both of these entrances, they were given unrewarded test trials with the previously unused entrances. Accurate searching from a novel entrance perspective would indicate that the birds had formed an allocentric representation of the goal and landmark relationships that could be accessed and used to navigate effectively from a new starting point. As an additional test of whether directional information acquired outside the apparatus contributed to successful landmark use, pigeons in the opaque carrier underwent another series of familiar and novel entrance tests but were disoriented before each trial. If successful landmark use after entering from a novel location was based on a sense of direction gained from passive motion in the carrier outside the arena, disorientation should reduce search accuracy. The transparent carrier group did not receive disorientation tests because visual cues in the room would have provided a means of reorienting before entering the arena.

Method

Subjects. Eight White King pigeons (*Columba livia*) obtained from Palmetto Pigeon Plant (Sumter, SC) aged 2–8 years served as subjects. The birds had various amounts of experience in operant experiments involving visual discriminations. For the duration of this experiment, a piece of black electrical tape approximately 4 cm long was fixed to the top of each pigeon's head with a small amount of rubber cement to aid the experimenters in discriminating the pigeon's head from the light-colored background of the arena and bedding. Pigeons were housed individually in a colony room on a 14:10-hr light–dark cycle with free access to water and grit, and were maintained at approximately 22 °C and at $85 \pm 2\%$ of their free-feeding body weights throughout the experiment. When the pigeons were not serving in an experiment, they were socially housed in an aviary with food and water available ad libitum.

Apparatus. Figure 1 shows the layout of the arena and the surrounding room. Pigeons were tested in a square white arena (1.5 m \times 1.5 m) with walls that were 40 cm high. A white curtain surrounded the arena from

approximately 20 cm below the top of the walls on the outside to the ceiling. The curtain was fixed to the arena with Velcro. Each wall of the arena contained an identical white guillotine-style door that was 30 cm wide and 33 cm high and was centered on the wall. The doors could be raised and lowered by an experimenter sitting in an adjacent control room. The arena floor was covered in granular cellulose bedding (Bed-o'-Cobs, The Andersons, Maumee, OH), approximately 6 cm deep. One blue, one red, and one white cylindrical landmark (9 cm diameter \times 47 cm high) stood on the floor surrounded by bedding. The top of each landmark was an inverted funnel to prevent the pigeons from perching on it. The blue landmark was in the center of the arena, the red landmark was in the southeast corner, and the white landmark was in the southwest corner. A white bottle lid, 4 cm in diameter, was attached to the floor of the arena halfway between the blue and red landmarks using Velcro. A white curtain covered the ceiling above the arena. A video camera protruded through the curtain and was centered above the arena, and four identical halogen lights were placed symmetrically around it.

The testing room was 3 m \times 2 m. A table served as the start platform and was located on the east wall of the room. A sliding door was located on the south wall of the room. Various cutouts from magazines were pasted on the walls to add features to the room. White noise speakers were centered above the four corners of the arena above and just outside the curtained enclosure. The carriers used in the experimental room were identical except that one was made of transparent Plexiglas and the other was made of opaque black Plexiglas. They measured 37 cm \times 30.5 cm \times 33.7 cm. Both carriers had a false back wall that could be raised by the experimenter to reveal a small dish with food when necessary. This area measured 6.4 cm \times 30.5 cm \times 33.7 cm, and the area where the pigeon stayed measured 30.5 cm \times 30.5 cm \times 33.7 cm. In the transparent box, white opaque tape covered about two thirds of the false back wall to prevent the pigeon in the carrier from seeing the food behind the wall before it was raised. Each carrier had a handle mounted on top in the center. Eight pieces of corn were used as a reward in the arena, and the carrier was baited with about 1 g of mixed grain.

The experimenter sat in an adjacent control room and watched the pigeon in the arena on a TV monitor connected to the camera centered over the arena and videotaped each trial. The experimenter also controlled the doors to the arena and carrier from the control room.

Procedure. The 8 pigeons were divided into two groups of 4 pigeons each. Birds in both groups were transported from the colony room to the testing room in a small opaque transport container and then placed in one of two carriers in the experimental room, which also functioned as start boxes for trials in the arena. Pigeons in one group were always placed in a transparent carrier at the beginning and for the duration of each session, and pigeons in the other group were always in an opaque carrier. All other aspects of the procedure were identical, except where noted next.

Pigeons first underwent a series of pretraining sessions. Throughout pretraining, each pigeon was placed in the carrier at the start platform and then transported by the experimenter to either the east or the west door at the start of the session and was not moved away from the door until the session was over. Two birds in each group were assigned to the east door and 2 birds were assigned to the west door for the pretraining phase. In this and all subsequent experiments, the experimenter transported the bird in the carrier by holding the carrier in front of her body with the baited reward chamber toward her and the pigeon compartment away from her. After the carrier was placed at the appropriate door, the experimenter left the room. With the carrier placed on the floor outside one of the doors to the arena, pigeons were first allowed to eat from the small food dish at the back of the chamber when the experimenter raised the back wall. When the pigeons were eating readily, they were trained to shuttle back and forth from the carrier to the arena. Once a pigeon was reliably entering the arena and returning when the experimenter raised the wall in the carrier to reveal the food there, the door to the arena was closed when the pigeon entered the arena. The goal food dish containing the corn reward was totally exposed

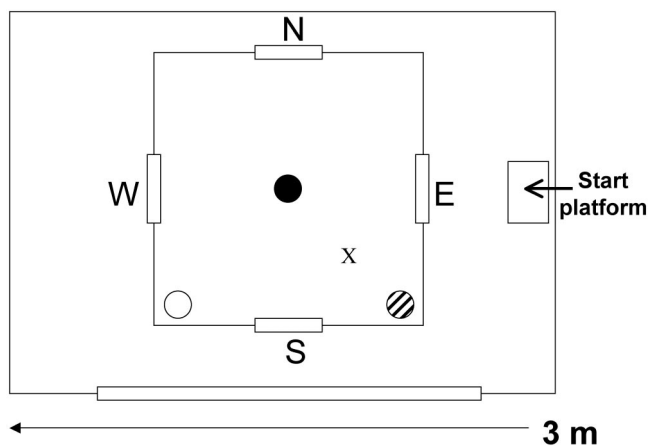


Figure 1. An overhead view of the arena and testing room. Arena entrances are marked with compass directions (N = north; S = south; W = west; E = east). For this and all other figures, X indicates the location of the buried goal, and the circles show the positions of the landmarks (solid black = blue landmark; white = white landmark; striped = red landmark). The experimenter entered and exited through a sliding door on the south wall.

at first, but the food and dish were progressively covered with more bedding over four trials each day. After 1 day when the pigeon found and ate totally buried food on all four trials, the next day consisted of four totally buried trials and the pigeon was transported back and forth between trials from the start platform to the same arena door used throughout pretraining.

The training phase followed the last pretraining day. Eight trials per day were carried out in this phase. In this and all subsequent phases, all trials were videotaped. Four trials per day were conducted with the pigeon entering the arena from the east door, and four trials were conducted using the west door. The order of doors was randomized over the eight trials. On each trial, the experimenter transported the pigeon in the carrier from the start platform to the appropriate door, exited the testing room, controlled the opening and closing of apparatus doors from the control room, and then transported the pigeon back to the start platform to set up for the next trial. The intertrial interval lasted approximately 4 min. For travel to the far west door, either a north or a south route around the arena was taken, with each route used an equal number of times in a session and in random order. From the control room, the experimenter recorded the number of searches, defined as sweeps of bedding by the pigeon's beak, until the pigeon began eating the food. After 4 consecutive days in which the number of searches after entering from the east door was not statistically different from the number of searches after entering the west door (as calculated using a paired *t* test), one unbaited probe trial per day was introduced. The probe trial always occurred in the last half of the session in a randomly determined trial. Probes from east and west occurred equally often in each successive block of four sessions. The food dish and corn were removed from the arena for the probe trial, and the pigeon was allowed to sweep 25 times, at which point the arena door was opened and the bird was returned to the carrier. Sessions with probe trials continued until the number of searches to find the food on nonprobe trials from east and west entrances did not differ significantly for 4 consecutive days.

Immediately following the training phase, a novel entrance test phase was conducted. Eight sessions of eight trials each were conducted in this phase. As in the previous phase, one trial per day was an unbaited probe trial during which the pigeon was given 25 searches. Over the eight sessions, two probe trials were conducted from each of the familiar east and west (one north route and one south route) entrances, and two probe trials were conducted from each of the novel north and south entrances. Travel to the north and south entrances was always the most direct route from the start platform to the door, resulting in routes that differed in travel direction but were equal in travel duration. The order of the entrances was randomized for each pigeon with the restriction that a pigeon never entered the novel entrances on consecutive days.

Following completion of the eight sessions, pigeons in the opaque carrier group received a retraining phase consisting of five sessions identical to those in the training phase, including unbaited probes. After the retraining sessions, the opaque carrier group was given a series of disorientation tests. Just as in the previous novel entrance test phase, one trial per session was a probe trial, and two probes were conducted from each entrance. When a pigeon in the carrier was removed from the start platform before the probe trial, it was carried to a random, predetermined corner of the testing room where the carrier was placed on a turntable and rotated for 1 min at 10 rpm. The pigeon was then transported to the appropriate arena entrance via the shortest route. The general behavior of pigeons that had been rotated was the same as oriented pigeons on other trials, and at no time did any pigeon appear disoriented or off balance. Each corner of the testing room was used for disorientation twice, and the disorientation location was different for each probe trial at a given entrance.

Probe test scoring. At the conclusion of testing, probe test trials were converted from analog videotape to digital files at 30 frames per second. The digital files were scored using software developed in Visual Basic by J. E. Sutton. As the digital file played, the experimenter used a mouse to click on the location of the black stripe on pigeon's head as the bird's beak

contacted the bedding during each search. A search was defined as a sweep of the bird's head that displaced bedding from the floor of the arena. The first 20 searches were scored, except where noted later. When necessary, the experimenter played the file forward and backward frame by frame to pinpoint the location of contact with the bedding. The software converted the location of each mouse click to an *x*-, *y*-coordinate in a 20 × 20 grid based on the area of the arena floor, and the coordinate was used to calculate the search error and search location measures (described next). Each square of the grid corresponded to approximately 7.5 cm² of area on the floor.

Dependent measures of search accuracy. Except where noted next, two dependent measures of accuracy were calculated for statistical tests using the search coordinates on probe test trials, search error and search location. Search error was the distance (in centimeters) of each search's coordinate from the goal coordinate and was calculated using the Pythagorean theorem. To quantify the locations of searches, a 30 cm × 30 cm area of the arena floor with the buried seed goal at its center was identified as the goal zone. A corresponding zone was identified in each of the other three quadrants of the arena, such that each zone was positioned the same distance and direction from the center landmark as the goal zone in the southeast quadrant. Search location was based on the proportion of searches falling in each of these four zones and permitted tests of whether there were more searches near the goal than in comparable areas in the other quadrants of the arena. Throughout this report, alpha was set at .05 for statistical tests.

Results and Discussion

Pretraining. Birds in the two groups spent a similar number of days in the pretraining phase. Birds in the transparent carrier group completed the phase in a mean of 12.50 days (*SD* = 4.80), and birds in the opaque carrier group completed the phase in a mean of 11.75 days (*SD* = 7.67). An independent samples *t* test showed that the groups did not differ statistically in number of days to complete the pretraining phase, *t*(6) = 0.87, *p* > .05.

Training: First session. After entering the arena from a single entrance during the pretraining phase, birds in both groups encountered a different entrance to the arena for the first time on the first day of the training phase. Pigeons in the transparent carrier group seemed to have little trouble finding the goal from this new entrance perspective, but pigeons in the opaque carrier group tended to search initially at a location that was the same direction and distance from the new entry point as the goal had been from the opposite door in the pretraining phase. To analyze this difference, the first trial from the new entrance (either east or west, whichever was not used in pretraining) on the first day of training was scored by recording the position of each pigeon's first 10 searches. Because food was present in the goal location on these training trials and many birds had found the food after 10–15 searches, only the first 10 searches were scored.

The mean search location for each pigeon was calculated by averaging the *x*- and *y*- coordinates of the 10 searches. Figure 2 shows the mean search location for each bird in the opaque carrier and transparent carrier groups on the first trip through a novel door. Using the Pythagorean theorem, the distance from each search to both the actual goal and the "virtual" goal was calculated, and the means for each group are displayed in the lower portion of Figure 2. The virtual goal was defined as the place birds should search if they had encoded the goal relative to their position at the start of a trial in pretraining (i.e., egocentrically) instead of relative to the landmarks. For instance, pigeons that were pretrained using

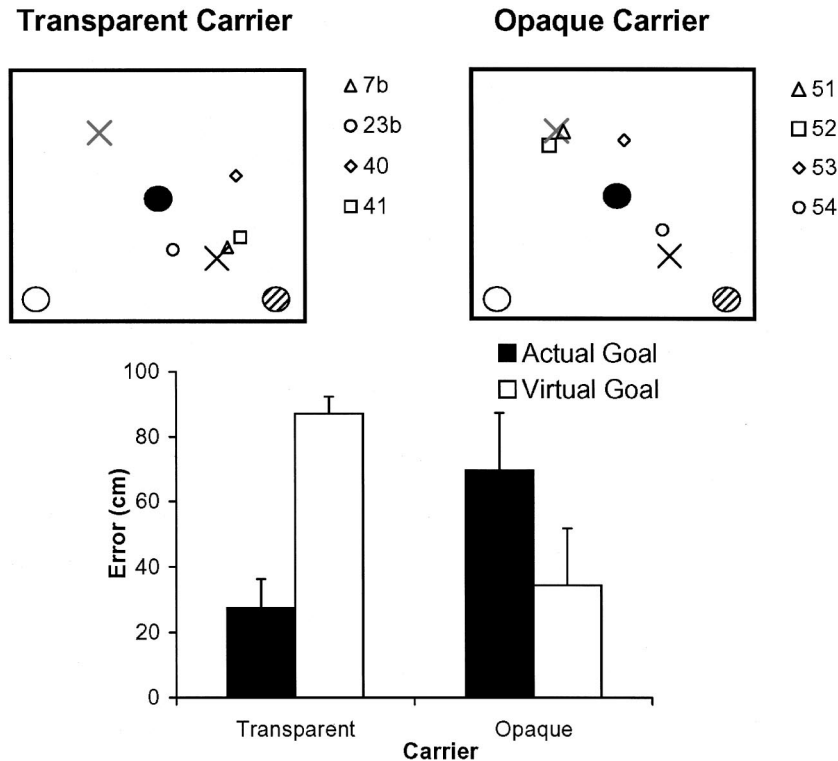


Figure 2. Mean search location for each bird on the 1st day of the training phase when entering from a novel direction and mean error distance of searches on Day 1 of training from the actual goal and the virtual goal (see text). Error bars indicate standard error of the mean.

the west entrance might encode the rule “walk 120 cm, turn slightly right, and search there.” A mixed two-factor analysis of variance (ANOVA) with carrier (2) and goal location (2) as factors revealed no significant main effects of carrier, $F(1, 6) = 3.89, p > .05$, or goal location, $F(1, 6) = 0.42, p > .05$, but there was a significant Carrier \times Goal Location interaction, $F(1, 6) = 6.40, p < .05$. Post hoc analyses using the Tukey’s honestly significant difference (HSD) test were carried out to investigate the source of the interaction. Comparisons of the carrier groups at each goal location revealed that the opaque carrier group searched significantly closer to the virtual goal than did the transparent carrier group ($p < .05$). Comparisons across goal location with group held constant were not significantly different.

Because the treatment of the transparent carrier and opaque carrier groups differed only in access to visual cues in the room outside the arena, it can be concluded that these cues strongly affected the pigeons’ initial search strategies inside the arena. In the absence of visual access to the surrounding room, the opaque carrier group initially learned to find the buried goal using an egocentric coding strategy that probably involved making a response based on movement in a certain direction and distance when the door opened at the beginning of a trial. In contrast, birds with full visual access to the room used a more allocentric strategy by encoding the goal using the landmarks. It is important to note that although the opaque carrier group’s initial searches were most often incorrect, all of the pigeons eventually found the buried food on every trial.

Training to criterion. In spite of differing in accuracy when they first entered the arena from a second entrance, the two groups of pigeons met the criterion of equal accuracy from the east and west entrances similarly quickly. Birds in the transparent carrier group completed the training phase in a mean of 9.75 days ($SD = 2.36$), and birds in the opaque carrier group completed training in a mean of 10 days ($SD = 1.63$). An independent samples t test showed that the two groups did not differ significantly in days to complete the training phase, $t(6) = 0.17, p > .05$.

Novel entrance tests: Search error. Both the transparent carrier group and the opaque carrier group searched accurately whether entering from a familiar entrance or a novel one in the test phase. Figure 3 shows the average error distance of searches by pigeons in the transparent carrier and opaque carrier groups at familiar and novel entrances. A mixed two-factor ANOVA with carrier (2) and entrance type (2) as factors revealed no significant main effect of carrier, $F(1, 6) = 1.10, p > .05$, and no entrance main effect or Carrier \times Entrance interaction ($F_s < 1$).

Novel entrance tests: Search location. Table 1 shows the proportion of total searches on probe trials that fell in each zone. If the birds were focusing their searches on the goal area, the proportion of searches in the southeast zone should be significantly higher than in other quadrants. A mixed ANOVA was carried out on the proportion data with carrier (2), entrance type (2), and zone (4) as factors. There was a significant main effect of zone, $F(3, 18) = 116.49, p < .05$, but no other main effects or interactions were significant (all $F_s < 1$). To investigate the main effect of

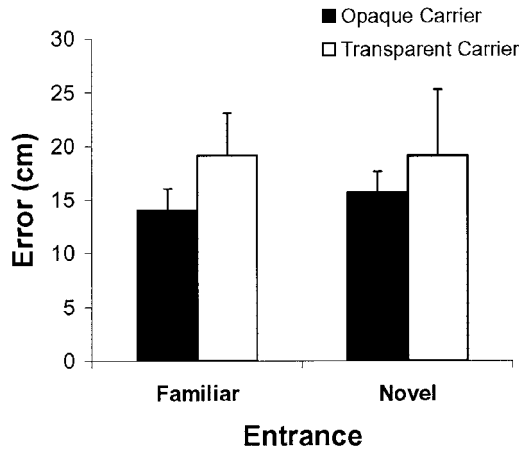


Figure 3. Mean error distance of searches for both groups of pigeons from familiar (east and west) and novel (north and south) entrances in Experiment 1. Error bars indicate standard error of the mean.

zone, post hoc Tukey pairwise comparisons were conducted on the proportion of searches in each zone and confirmed that significantly more searches occurred in the southeast zone than in any other zone in the arena ($ps < .01$). No other comparisons were significantly different. It should be noted that the zone measure did not capture every search, but it accounted for most searches by both the transparent carrier group (familiar entrances = 82%; novel entrances = 84%) and the opaque carrier group (familiar entrances = 88%; novel entrances = 87%).

The opaque carrier group’s accuracy indicates that visual access to the arena surroundings only affected navigation within the arena at first. Experience entering from two opposite directions or being moved around the room in consistent ways resulted in a new, more allocentric landmark-based coding strategy. This new strategy allowed the pigeons in the opaque carrier group to search accurately from novel entrance directions in the test phase, unlike on the initial training day.

It might be suggested that the pigeons in both groups learned to use some correlate of the distance they were carried from the holding platform to the east versus west starting locations as a conditional cue indicating where to move once in the arena. Such a conditional rule might be “long travel means head to the right, short travel means head to the left.” However, this cannot be all that the pigeons had learned because this account does not explain how the novel (and equal) travel times or distances to the north and south entrances could by themselves have cued the birds on how to move once in the arena. For the transparent carrier group, a sense of position in the extra-arena world could also have been based on the specific visual cues outside the familiar east and west entrances, but, again, it is unclear how the pigeons could use these cues alone to tell them where to go when placed at novel entrances. Successful performance from the novel north and south entrances must therefore have been based on either the pigeons’ sense of their location relative to the arena and the goal while being moved around outside the arena or a representation of the location of the goal gradually built from experience viewing the landmarks from different perspectives with no reference to position in the larger environment.

Disorientation tests (opaque carrier group only). Although the novel entrance tests showed that visual cues outside the arena were not necessary for successful navigation from the novel entrances, the role of an internal sense of direction remains unclear. One way to test the role of an internal sense of direction for the opaque carrier group is to explicitly disorient the pigeons before they enter the arena. If the birds had developed an internal sense of direction and were relying on it to determine where to search once in the arena, their search accuracy should be reduced by rotation prior to being placed by an entrance.

Search error. Figure 4 shows the mean error distance of searches for pigeons in the opaque carrier group after rotation at familiar and novel entrances, along with the same birds’ performance on probe tests in the previous novel entrance phase of testing (when they were not rotated before entering the arena). A repeated-measures ANOVA with entrance type (2) and rotation condition (2) as factors showed no main effect of rotation, $F(1,$

Table 1
Proportion of Searches Falling in Zones on Unbaited Probe Trials in Experiment 1

Group	Zone								Total in zones
	NW		NE		SE		SW		
	M	SD	M	SD	M	SD	M	SD	
Transparent carrier									
Familiar	.00	.000	.04	.06	.73	.22	.05	.07	.82
Novel	.02	.04	.06	.12	.73	.33	.03	.03	.84
Opaque carrier									
No rotation									
Familiar	.00	0	.01	.02	.87	.10	.00	0	.88
Novel	.00	0	.02	.03	.80	.17	.05	.05	.87
Rotation test									
Familiar	.00	.00	.00	.00	.74	.11	.11	.13	.85
Novel	.05	.09	.01	.02	.68	.14	.11	.11	.85

Note. Goal was located in southeast zone on baseline training trials. NW = northwest; NE = northeast; SE = southeast; SW = southwest.

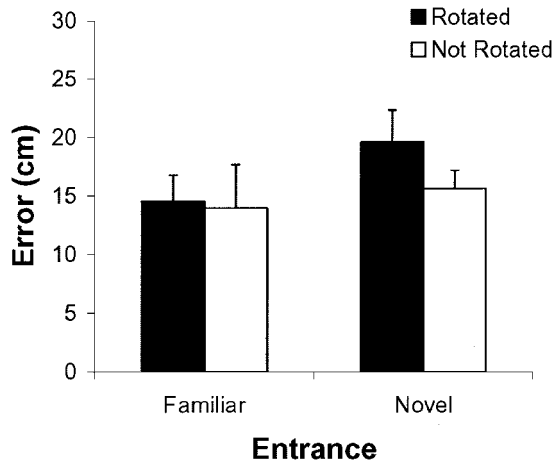


Figure 4. Mean error distance of searches for opaque carrier pigeons on trials with and without rotation shown for familiar (east and west) and novel (north and south) entrances in Experiment 1. Error bars indicate standard error of the mean.

3) = 1.05, $p > .05$, no main effect of entrance type, $F(1, 3) = 1.66$, $p > .05$, and no Entrance \times Rotation interaction, $F(1, 3) = 1.33$, $p > .05$.

Search locations. The proportion of total searches in each zone of the arena on rotation probe trials from both types of entrance is displayed in Table 1. The zone data were analyzed in a repeated-measures ANOVA with rotation condition (2), entrance type (2), and zone (4) as factors. There was a significant main effect of zone, $F(3, 9) = 263.43$, $p < .05$, and a significant Rotation \times Zone interaction, $F(3, 9) = 4.75$, $p < .05$. All other main effects and interactions were not significant ($F_s < 1$). A series of post hoc Tukey's HSD tests was conducted to investigate the source of the Rotation \times Zone interaction. First, pairwise comparisons of the proportions of searches across zones were compared for each rotation condition and showed that more searches were directed to the southeast goal zone than any other zone under both rotation conditions (all $p_s < .01$). Next, tests were conducted to determine whether rotation condition affected the proportion of searches in individual zones. Pigeons directed a significantly higher proportion of searches to the southeast goal zone when they were not rotated ($M = .84$, $SD = .06$) compared with when they were rotated ($M = .71$, $SD = .10$), but no other zones showed an effect of rotation. Finally, it should be noted that the zone measure captured a similar proportion of searches under rotated conditions (85%) and nonrotated conditions (87%).

Explicit rotation before entering the arena had a subtle effect on search accuracy relative to nonrotated trials. While the overall distance of errors was the same, and more searches were directed to the southeast goal zone than any other zone, rotation seems to have resulted in less focus in the immediate vicinity of the goal. Still, the effect of rotation was slight, and cues from the landmarks were sufficient to allow disoriented pigeons to search fairly accurately. These results are consistent with reports that, under some circumstances, disoriented rats are able to use landmarks (Dudchenko et al., 1997; Huxter et al., 2001), but they also indicate that birds use information based on their internal sense of direction or position in the extra-arena environment to locate the goal.

Experiment 2

Experiment 2 was designed to investigate the relative importance of an internal sense of direction and landmark piloting with tests that could be conducted with both groups of pigeons. On probe tests from the relatively novel north and south doors, the landmarks were rotated 180° in the arena, putting information about the goal's location from the landmarks and from the larger extra-arena environment in conflict. Thus, for example, a bird might enter the arena from the north but see the landmarks arranged as if viewed from the south. The question of interest was whether pigeons would shift their searches to maintain the same relation to the rotated landmarks (search in the landmark-based *rotationally correct* location) or would search relative to the stable extra-arena environment (the *globally correct* location), and whether access to visual cues outside the arena would affect these responses. For instance, if transparent carrier pigeons rely more heavily on extra-arena cues in the task, we might expect them to search at the globally correct location more than the opaque carrier group.

Method

Subjects. The 8 pigeons from Experiment 1 served in this experiment and were housed and maintained in an identical manner.

Apparatus. The arena, landmarks, carriers, and all other aspects of the apparatus were identical to those in Experiment 1.

Procedure. Immediately following the completion of Experiment 1, all pigeons were given 5 retraining days, with sessions that were identical to the training phase session of Experiment 1. On the 6th day, landmark rotation testing began. This testing phase proceeded as had the novel entrance testing phase of Experiment 1, with two probe trials from each door over 8 days. On the north and south probe trials, however, the red and white landmarks were rotated 180° in the arena. The blue landmark remained in the center.

Results and Discussion

Search error. Figure 5 shows the mean error distance of searches on probe trials with the landmarks rotated for the transparent carrier and opaque carrier groups when measured from the globally correct location and the landmark-based rotationally correct location. A mixed ANOVA with carrier (2) and goal position (2) as factors revealed a significant main effect of carrier, $F(1, 6) = 28.48$, $p < .05$, and a significant main effect of goal position, $F(1, 6) = 8.31$, $p < .05$. There was no Carrier \times Goal Position interaction, $F(1, 6) = 1.65$, $p > .05$. Overall, pigeons in both carrier groups searched significantly closer to the rotationally correct goal location indicated by the landmarks ($M = 36.71$, $SD = 16.89$) than to the globally correct location ($M = 68.37$, $SD = 15.85$). Thus, both groups of pigeons relied more heavily on cues from the landmarks when searching than on a sense of the goal's location with respect to the larger environment. In addition, the transparent carrier group showed significantly more error overall ($M = 54.49$, $SD = 1.23$) than did the opaque carrier group ($M = 50.70$, $SD = 0.61$). This difference may indicate that the transparent carrier birds were generally more disrupted by the landmark rotation than the opaque carrier birds, but we believe this effect should be interpreted with caution given the small absolute difference between the means (less than 4 cm).

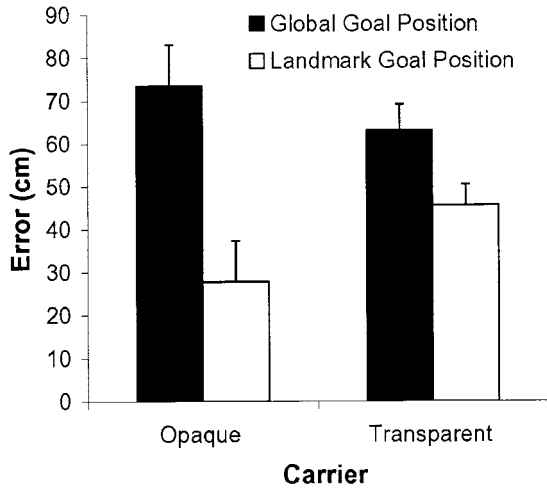


Figure 5. Mean error distance from the landmark-indicated rotationally correct goal position and from the goal position indicated by global cues for both carrier groups in Experiment 2. Error bars indicate standard error of the mean.

Search locations. Table 2 shows the proportion of searches in each zone on trials with the landmarks rotated. To address whether the pigeons directed more searches to the rotationally correct zone (northwest) or to the globally correct zone (southeast), the proportion of searches in all four zones was tested in a Carrier (2) × Zone (4) mixed ANOVA. There was a main effect of zone, $F(3, 18) = 22.94, p < .05$, and a main effect of carrier, $F(1, 6) = 27.57, p < .05$. The Zone × Carrier interaction only approached significance, $F(3, 18) = 2.68, p = .07$. The main effect of carrier indicates that the average proportion of searches accounted for by zones was higher for the opaque group ($M = .24, SD = .01$) than for the transparent group ($M = .20, SD = .01$). This is a reflection of the percentage of total searches accounted for by the zone measure, which was higher for the opaque group (95%) than for the transparent group (79%). Post hoc Tukey pairwise comparisons were conducted on proportions of searches in the four zones to investigate the main effect of zone. The northwest, rotationally correct, zone had a higher proportion of searches than any other zone (all $ps < .01$), and no other zones were significantly different.

Both the search error distance and search location data indicate a strong influence of landmark cues on searching by both groups of pigeons. If visual cues outside the arena had afforded the transparent carrier group an enhanced internal sense of direction with which to encode the goal relative to the global environment, it might be expected that those pigeons would search significantly more at the globally correct location than the opaque carrier group. Despite the suggestion of interaction in Figure 5, our statistical results showed no clear effect of access to visual cues outside the arena on searching. It should be noted that both groups of birds did direct some proportion of total searches to the globally correct southeast zone (see Table 2), indicating that while the landmarks guided the majority of searches, they had indeed encoded the goal with respect to the global environment.

It appears that even with a strong internal sense of direction based on visual cues outside an arena, proximal landmarks inside an arena exerted stronger control over searching than more global cues based on an internal sense of direction. This is consistent with reports from experiments in which birds had full visual access to the extra-arena environment at all times. For example, Spetch and Edwards (1988) found stronger control by local cues than global room cues when the two were put in conflict, and Gould-Beierle and Kamil (1999) found that Clark’s nutcrackers used a proximal landmark as a guide when the landmark was shifted within an experimental room.

Experiment 3

Based on the results of Experiments 1 and 2, it might be concluded that cues outside the arena contribute very little to finding a goal when landmarks are available. However, when the landmarks were rotated, there was still some responding to the globally correct location. In Experiment 3, pigeons were tested with the most informative landmarks (red and white) removed to directly investigate the degree to which the goal’s location had been encoded relative to the more global reference frame. If the pigeons continued to search accurately without landmark cues, then the birds must have been using an internal sense of their global direction or position.

Method

Subjects. Four pigeons in the opaque carrier group and 3 pigeons in the transparent carrier group from previous experiments served in this exper-

Table 2
Proportion of Probe Trial Searches in Each Zone With Landmarks Rotated 180° in Experiment 2

Group	Zone								Total in zones
	NW ^a		NE		SE ^b		SW		
	M	SD	M	SD	M	SD	M	SD	
Transparent carrier	.46	.08	.09	.11	.21	.10	.03	.05	.79
Opaque carrier	.78	.24	.02	.02	.15	.23	.00	.00	.95

Note. NW = northwest; NE = northeast; SE = southeast; SW = southwest.

^a The location of the goal zone with respect to the rotated landmarks. ^b The location of the goal zone on baseline training trials and with respect to the global environment.

iment. The 4th bird in the transparent carrier group was dropped because of failure to enter and exit the apparatus and search for the food. The pigeons were housed and maintained in an identical manner to the previous experiments.

Apparatus. The apparatus was the same as in previous experiments.

Procedure. Immediately following the completion of Experiment 2, the pigeons were given 5 retraining days. On the 6th day, landmark removal testing began. The eight landmark removal test sessions were identical to sessions in the landmark rotation phase of Experiment 2, except that on the north and south entrance probe trials, the red and white landmarks were removed from the arena. The blue landmark was left in place because it was centered in the arena and provided no directional information.

Results and Discussion

Search error. The opaque carrier group’s searches on probe trials with landmarks removed were an average of 30.27 cm (*SD* = 7.42) away from the goal, and the transparent carrier group’s searches were an average of 27.07 cm (*SD* = 17.39) away from the goal. An independent samples *t* test showed no significant difference in the amount of error distance between the groups, *t*(5) = 0.34, *p* > .05.

Search location. Table 3 displays the proportion of searches on landmark-removal probe tests falling in each zone for each group. A mixed ANOVA with carrier (2) and zone (4) as factors was carried out on the proportion of searches in each zone on probe tests. There was a significant main effect of carrier, *F*(1, 5) = 30.27, *p* < .05, and a significant main effect of zone, *F*(3, 15) = 12.64, *p* < .05, but no Carrier × Zone interaction (*F* < 1). The effect of carrier indicates that the average proportion of searches accounted for in a zone was higher for the transparent carrier group (*M* = .22, *SD* = .01) than for the opaque carrier group (*M* = .17, *SD* = .02). As in Experiment 2, this reflects a difference between the percentage of total searches accounted for by the zones for the groups (transparent group = 88%; opaque group = 66%). Post hoc Tukey pairwise tests were conducted on the proportions of searches in the four zones to investigate the main effect of zone. The southeast goal zone had significantly more searches than all other zones (all *ps* < .01), and no other pairs of zones were significantly different.

With no informative landmarks present, pigeons in both groups searched in the goal location based on their internal sense of

direction in the larger environment (though they were not perfect). It seems that while landmark cues in Experiment 2 controlled searches when they conflicted with information acquired outside the arena, the birds indeed encoded the location of the goal with respect to the larger environment and used that information when landmarks were unavailable. The slightly less diffuse search by the transparent carrier group in the landmark removal test suggests that orientation based on a combination of visual cues and vestibular (or other) cues from passive movement is more accurate than orientation without visual cues. In contrast, when the landmarks were present but rotated, searching by the opaque carrier group was less diffuse than that of the transparent carrier group. This is consistent with the possibility that in the absence of the visual component of the global positional cues, the opaque carrier birds relied more on the landmarks than did the transparent carrier birds.

Experiment 4

In Experiment 3, the pigeons searched fairly accurately in the absence of landmark information and we concluded that they relied on an internal sense of direction, but internal sense of direction was not explicitly manipulated. In Experiment 4, the opaque group birds were retrained and then given tests with the landmarks removed (as in Experiment 3) under disoriented conditions. If the pigeons had been relying on their sense of direction to search in Experiment 3, and the rotation procedure was truly disorienting, searches under these conditions should be randomly distributed around the arena. Furthermore, these tests could address whether something besides an internal sense of direction, perhaps uncontrolled, unintended cues in the arena or surrounding space, was guiding the birds’ searches. In that case, we should see little effect of adding disorientation to the no-landmarks test condition. It should be noted that by this point, the pigeons were highly experienced at this task, perhaps making it more likely that sensitivity to alternative cues undetectable to experimenters had developed. To avoid giving a large number of unrewarded tests, and because substantial data had been collected in previous experiments, we focused on tests conducted under disoriented conditions with the landmarks removed in this experiment.

Table 3
Proportion of Probe Trial Searches in Each Zone With Landmarks Removed in Experiments 3 and 4

Group	Zone								Total in zones
	NW		NE		SE		SW		
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	
Transparent carrier									
Experiment 3	.01	.01	.15	.24	.62	.25	.10	.14	.88
Opaque Carrier									
Experiment 3	.01	.01	.11	.12	.44	.16	.10	.11	.66
Experiment 4	.09	.08	.14	.16	.34	.19	.09	.08	.66

Note. Goal was located in southeast zone on baseline training trials. NW = northwest; NE = northeast; SE = southeast; SW = southwest.

Method

Subjects. The 4 pigeons in the opaque carrier group served in this experiment. The pigeons were housed and maintained in an identical manner to the previous experiments.

Apparatus. The apparatus was the same as in previous experiments.

Procedure. A few weeks after the completion of Experiment 3, the pigeons were given 5 retraining days and were performing at the same baseline level of accuracy as in previous experiments. On the 6th day, landmark removal testing began. The eight landmark removal test sessions were identical to the test sessions in Experiment 3, except that the birds were rotated 10 times on a turntable after being removed from the start platform and before being placed at the entrance to the arena on the test trials. As in the disorientation tests of Experiment 1, the turntable was in a randomly determined corner of the room each day, and a different corner was used for each entrance.

Results and Discussion

Search error. The average distance of searches to the goal on probe tests was 40.65 cm ($SD = 14.41$), a greater distance than in previous experiments (with the exception of landmark rotation tests in Experiment 2).

Search location. The proportion of searches directed to each zone of the arena on probe trials is displayed in Table 3. A repeated-measures ANOVA with zone (4) as the repeated factor revealed no significant effect of zone, $F(3, 9) = 2.51, p > .05$. Inspection of Table 3 shows that the pigeons did direct about 34% of their searches to the correct zone, but enough searches were also distributed around the arena to preclude a significant effect of zone. The scattered pattern of searches is further demonstrated by comparing the results of Experiment 3 and Experiment 4 in the bottom panel of Table 3. It is evident that rotation produced more focused searches in the incorrect northeast and northwest quadrants than in nonrotated trials.

While not producing a completely random distribution of searches (e.g., equal proportions of searches in each zone), disorientation affected the pigeons' ability to focus on the appropriate area of the arena and produced the first nonsignificant effect of zone in the series of experiments. It is possible that in addition, the birds had gradually learned to use some environmental cues not perceived by the experimenters to avoid the west side of the arena.

General Discussion

Literature reviewed in the introduction shows that rats and other small mammals can orient using vestibular information acquired during passive transport in the light or in the dark. In addition, when they are systematically disoriented during training or have vestibular lesions they will rely on available landmarks. When vestibular information conflicts with information from landmarks, rats and hamsters may use both kinds of information in a hierarchical manner (e.g., Maaswinkel & Whishaw, 1999; see also Etienne & Jeffery, 2004). Such findings support suggestions that a sense of direction acquired through self-motion cues plays an important role in spatial learning. However, although landmark use has been studied extensively in pigeons, Clark's nutcrackers, and other avian species, the existing literature is almost silent on the role of a sense of direction in landmark use by birds. One much-cited exception indicates that visual flow, rather than vestibular

stimulation, may be the primary source of distance and direction information for birds during passive transport.

In the four experiments reported in this article, we investigated the effect of information acquired during passive transport in the light and in the dark on pigeons' landmark use. Experiment 1 demonstrated that pigeons denied visual access to the surroundings of an enclosed arena could encode the landmarks and goal allocentrically after experience from multiple entrance points. Furthermore, a reliable sense of direction seemed to play a minor role for accurately locating the goal within the arena with landmarks present. Experiments 2, 3, and 4 investigated the relative importance of landmark information and global reference frame information derived from a sense of direction. Pigeons used landmarks when they were present—even when those landmarks led them to a new location—but were able to fall back on knowledge of the goal's location with respect to the larger environment when the landmarks were absent.

On the basis of the evidence from geese mentioned previously, it was hypothesized that visual cues in the area surrounding the arena would facilitate the formation of a sense of direction that would continue to inform the birds' searching once they were in the arena. In fact, visual cues outside the arena made the most difference early in training, when the birds were taken to a new entrance for the first time. The first trial from a new perspective revealed that pigeons without visual access to the arena surroundings had developed a response strategy, whereas pigeons with visual access searched using a place strategy. This finding is in line with results from the path integration experiments with geese (von St. Paul, 1982), where one outward trip with visual cues blocked resulted in random, instead of homeward, orientation. The pigeons in the opaque carrier group were eventually able to approach the landmarks from novel directions and search accurately, and perhaps if the geese had repeated the same outward journey in the cart a number of times they would have oriented homeward even without visual cues in transit.

The group differences early in training point to the dominance of visual information for the initial establishment of a sense of direction in birds. It is known that birds are sensitive to optic flow, and that signals from the visual and vestibular systems are integrated (reviewed by Wallman & Letelier, 1993). Our data suggest that visual input is most important for navigation in novel situations, and that vestibular cues are just as effective after experience without visual information. It is worth noting that the motion experience by both groups was a result of being passively moved by the experimenter. If the pigeons had produced the motion themselves by walking to the various entrances, for instance, the initial search decrements seen in the opaque carrier group might not have occurred. That is, input from self-motion may be more salient than input from passive motion and allow birds to update their position more rapidly in the absence of visual cues. Future tests might include a direct comparison of passive and active motion in birds, although the latter is probably only practical in lighted surroundings when birds have access to visual cues.

Throughout this article, we have referred to the information from inertial and available visual cues during passive transport as providing an internal sense of position or sense of direction. In insects and mammals, path integration on the basis of self-motion cues provides both direction and distance information. For instance, if a desert ant is displaced to a test field before its home-

ward journey, it runs straight in the direction that should lead to the nest and for approximately the right distance before breaking into a spiraling path around the area where the nest entrance would have been had the ant not been displaced (Muller & Wehner, 1988). The ant thus reveals knowledge of both the direction and the distance to the nest, that is, the position of the nest relative to its own position. However, in relatively small symmetrical spaces in the laboratory, sense of direction is usually all that is tested. For example, in the study by Golob et al. (2001) mentioned in the introduction, the rats needed only directional cues to find the correct corner of a square box. In the present experiments, cues obtained during passive transport clearly provided the pigeons with information that they used to direct their search once in the arena. The finding that rotating the birds before they entered the arena degraded accuracy shows that they were normally using a sense of which way they were heading when they entered the arena (i.e., a sense of direction) to locate the goal. It is unclear from the present results whether they also had a sense of their position and that of the goal within the wider world.

Both visually perceived landmarks and a sense of direction were used by pigeons in the search task reported here. When the two types of information conflicted, pigeons under both visual conditions primarily followed the landmarks. Also, when only cues from passive movement were available, pigeons still searched reasonably accurately. When only the landmark cues were available because sense of direction was disrupted through rotation, searching was still fairly accurate. Further research will be required to determine precisely the relative weighting of landmark and internal direction cues in birds, but the search pattern on conflict trials in the current experiments suggests a stronger tendency to rely on landmark cues in an uncertain situation, especially in animals deprived of static or dynamic visual cues to their global position. In addition, it will be important to carry out experiments in birds' natural environments to investigate the role of the sun compass or other polarizing cues in inertial navigation because pigeons do seem to utilize such cues when available (Bingman & Jones, 1994).

Whether, as proposed by some researchers (e.g., Gallistel & Cramer, 1996; Knierim et al., 1995), information from inertial navigation forms a framework onto which landmark information is later added is not entirely clear from the current data set. What is clear, however, is that both systems are in operation once successful navigation is evidenced, and each process is available to the birds in isolation. Considerable research reviewed in the introduction to this article has shown that self-motion cues play an important role in spatial learning by small mammals in the laboratory. The present findings show that they also play a role in short-distance navigation in one species of bird.

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