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Animals can use a number of cues to remember a vital location, such as a food source or a nest. As important as encoding these cues is the ability to select which cues a navigator ought to rely on more and which less. For example, landmarks are key visual cues that can guide a navigator when it has lost perceptual contact with its goal. It makes intuitive sense, and it has been confirmed by studies (Bennett, 1993; Chamizo, Manteiga, Rodrigo, & Mackintosh, 2006; Cheng, Collett, Pickhard, & Wehner, 1987; Gould-Beierle, & Kamil, 1999; Spetch, 1995), that landmarks closer to a goal are relied on more heavily than landmarks farther from the goal. Searching error increases with increased goal-landmark distances, and therefore it is ecologically advantageous to weigh proximal landmarks more. Similarly, larger landmarks are relied on more than smaller ones (Bennett, 1993; Chamizo, Rodrigo, Peris, & Grau, 2006; Cheng et al., 1987; Gouteux, Thinus-Blanc, & Vauclair, 2001). This is also adaptive because a larger landmark is generally more stable, it is less likely to be displaced by weather agents and can be seen from a farther distance; therefore, it would have greater predictive value for determining a goal location.
I
n some instances, animals must combine multiple cues to locate a goal. For example, a target corner in a perfectly rectangular room cannot be distinguished from its opposite corner unless a feature cue is added to the room, e. g., coloring one wall differently from the other three walls. To identify the goal/correct corner, a navigator would have to use the geometric information provided by the rectangular environment (which specifies a pair of opposite, potentially correct corners) and combine it with information provided by the colored wall (among the two geometric corners, the goal is the closer or the farther relative to the feature). Although it has been proposed that geometric information is processed separately from feature cues, via a "geometric module" (Cheng, 1986; Gallistel, 1990; Hermer & Spelke, 1994, 1996; Wang & Spelke, 2002), a vast amount of data demonstrate that animals are able to combine information from the two sources (birds: Kelly, Spetch, & Heth, 1998; Vallortigara, Zanforlin, & Pasti, 1990; fish: Sovrano, Bisazza, & Vallortigara, 2002; monkeys: Gouteux et al., 2001; humans: Learmonth, Newcombe, & Huttenlocher, 2001; Ratliff & Newcombe, 2008).

Not only can geometry and feature information be combined, but there is also evidence that they are integrated in a flexible manner, with each cue weighed according to reliability, salience, variability, and prior experience (Newcombe & Huttenlocher, 2006; Newcombe & Ratliff, 2007). Two examples illustrate this point. Using the prototypical rectangular enclosure with feature cues on the walls, studies have demonstrated that subjects tend to rely more on feature than geometric cues as the size of the enclosure increases (Learmonth, Nadel, & Newcombe, 2002; Vallortigara, Feruglio, & Sovrano, 2005; Sovrano, Bisazza, Vallortigara, 2005; Ratliff & Newcombe, 2007). This is probably related to the fact that, in larger enclosures, a

feature cue on the boundary tends to be generally farther away from a navigator, providing a more stable directional reference (Ratliff & Newcombe, 2007; Wang & Spelke, 2002). Therefore, in large environments it would be more advantageous to rely on feature cues, whereas in a smaller environment a feature could be less informative. In a similar manner, holding the size of the enclosure constant, more weight is assigned to the feature cue—compared to geometry—when the goal is closer to the feature than when it is farther away (Cheng, 1986; Gray, Blomfield, Ferrey, Spetch & Sturdy, 2005; Nardi & Bingman, 2007; Vallortigara et al., 1990). This goal-feature proximity effect clearly resembles the above mentioned greater reliance on landmarks closer to the goal. In sum, the relative usefulness of geometry or feature cues can affect an animal's goal finding strategy, supporting the hypothesis that the nervous system integrates the two sources of information into a single, adaptive and flexible representation ("adaptive combination view"; Newcombe & Huttenlocher, 2006). It has also been proposed that spatial cues are integrated in a statistically optimal manner, with weights assigned to cues in order to reduce variance (Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Nardini, Jones, Bedford, & Braddick, 2008).

Most studies on spatial learning have been carried out in horizontal environments and very little attention has been given to what may occur on vertically extended surfaces. When a navigable surface is tilted, a new spatial cue is added, which provides the navigator with an allocentric, directional frame of reference that can be used for reorientation and for encoding a goal location (Jacobs & Schenk, 2003). Theoretically, any compass-like direction extracted from the slope gradient can be used as a reference (uphill, downhill, or any bearing in between; Restat, Steck, Mochnatzki, & Mallot, 2004). Goal location studies on pigeons have suggested that, among an array of four potential hiding places, a goal is encoded based on its position with respect to the vertical (uphill–downhill) and orthogonal (left–right) axes of the slope gradient (for an example, see Figure 1B; Nardi & Bingman, 2009a, 2009b). The vertical axis of the slope is the most salient, as pigeons committed most search errors to the location with a correct vertical coordinate (uphill or downhill), but a wrong orthogonal coordinate (left or right; Nardi & Bingman, 2009a). Comparatively, this parallels the primacy of the vertical axis found in place learning in rats (Grobéty & Schenk, 1992) and in spatial reference frames in humans (Carlson & Van Deman, 2008; Franklin & Tversky, 1990). The ecological reason for this priority is that the vertical axis identifies the direction of steepest descent of the slope, moving along which most energy is required. Pigeons also encoded the location of the goal along the orthogonal axis, as they learned to distinguish two locations with the same vertical coordinate. The orthogonal axis can be considered secondary because it identifies points of equal elevation, it is symmetrical (no ascent or descent in either direction) and, theoretically, because it can be derived from the vertical axis ("right" is 90° clockwise with respect to the uphill direction, "left" is 90° counterclockwise). By using such a bicoordinate representation, pigeons can encode a goal from a square or trapezoid arrangement of potential hiding places on a slope (see Figure 1B; Nardi & Bingman, 2009a, 2009b).
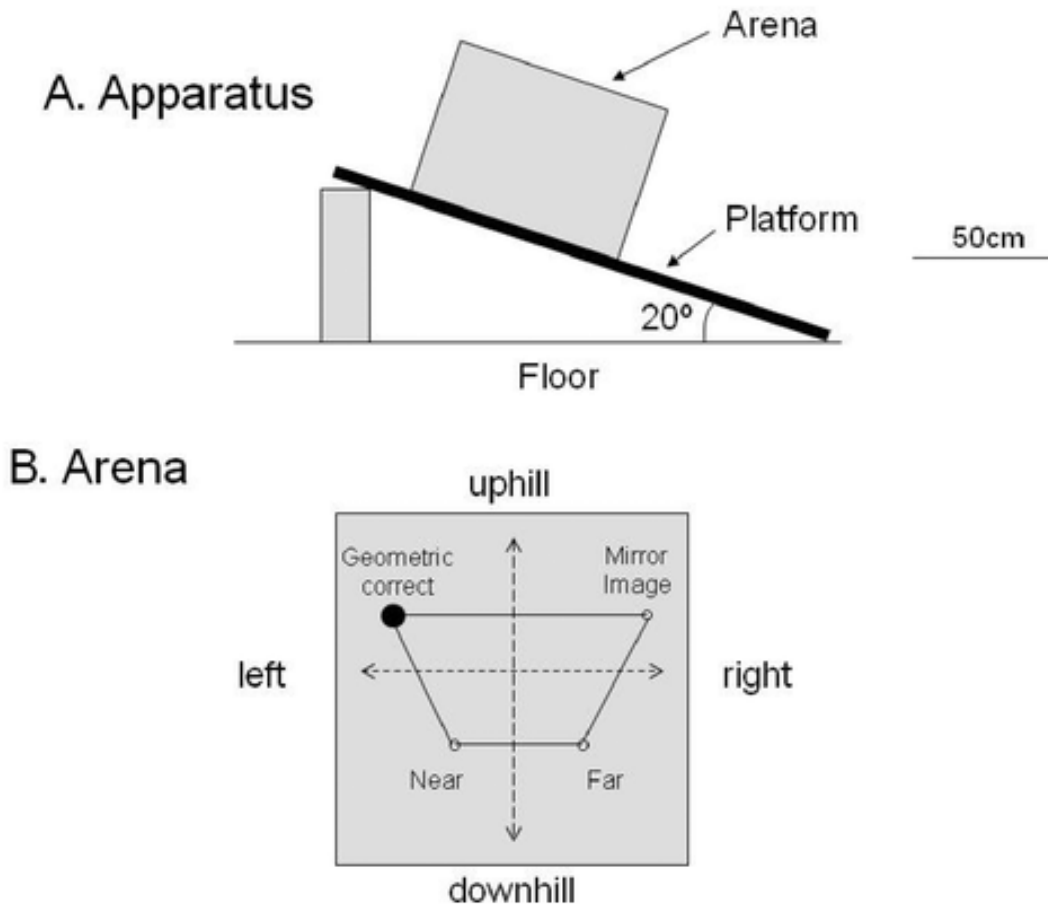
Figure 1. A: Schematic representation of the experimental environment viewed from the side. B: Schematic representation of the arena viewed from above. The geometric correct corner labels the reinforced corner. The mirror image corner labels the other acute, but geometrically incorrect, corner. The near and the far corner label the other two, obtuse corners. Because the floor is slanted, each corner can also be identified based on its position with respect to the vertical (uphill–downhill) and orthogonal (left–right) axes of the slope. In this case, the geometric correct corner is uphill/left, the mirror image corner is uphill/right, the near corner is downhill/left, and the far corner is downhill/right.

To date, the use of slope for determining a goal location has been shown in rats (Miniaci, Scotto, & Bures, 1999; Moghaddam, Kaminsky, Zahalka, & Bures, 1996), pigeons (Nardi & Bingman, 2009a), and human adults (Restat et al., 2004). Slope is an ecologically relevant cue because we do not live in a flat world; geographical slants are part of the lay of the land in natural environments. A slope can be perceived by a combination of kinesthetic, proprioceptive, vestibular, and visual stimuli; we refer to these multimodal cues collectively as slope cues or slope information. Slope information is nongeometric because it does not involve the relationship between surfaces and points (Gallistel, 1990); it can be considered a gravity-dependent, feature cue. From a neurological point of view, a goal
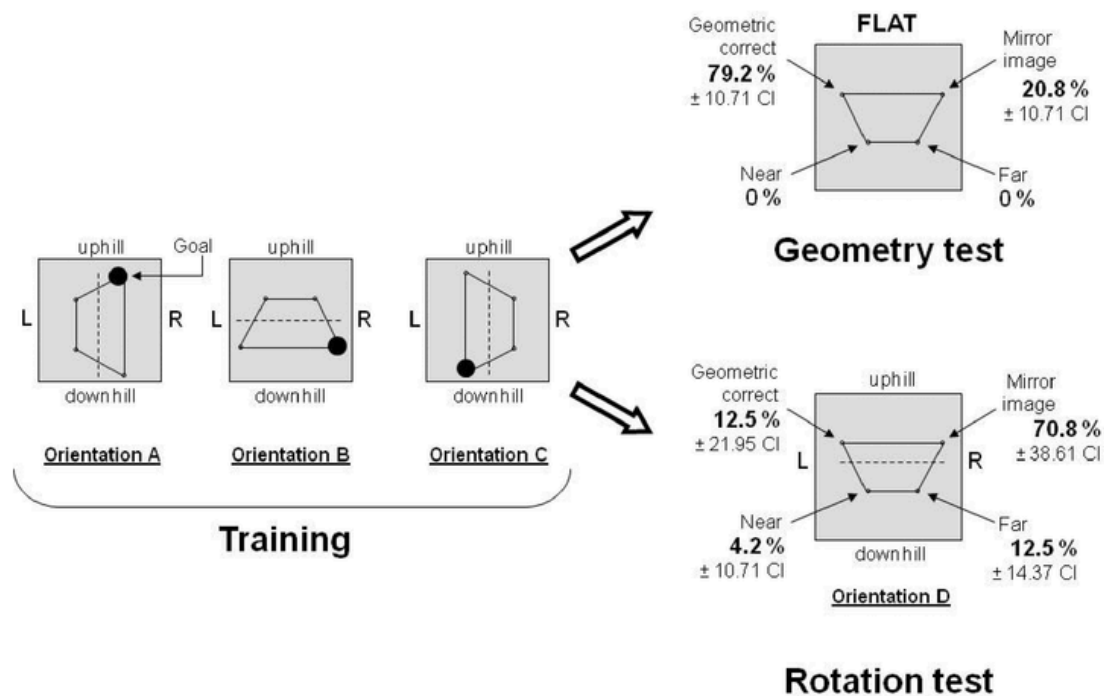
representation based on slope is hippocampal independent (Nardi & Bingman, 2009b), just like goal representation based on visual feature cues (McGregor, Hayward, Pearce, & Good, 2004; Vargas, Petruso, & Bingman, 2004).

Recently, Nardi and Bingman (2009a) investigated the relationship between slope and geometric information. Pigeons had to locate a goal in a corner of a trapezoid arena that was placed horizontally or on a sloped floor. Like in many geometry studies, the goal could be determined by its position with respect to the shape of the arena (geometrically unambiguous). However, in the sloped condition, the goal could also be located by its position with respect to the vertical (uphill–downhill) and orthogonal (left–right) axes of the slope gradient (e.g., the goal is uphill on the left). Pigeons learned the task more than four times faster when the arena was on the slope. Clearly slope added an exploitable cue to the environment, so salient that it rendered task acquisition much easier. More important, when slope and geometric information were set in conflict, pigeons searched solely according to slope, and the geometric correct corner was never chosen. This unresponsiveness to geometry during conflict tests clashes with many horizontal studies that have proposed geometry to be the preferred means of reorientation (Cheng, 1986; Gallistel, 1990; Hermer & Spelke, 1994, 1996; Wang & Spelke, 2002). In particular, in pigeons, when conflict between geometry and visual feature cues occurs, it is geometry that controls behavior (Vargas et al., 2004; Nardi & Bingman, 2007), or at least some choices are still directed to the geometric correct corner (Kelly et al., 1998). By contrast, there was no evidence that geometry had any control over behavior when the floor was slanted (Nardi & Bingman, 2009a). According to Cheng and Newcombe (2005), this could be an indication that slope and geometry are not integrated in a unified representation, but are two, modular representations that guide behavior. The purpose of the present study was to test this possibility.

A basic tenet of principles of associative learning and of models of spatial learning (adaptive combination view: Newcombe & Huttenlocher, 2006; operant model of geometric learning: Miller & Shettleworth, 2007), is that the associative strength of a cue is critically dependent on its predictive value. After all, why rely on a feature cue or on the shape of the arena if the goal cannot be localized based on that information? In Nardi and Bingman's study (2009a), slope and geometry were equally good predictors of the goal location. In the present study, using the same apparatus and an analogous methodology, we drastically decreased the predictive value of slope. If the two cues are integrated (combined in a flexible representation sensitive to the usefulness of the cues; Cheng & Newcombe, 2005), now that geometry is the only good predictor of the goal, we would expect geometry to control behavior. Conversely, if under conditions in which slope is a poor predictor of goal location, pigeons still fail to rely on geometry—the good predictor—this would strongly suggest that slope is the dominant cue and that, perhaps, slope information is not integrated with geometry.

Experiment 1

Pigeons were trained to locate food hidden in a corner of an isosceles trapezoid arena, which was placed on a surface slanted by 20° (see Figure 1). The arena was presented with three different orientations on the slope. Among the array of four corners, therefore, the goal corner did not have a fixed position with respect to the slope. Following the example in Figure 2, in some trials the goal was uphill on the right (Orientation A), in other trials it was downhill on the right (Orientation B), and in other it was downhill on the left (Orientation C). Therefore, position relative to the slope was not a good predictor of goal location. By contrast, the goal corner could be consistently predicted by its position with respect to the geometric shape of the arena (the corner with a short wall on the left and a long wall on the right) in all three orientations (see Figure 1B and Figure 2). After training, pigeons were tested on a flat surface to verify if they had learned geometry. Crucially, they were also tested with a novel orientation of the arena on the slope, an orientation not presented during training. If pigeon search behavior was controlled by geometry—the good predictor—then in the novel orientation they should show a preference for the geometric correct corner.

Geometry test

FLAT

Geometric correct **79.2%** ± 10.71 CI

Mirror image **20.8%** ± 10.71 CI

Near **0%**

Far **0%**

Training

uphill	Goal	uphill		uphill	
L	R	L	R	L	R
downhill		downhill		downhill	
Orientation A		Orientation B		Orientation C	

Rotation test

uphill

Geometric correct **12.5%** ± 21.95 CI

Mirror image **70.8%** ± 38.61 CI

L   R

Near **4.2%** ± 10.71 CI

downhill

Far **12.5%** ± 14.37 CI

Orientation D

Figure 2. Experimental procedure for training and testing in Experiment 1. Each orientation of the arena on the slope is represented with its principal axis (dashed line). The goal corner during training is marked with a black dot. Pigeons were trained with three different orientations of the arena with respect to the slope. In Orientation A, the goal is uphill/right, in Orientation B it is downhill/right and in Orientation C it is downhill/left. In the geometry test the arena was placed horizontally on the floor. In the rotation test, a novel orientation was used (Orientation D, for which the geometric correct corner is uphill/left). Notice that Orientations A and C have the principal axis of the arena aligned (parallel to the

vertical axis of the slope), and that Orientations B and D have the principal axis aligned (perpendicular to the vertical axis of the slope). Here the orientation for the rotation test has the principal axis of the arena perpendicular to the vertical axis of the slope. However, for half of the subjects, the test orientation had the principal axis parallel to the vertical axis of the slope (Orientation A or C), and for the other half it had the principal axis perpendicular to the vertical axis of the slope (Orientation B or D). Furthermore, for half of the pigeons the geometric correct corner in the rotation test was uphill, and for the other half it was downhill. The mean percentage of choices for each test is indicated in each corner (±95% confidence intervals). In the geometry test, only the acute corners were chosen, and the geometric correct corner was chosen significantly more than the mirror image corner. In the rotation test, the mirror image corner was chosen significantly more than any other corner (no other differences were significant).

Method
Apparatus

The apparatus used in this study was identical to that used by Nardi and Bingman (2009a). The experimental environment consisted of a square, wooden platform (183 × 183 cm, 10 cm high above the floor) surrounded by circular curtains. A video camera attached to the ceiling, directly above the center of the platform, was used to observe and record the behavior of the subjects. An isosceles trapezoid arena, with no ceiling or floor, was placed on the platform (see Figure 1). The four walls of the arena (61 cm high) were made of pink Styrofoam (4 cm thick; Dow Chemical, Midland, MI), and were attached to create an isosceles trapezoid environment (longer base 165 cm, shorter base 87 cm, sides 92 cm). The platform was tilted 20° degrees with respect to the floor by placing one side of the platform on a wooden stage. The test environment was illuminated by a 75 W light bulb attached to the ceiling above the center of the platform (next to the camera). Four red feeders (7.6 cm in diameter and 4.3 cm in height) were placed in the corners of the arena.

Subjects

Six experimentally naïve homing pigeons (Columba livia) were used. During the experiment, pigeons were maintained at 85% of their free-feeding body weight and given free access to grit and water. All procedures were carried out in accordance with National Institute of Health guidelines and approved by the Bowling Green State University Institutional Animal Care and Use Committee.

Habituation

In this phase the platform was placed horizontally on the floor. On reaching 85% of their normal body weight, the pigeons were taken through a habituation procedure (one trial/day). A pigeon was transported in a carrying cage inside the darkened experimental room and slowly rotated (approximately 10 to 12 rpm) on a swivel chair for 1 min to prevent any use of inertial vector orientation. The pigeon was

then introduced into the experimental environment. The light in the experimental environment was turned on, and the pigeon was allowed to explore the environment for 20 min. On the first 2 days of the habituation procedure, the arena was not used and the pigeon could explore the entire experimental platform. Starting from Day 3, the trapezoid arena was placed on the platform and the pigeon was introduced into the arena. During habituation, two feeders were placed in the center of the platform (in the center of the arena from Day 3). On the first day, pieces of food (dry food pellets; Purina Pigeon Chow, Ralston-Purina, St. Louis, MO) were scattered in and around the feeders to encourage the birds to explore the feeders. During the remaining days of the habituation procedure, food was placed only inside the feeders. As a pigeon learned to eat from the feeders, the food was gradually covered with grit until it was completely covered. The habituation phase ended when a pigeon completely ate the grit-covered food from both feeders within 5 min. All pigeons concluded habituation in 4 or 5 days.

Training

Training consisted of nine daily sessions. The platform was tilted 20° degrees with respect to the floor by placing one side of the platform on a wooden stage. The elevated side of the platform changed randomly from trial to trial, such that birds were not able to associate any uncontrolled feature of the platform with the slope gradient. Also, throughout both training and testing phases of the experiment, the arena was turned upside-down randomly from trial to trial, such that the edge that was in contact with the platform on one trial was now oriented to the ceiling. This procedure was carried out to reduce the likelihood of birds using any possible uncontrolled feature of the arena (e.g., scratches or marks) to locate the goal. For each subject the arena was presented in three of four discrete 90° orientations with respect to the slope (see Figure 2). A daily training session was composed of nine trials, three trials for each orientation. Each orientation was presented in random order, with the constraint that the same orientation could not be presented on consecutive trials. A feeder was positioned at each corner of the arena. Each pigeon's daily amount of food (typically 20 to 25 g) was rationed out through the daily trials and placed in one feeder. This goal feeder contained food covered by grit; the other three feeders were filled only with grit. It has been shown that corners of an environment might carry a different perceptual salience depending on angle size (Tommasi & Polli, 2004). To avoid a potentially different level of stimulus control gained by the goal corner angle, each pigeon was randomly assigned one of the two acute corners as the goal. The goal feeder always maintained the same position with respect to the geometric shape of the arena. At the beginning of each trial, a bird was slowly rotated on a swivel chair in the dark. The pigeon was then placed inside the darkened arena near the midpoint of one of the four sides; each trial started from a different side of the arena (in random order, counterbalanced across sessions and each orientation). This procedure was carried out to prevent birds from using other learned, idiothetic associations, such as locating the goal by always turning to the same side. Once the light was turned on, the pigeon was free to search for the correct, baited feeder. A feeder choice was scored when a pigeon pecked inside a

feeder. For each trial a pigeon was always allowed to find and eat from the correct feeder; however, a trial was considered correct only when the first choice was to the baited feeder. After a trial was completed, the light was turned off and the pigeon was taken out of the experimental environment. The approximate time between trials for each bird was 5 to 10 min.

Testing

After the nine training sessions, four test sessions were conducted. A daily test session was composed of nine reinforced training trials, plus two unreinforced test trials (a total of 11 trials per session now). The fourth and the eighth trial of the session were the test trials. The unreinforced test trials ended once a pigeon pecked in two different feeders, or 3 min after a first choice. On each test session, two types of test trials (see below) were presented, such that by the end of the experiment each subject was given four trials of each test trial type (for each test trial a bird entered the arena from a different side). The test trial types were presented in random order, counterbalanced across subjects. The two test trial types are given in the following sections.

Geometry test

As shown in Figure 2, the platform was placed horizontally on the floor. The purpose of this test was to determine if a pigeon had encoded the geometric information provided by the walls of the arena (the shape of the environment) during training with multiple-arena orientations on a slope.

Novel orientation test (for brevity referred to as Rotation test)

As shown in Figure 2, the arena was placed on the slope with a new orientation that was not presented during training. For three pigeons the test orientation was one in which the principal axis was parallel to the vertical axis of the slope. For the other three pigeons, the test orientation was one in which the principal axis was perpendicular to the vertical axis of the slope (see Figure 2). Furthermore, the location of the goal during training was counterbalanced across subjects such that, in the novel orientation, half of the birds had the geometric correct corner uphill, and for the other half it was downhill. This test assessed if goal search based on geometric shape information would transfer to a novel orientation of the arena on the slope. For all tests mean values are always presented with 95% confidence intervals (CI).

Results
Acquisition

For each pigeon, the percentage of correct trials during the training sessions was averaged per block of three sessions (Block 1: Sessions 1–3; Block 2: sessions 4–6; Block 3: Sessions 7–9). Furthermore, the percentage of correct trials during the

reinforced trials of a test session was averaged across the four test sessions (Block 4: Sessions 10–13). A within-subjects analysis of variance (ANOVA) revealed a significant effect of session block on the percentage of correct trials, $F(3, 15) = 23.73$, MSE = 136.38, $p < .001$, η p2 = .83. The percentage of correct trials increased monotonically across the blocks (see Figure 3A). Results of pairwise t tests with Sidak adjustment showed a significant step of increase in performance from session Block 2 to Block 3, $p < .05$ (Figure 3A).
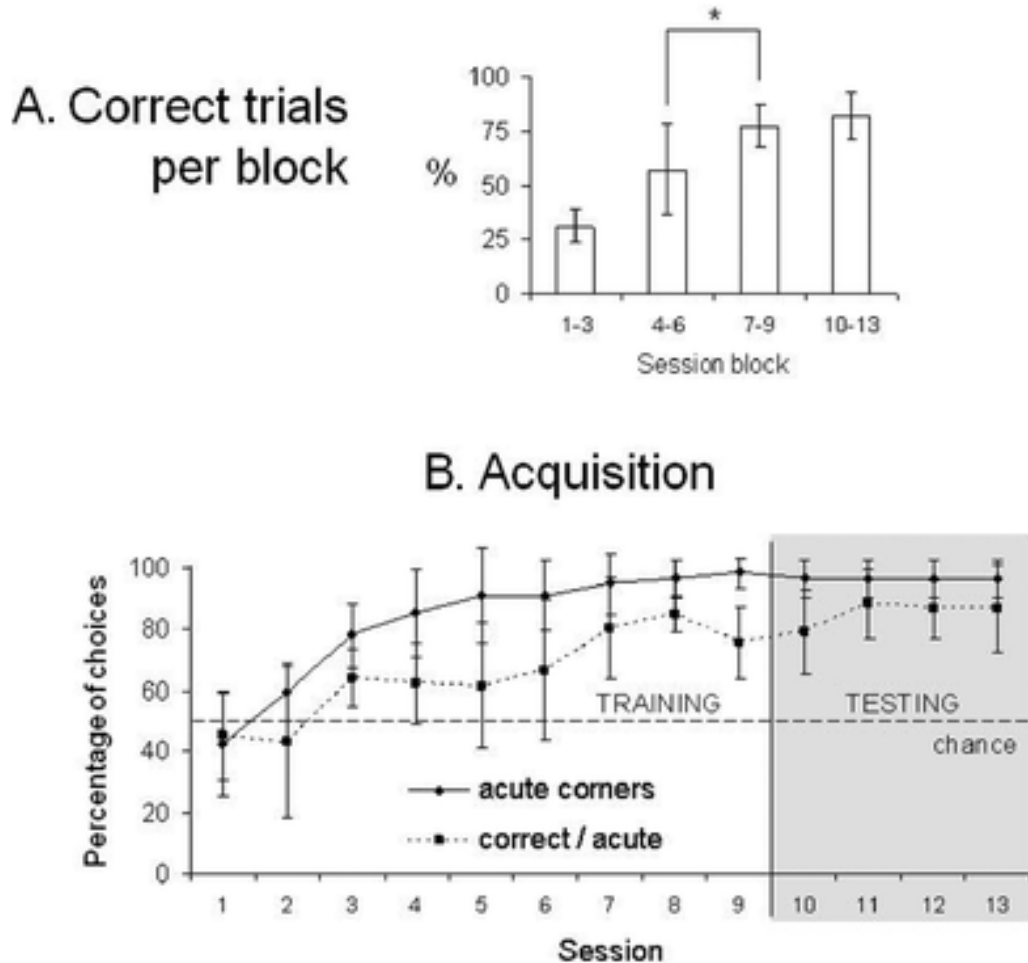
Figure 3. A: Mean percentage of correct trials (±95% confidence intervals) per session block during training (Blocks 1–3) and during the reinforced trials of testing (Block 4) in Experiment 1. There was a statistically significant step of increase in performance from Session Block 2 to Session Block 3 (* $p < .05$). B: Mean percentage of choices (±95% confidence intervals) during the nine training sessions and the reinforced trials of the four test sessions in Experiment 1. The solid line represents the percentage of choices to the acute corners, as opposed to obtuse corners (i.e., acute/total). The dotted line represents, among searches to the acute corners, the percentage of choices to the geometric correct corner, as opposed to the mirror image corner (i.e., correct/acute). For example, in Session 5 the mean percentage of choices to the acute corners is approximately 91%, of which approximately 61% are

directed to the geometric correct corner (therefore, the remaining 39% are directed to the mirror image corner). The chance level for both curves is 50% because, assuming an equal distribution of choices among the four corners, the acute corners should be visited half of the times (considering overall choices), and the geometric correct corner should be visited half of the times (considering choices only to acute corners).

Figure 3B shows the learning curve for the task broken down into two components: the percentage of choices directed to acute corners—as opposed to obtuse corners—and, considering only the searches at the acute corners, the percentage of choices directed to the geometric correct corner—as opposed to the mirror image corner. During the first training session, the distribution of choices to the acute and the obtuse corners was not significantly different from an equal distribution, binomial test, $p > .05$. Furthermore, the distribution of searches at the two acute corners was not significantly different from an equal distribution, binomial test, $p > .05$. From Session 3, pigeons were choosing the two acute corners significantly more than the two obtuse corners, binomial test, $p < .001$. From Session 6, pigeons were choosing the geometric correct corner significantly more than expected by an equal distribution of searches between the two acute corners, binomial test, $p < .05$. In the last training session (Session 9), an obtuse corner was chosen only once by the pigeons as a group, and searches at the geometric correct corner (M = 74.1% ± 12.03 CI) were significantly more than searches at the mirror image corner (M = 24.1% ± 11.46 CI), binomial test, $p < .001$.

For each pigeon, the distribution of correct trials across the three training orientations was not significantly different from an equal distribution, highest chi-square value for any one pigeon: $\chi 2(2, n = 47) = 5.66$, $p > .05$.

Testing

When tested on a flat surface (geometry test), pigeons searched only at the acute corners, and subjects overwhelmingly chose the geometric correct corner (M = 79.2% ± 10.72 CI) over the mirror image corner (M = 20.8% ± 10.72 CI). This difference was statistically significant, binomial test, $p < .01$ (see Figure 2). When tested in the novel orientation of the arena with respect to the slope (rotation test), surprisingly, pigeons as a group directed more than two thirds of the searches to the mirror image corner (M = 70.8% ± 38.61 CI). This was the only corner chosen above chance, binomial test, $p < .001$ (see Figure 2). Results of pairwise binomial tests with Bonferroni's adjustment show that the mirror image corner was chosen significantly more than any other corner, $p < .01$; all other differences between corners were not statistically significant, $p > .05$.

Discussion

In the course of nine sessions (27 trials per each orientation), pigeons learned to locate a reward in a corner of an isosceles trapezoid arena presented in three different orientations on a slope. Subjects learned to discriminate between acute and obtuse corners, a distinction that could be based on the local cue of corner angle (see Pearce, Good, Jones, & McGregor, 2004; Tommasi & Polli, 2004). More important, they learned to distinguish the geometric correct corner from its mirror image, although both share the same local cue—an acute angle. To do so, they had to encode the metric properties of the arena (length of the walls) and combine it with sense (distinction of left and right; e.g., the geometric correct corner had a long wall to the right and a short wall to the left, whereas the mirror image corner had a long wall to the left and a short wall to the right; Cheng & Gallistel, 1984; Sovrano & Vallortigara, 2006).

It is important to note that performance of each pigeon did not vary significantly across the three training orientations with respect to slope. In other words, subjects did not have a preferred orientation in which they learned the goal location better or more rapidly than the other orientations. For this reason, it can be excluded that pigeons were biased to direct searches, across all orientations, to a single location with respect to the slope gradient (e.g., always going to the uppermost corner on the right), or that they were following a search route energetically less expensive (i.e., always going downhill). Furthermore, because the starting point in the arena varied from trial to trial, it can also be excluded that pigeons were following an idiothetic association (e.g., always turning to the same side) to find the goal.

The geometry test clearly revealed that, although the arena was presented in three different slope orientations, pigeons successfully encoded the goal location with respect to the geometric shape provided by the arena. When subjects did not choose the geometric correct corner, the mirror image was the only other corner chosen. This suggests that the local cues of the correct corner (acute angle) were easier to associate with the goal than the geometric cues necessary to distinguish between the correct and the mirror image corner.

When tested in the novel orientation (rotation test), subjects did not choose the geometric correct corner more than expected by chance. Although the pigeons learned to associate the geometric cues of the correct corner with the goal, as demonstrated by the geometry test, this association did not transfer to the novel orientation of the arena on the slope. Previous studies have shown that geometric information can generalize to a novel context, such as to an arena with a different shape (McGregor, Jones, Good, & Pearce, 2006; Pearce et al., 2004; Tommasi & Polli, 2004) or a different size (Kelly & Spetch, 2001). Furthermore, pigeons are able to transfer goal searching based on geometric cues even to an arena in which feature cues, which have been associated with the goal location during training, are arranged differently (Nardi & Bingman, 2007; Vargas et al., 2004). Therefore, it is surprising that generalization of geometric information did not occur when a stimulus—the arena orientation on a slope—which was not a good predictor of the goal, was different from training. We find it interesting that choices in the novel

orientation were not equally distributed among the corners, but were directed to the mirror image corner significantly more than any other corner. Because of this systematic error, it is unlikely that the lack of generalization is due to a generalization decrement (Pearce, 1987). We propose two interpretations of this surprising result.

Using an apparatus identical to the present experiment, Nardi and Bingman (2009a) showed that pigeons learned to locate the goal with respect to its position on the slope gradient (e.g., the goal feeder is uphill on the left) in an average of 26 trials. In that study the arena was presented in a single orientation. Because in the present experiment pigeons were exposed to each orientation for 27 trials, they had enough training to encode a slope-based representation for each of the three orientations. Following the example shown in Figure 2, subjects might have learned that in Orientation A the goal corner was uphill/right, that in Orientation B it was downhill/right, and that in Orientation C it was downhill/left. These positions with respect to the slope would map onto three corners of the arena in the novel orientation (Orientation D): the mirror image, the far, and the near corner, respectively. If, among these candidate corners, pigeons attempted to match as many cues as possible with the goal corner during training, then they would commit a systematic error to the mirror image corner because it is the only acute corner of the three. In sum, this hypothesis supposes that, in the novel orientation, pigeons were matching the goal's position on the slope plus local cue (corner angle). We will refer to this as the slope-position hypothesis.

An alternative hypothesis could be that pigeons in the novel orientation (Orientation D, see Figure 2) were following the slope-based representation associated only with Orientation B, because in these two orientations the principal axis (or main axis of elongation; see Gallistel, 1990) of the arena is aligned with respect to the slope. Therefore, in the novel orientation, pigeons' choices would be biased toward the mirror image corner (uphill/right), because that is the acute corner closest to the goal position specified by Orientation B (i.e., downhill/right). This hypothesis is supported by the claim that animals orient by extracting global geometric parameters from the environment, such as its principal axis (Gallistel, 1990), and by the fact that transfer of goal searching from one shape of the arena to another can be explained—at least in some cases—by the alignment of the principal axes (Cheng & Gallistel, 2005). Basically, this hypothesis supposes that pigeons were matching the arena's principal axis plus local cue. We refer to this as the principal-axis hypothesis.

In essence, these two competing hypothesis differ in the number of slope-based representations "activated" in the novel orientation. For the slope-position hypothesis, all slope-based representations learned during training are guiding behavior (one for each training orientation); for the principal-axis hypothesis, only one slope-based representation is guiding behavior—the one associated to the training orientation matching the principal axis of the arena. However, the basic stipulation for both these hypothesis is that, during training, pigeons encoded a

slope-based goal representation (i.e., the goal's position with respect to the slope) for each orientation. The purpose of Experiment 2 was to test this assumption. In addition, Experiment 2 was designed to determine which of the two above mentioned hypotheses offers a better explanation for the type of representation acquired by the pigeons.

Experiment 2

Following a similar procedure as in Experiment 1, pigeons were now trained with two, 180°-opposite orientations of the arena on the slope. After having received the same number of trials for each orientation as in Experiment 1 (27 trials), they were tested with a novel orientation in which the principal axis was perpendicular to both training orientations with respect to the slope (see Figure 4). Under this condition, the principal-axis and slope-position hypothesis would predict two different outcomes in the rotation test trials. The principal-axis hypothesis assumes that pigeons follow the slope-based representation of the training orientation matching the principal axis of the arena. However, now the principal axis of the test orientation is not aligned to any training orientation. Because there is no match based on the principal axis, no preference for a slope-based representation would be predicted; pigeons should choose only based on the local cue and searches should be equally distributed between the geometric correct and mirror image corner. By contrast, if pigeons match the slope position of the goal (slope-position hypothesis), a bias to the mirror image corner should still appear in the novel orientation test. In fact, as shown in Figure 4, if during training subjects encoded the goal as uphill/right (for Orientation A) and downhill/left (for Orientation C), two corners of the novel arena orientation (Orientation D) would map onto these positions: the mirror image and the near corner, respectively. Among these two candidate corners, pigeons would choose the mirror image corner because it is the only acute corner.

In Experiment 2 an additional test was included to determine if pigeons encoded a slope-based goal representation for each orientation. Subjects were tested on the slope but using a square arena, which provides no useful geometric cues to distinguish any corner from the others. If pigeons learned to locate the goal by its position with respect to the slope, we would expect a preference, among the four geometrically identical corners, for the two that map onto the goal positions with respect to the slope. For example, for a pigeon whose goal was uphill/right in one orientation and downhill/left in the other, we would expect a higher proportion of searches at the uphill/right and downhill/left corners of the square arena than at the other two corners that do not map onto the goal locations (see Figure 4, square test).
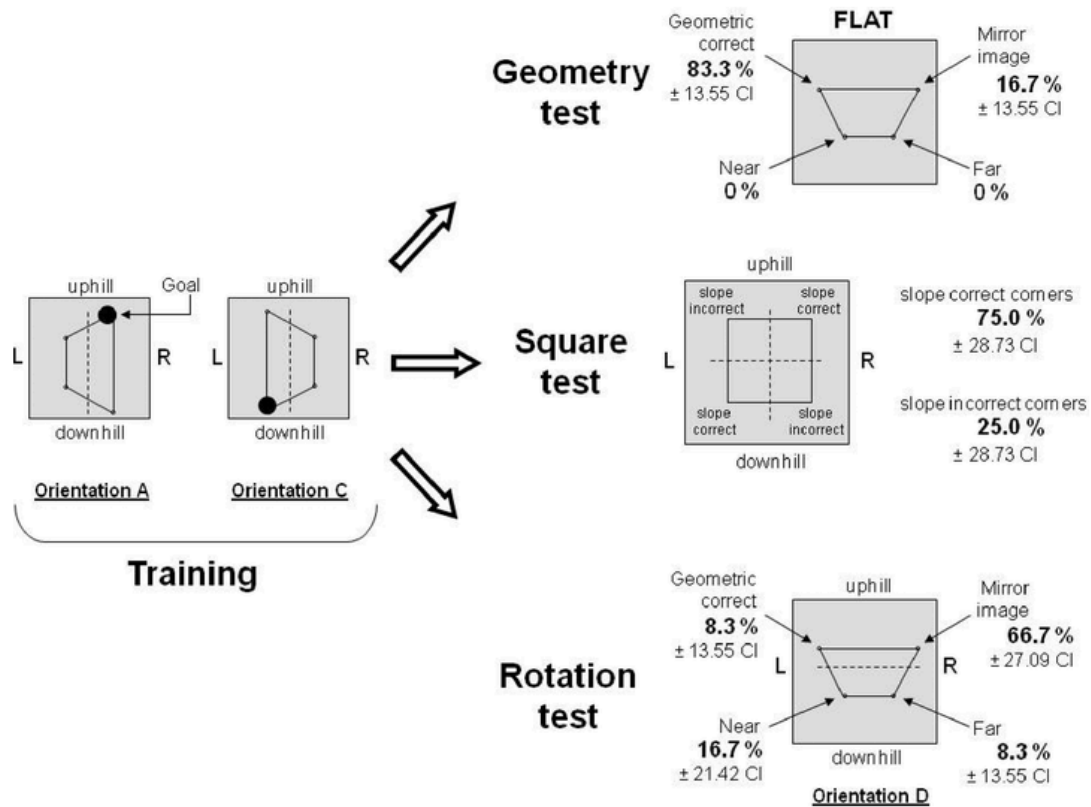
Figure 4. Experimental procedure for training and testing in Experiment 2. Each orientation of the arena on the slope is represented with its principal axis (dashed line). The goal corner during training is marked with a black dot. Pigeons were trained with two different orientations of the arena with respect to the slope. In Orientation A, the goal is uphill/right and in Orientation C it is downhill/left. In the geometry test, the arena was placed horizontally on the floor. In the square test, a square arena was used on the slope instead of the usual trapezoid. In the rotation test, a novel orientation was used (Orientation D, for which the geometric correct corner is uphill/left). In Experiment 2, the principal axis of the test orientation did not match either of the training orientations. In fact, notice that Orientations A and C have the principal axis of the arena aligned (parallel to the vertical axis of the slope), and that Orientation D instead has the principal axis perpendicular to the vertical axis of the slope. For half of the subjects, the test orientation had the principal axis parallel to the vertical axis of the slope (Orientation A or C), and for the other half it had the principal axis perpendicular to the vertical axis of the slope (Orientation B or D). Furthermore, for half of the pigeons the geometric correct corner in the rotation test was uphill, and for the other half it was downhill. For each test are indicated the mean percentage of choices to each corner (±95% confidence intervals). In the geometry test, only the acute corners were chosen, and the geometric correct corner was chosen significantly more than the mirror image corner. In the square test, two corners of the square map onto the goal's position with respect to slope: the uphill/right corner (for Orientation A) and the downhill/left corner (for Orientation C); these are called slope correct corners. The slope correct corners were chosen significantly more than the other two slope

incorrect corners. In the rotation test, the mirror image corner was chosen significantly more than any other corner (no other differences were significant).

Method

Six experimentally naïve homing pigeons were used. The apparatus was identical to Experiment 1. The experimental procedures were the same as Experiment 1, except for the following differences.

Training

Pigeons were trained with two of four discrete 90° orientations of the arena with respect to the slope. The two orientations had the principal axis aligned with respect to the slope (i.e., they were 180°-opposite orientations). Following the example in Figure 4, three pigeons were trained with Orientations A and C, the other three with Orientations B and D. Each pigeon was assigned one of the two acute corners as the goal.

During training, pigeons had the same exposure to each orientation as in Experiment 1 (a total of 27 trials for each orientation). Training consisted of six sessions composed of eight trials (four trials per each orientation, in randomized order) and a last session composed of six trials (three trials per each orientation). Testing

Four test sessions were conducted, each composed of six training trials plus three, unreinforced test trials (a total of nine trials per session). Trials 3, 6, and 9 were test trials. Three types of test trials were presented in each session, such that by the end of the experiment each subject was given four trials of each test type (see Figure 4).

Rotation test

Pigeons were tested with a novel orientation of the arena, not presented during training. For three pigeons the novel orientation had the principal axis parallel to the vertical axis of the slope (Orientation A or C), for the other three pigeons the main axis was perpendicular to the vertical axis of the slope (Orientation B or D). Furthermore, the location of the goal during training was counterbalanced across subjects such that, in the rotation test, for half of the birds the geometric correct corner was uphill, and for the other half it was downhill. More importantly, the principal axis of the arena in the novel orientation did not match either of the training orientations. Therefore, this test could determine which of the two hypotheses outlined in Experiment 1 is the most convincing. According to the slope-position hypothesis, choices should be mostly directed to the mirror image corner (as in Experiment 1). In fact, the goal position relative to the slope maps onto two corners of the arena in the novel orientation: the mirror image and the near corner, respectively (see Figure 4). Searches should be directed to the mirror image corner because it is the only one of the two that matches the local cue of the goal (an acute

corner). In contrast, according to the principal-axis hypothesis, because the novel orientation does not match the principal axis of any training orientation, there should be no bias toward any one acute corner; pigeons should search equally at the geometric correct and mirror image corners.

Square test

Pigeons were tested on the slope using a square arena instead of the training-trapezoid arena (each side was 112 cm, which was the approximate average length of the sides of the trapezoid). Having two axes of symmetry, a square arena does not provide any geometric information that cold be used to locate the goal. This test was introduced to test the hypothesis that pigeons developed a slope-based search strategy for each orientation. If so, we would expect pigeons to prefer, among the four geometrically identical corners, the two that have the same position as the goal with respect to the slope. As in the other test types, for each trial a pigeon started from a different side of the arena.

Geometry test

This was identical to Experiment 1.

Results
Acquisition

For each pigeon, the percentage of correct trials per session was averaged per block of training sessions (Block 1: Sessions 1–2; Block 2: Sessions 3–4; Block 3: Sessions 5–7). Furthermore, the percentage of correct trials during the reinforced trials of a test session was averaged across the four test sessions (Block 4: Sessions 8–11). A within-subjects ANOVA revealed a significant effect of session block on the percentage of correct trials, $F(3, 15) = 95.82$, $MSE = 4,149.15$, $p < .001$, $\eta p2 = .95$. The percentage of correct trials increased monotonically across the blocks (see Figure 5A). Results of pairwise t tests with the Sidak adjustment showed that there was a significant step of increase in performance from Block 1 to Block 2, $p < .01$, and from Block 2 to Block 3, $p < .01$.

Figure 5B shows the learning curve for the task broken down into two components: The percentage of choices directed to acute corners—as opposed to obtuse corners—and, considering only searches at the acute corners, the percentage of choices directed to the geometric correct corner—as opposed to the mirror image corner. In the first training session, the distribution of choices to acute and obtuse corners was not significantly different from an equal distribution, binomial test, $p > .05$, and the distribution of choices between the two acute corners was not significantly different from an equal distribution, binomial test, $p > .05$. Starting from Session 3, pigeons were choosing the acute corners significantly more than the obtuse corners, binomial test, $p < .05$. Also, starting from Session 3, considering only searches at the acute corners, pigeons were choosing the geometric correct corner

significantly more than the mirror image corner, binomial test, p < .001. In the last training session (Session 7), an obtuse corner was chosen only once by the pigeons as a group—in all other trials an acute corner was chosen—and searches at the geometric correct corner (M = 91.7% ± 9.58 CI) were significantly more than searches at the mirror image corner (M = 5.6% ± 9.03 CI), binomial test, p < .001.
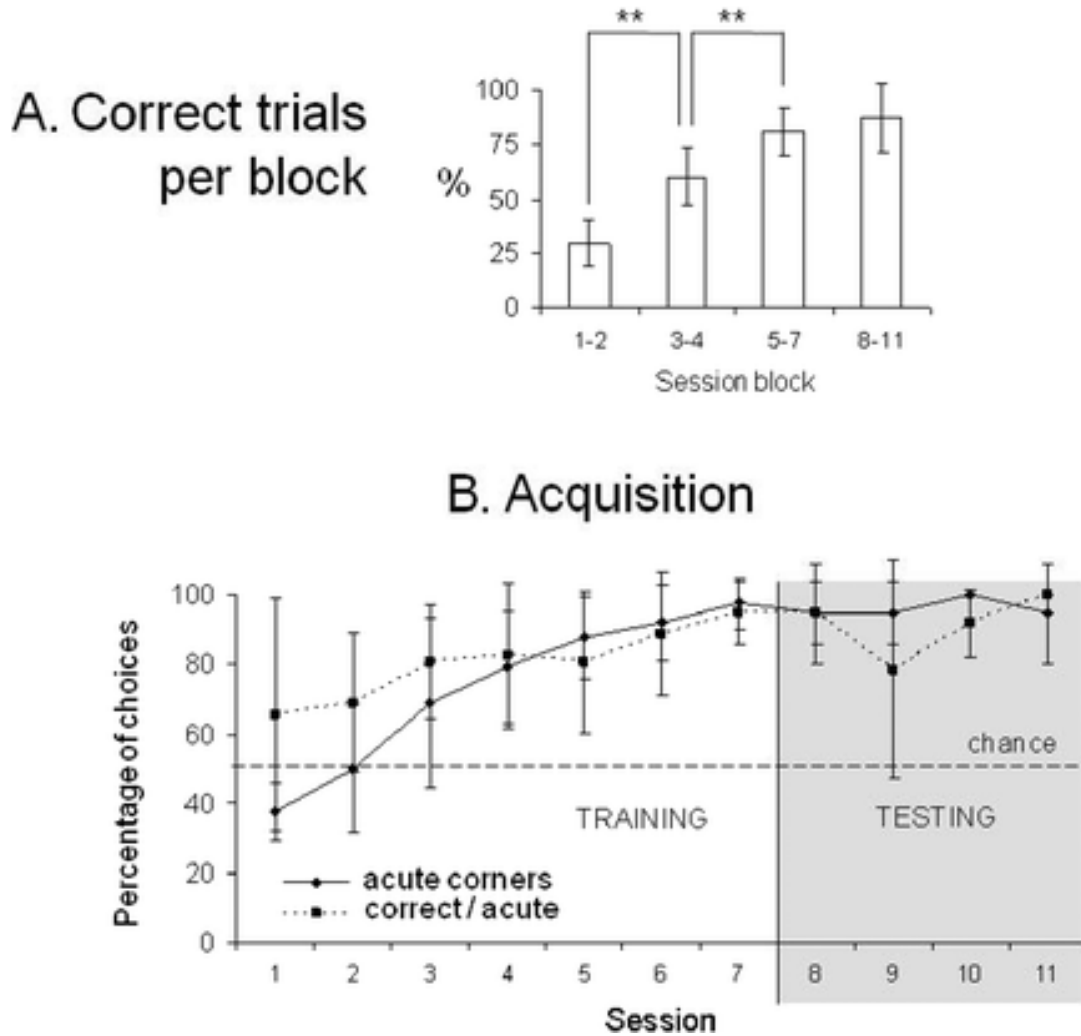
Figure 5. A: Mean percentage of correct trials (±95% confidence intervals) per session block during training (Blocks 1–3) and during the reinforced trials of testing (Block 4) in Experiment 2. There was a statistically significant step of increase in performance from Session Block 1 to 2, and from Block 2 to 3 (** p < .01). B: Mean percentage of choices (±95% confidence intervals) during the seven training sessions and the reinforced trials of the four test sessions in Experiment 2. The solid line represents the percentage of choices to the acute corners, as opposed to obtuse corners (i.e., acute/total). The dotted line represents, among searches to the acute corners, the percentage of choices to the geometric correct corner, as opposed to the mirror image corner (i.e., correct/acute).

Throughout training, for five of the pigeons the distribution of correct trials across the two training orientations was not significantly different from an equal distribution, highest chi-square value for any one pigeon: $\chi^2(1, n = 36) = 1.00$, $p > .05$. However, one pigeon completed significantly more correct trials in one orientation, $\chi^2(1, n = 22) = 4.55$, $p < .05$. In the first five training sessions this outlier completed 12 correct trials in one orientation and only one correct trial in the other. However, during the last part of training this bias was eliminated as the total number of correct trials in the last two training sessions was equally divided between the two orientations (five and five). Therefore, it can be concluded that, for the pigeons as a group, the correct trials were distributed approximately equally across the two training orientations, and that at the end of training all pigeons learned the task in both orientations.

Testing

Geometry test

When tested on a flat surface, pigeons chose only the acute corners of the arena. Subjects searched overwhelmingly more at the geometric correct corner (M = 83.3% ± 13.55 CI) than at the mirror image corner, binomial test, $p < .01$ (see Figure 4).

Square test

When tested with the square arena, for each pigeon there was a pair of opposite corners that, with respect to the slope, mapped onto the goal location during training (see Figure 4). For example, if the goal was uphill/left in one training orientation and downhill/right in the other, these locations would map, respectively, onto the uphill/left and downhill/right corners of the square arena (called slope correct corners). Searches at the slope correct corners (M = 75.0% ± 28.73 CI) surpassed significantly those to the slope incorrect corners, binomial test, $p < .05$.

Rotation test

When tested in the novel orientation of the arena with respect to the slope, pigeons as a group directed two thirds of the searches to the mirror image corner (M = 66.7% ± 27.09 CI). This was the only corner chosen above chance, binomial test, $p < .001$ (see Figure 4). Results of pairwise binomial tests with Bonferroni's adjustment show that the mirror image corner was chosen significantly more than any other corner, $p < .05$; all other differences between corners were not statistically significant, $p > .05$.

Discussion

Similar to Experiment 1, pigeons learned to locate the goal in a corner of an isosceles trapezoid arena presented in two different orientations on a slope. Furthermore, the geometry test showed that pigeons encoded geometry and were able to use it on a flat surface.

When tested on the slope but without geometric information (square test), out of the four identical corners, pigeons chose significantly more the two that mapped onto the goal positions with respect to the slope. Similarly, Nardi and Bingman (2009a) reported a preference for the slope correct corner in the square test, but in that case only one training orientation was used. The present result shows that, even when trained with multiple orientations of the arena, pigeons do encode the goal locations relative to the slope gradient.

When tested in the novel orientation (rotation test), the systematic error to the mirror image corner appeared again, just as it did in Experiment 1 using three training orientations. However, crucially, in Experiment 2 the novel orientation did not match the principal axis of either training orientation. Therefore, the systematic bias cannot be explained by a process of matching the arena's principal axis plus local cue, and the principal-axis hypothesis can be discarded. Instead, the preference for the mirror image corner can still be explained by a process of matching the goal's position on the slope plus local cue (slope-position hypothesis). Following the example in Figure 4, if during training subjects encoded that the goal was uphill/right (for Orientation A) and downhill/left (for Orientation C), two corners of the novel arena orientation (Orientation D) would map onto these positions: the mirror image and the near corner, respectively. Among these two candidate corners, pigeons would choose the mirror image corner because it is the only acute corner.

Overall, these results provide support for the slope-position hypothesis: pigeons encoded a slope-based representation for each training orientation, and these representations—together with local cue—were driving search behavior in the novel orientation of the arena on the slope.

General Discussion

Nardi and Bingman (2009a) showed that, when geometry and slope equally predicted a goal location, pigeons tested in a novel arena orientation displayed a large preference for the correct corner according to the slope gradient, even if it was geometrically incorrect. This could be due to a number of incidental factors, such as the floor inclination used in the study (20°) and the arena shape, which might have favored using a slope-based representation rather than relying on the geometric shape of the arena. Crucially, in the present study, slope was rendered a poor predictor of the goal location. The arena did not have a fixed orientation on the slope, so that the position of the goal varied unpredictably with respect to slope gradient. In Experiment 1, the goal assumed three different positions relative to the slope. Because the goal location was instead fixed relative to the shape of the arena, geometry can be consider three times as predictive as slope in determining where

the goal was. In Experiment 2, the goal assumed two different positions relative to the slope; therefore, geometry was twice as predictive as slope. A reading of associative learning principles that gives most emphasis to predictive validity would now expect behavior to be controlled by the more informative cue—geometry.

When tested in the novel arena orientation on the slope, pigeons were responding to the local cue of the corner angle, as they chose an acute corner. This shows that the association between reward and acute corner was able to withstand changes in orientation context. The strength of this association is also supported by pigeons' rapid learning to choose an acute corner during training, and by the fact that, in the geometry tests, searches were limited to the acute corners.

However, the key issue was whether pigeons would be able to distinguish, among the two acute corners, the geometrically correct, reinforced corner from its mirror image (geometric information). It is important to note that the geometric correct/mirror image corner distinction in the isosceles trapezoid arena is the same as the geometric correct/geometric incorrect corner distinction in the prototypical rectangular arenas; in both cases there is a same angle, but an opposite left–right (sense) arrangement of identical walls (e.g., short wall to the left, long wall to the right; Cheng & Gallistel, 1984; Sovrano & Vallortigara, 2006). Crucially, the geometric correct corner was never chosen above chance in a novel orientation of the arena on the slope. Therefore, both experiments consistently show that geometry failed to control behavior. Pigeons clearly associated the geometric correct corner with the goal, as they did use geometry on a flat surface (geometry test); however, there is no evidence that this association was used on the slope.

This finding has a nice parallel in two touch-screen studies. Human adults (Kelly & Spetch, 2004a) and pigeons (Kelly & Spetch, 2004b) were shown images of a rectangular environment on a touch-screen monitor and were trained to locate the goal in one corner. The rectangle on the screen was presented in multiple orientations with respect to the screen (discrete rotations of 45°). Subjects learned the task after many trials, but when tested with a novel orientation—not presented during training—they failed to identify the geometric correct corners and chose by chance. Even though a very different experimental set-up was used (2D computer images instead of a real-world 3D environment), these touch-screen studies resemble the present study because in both cases stimuli were presented with a vertical component (vertically oriented computer monitor and slanted, navigable surface) and in both circumstances geometry failed to control behavior.

In the present study, a systematic preference for the mirror image corner was revealed when pigeons were trained with three (Experiment 1) or with two (Experiment 2) arena-orientations on the slope. These results have been interpreted as showing that subjects were responding, in the novel orientation, to a nongeometric association. Birds encoded the goal position with respect to the slope in each training orientation. Then, in the novel orientation they were choosing the corner that matched two criteria: (1) it had to have one of the goal positions with

respect to the slope, and (2) it had to have the same local cue as the goal (an acute corner). Such a slope-position plus local-cue matching strategy can explain the surprising systematic error to the mirror image corner in both experiments. Furthermore, this mechanism is supported by the result of the square test (Experiment 2), which showed that pigeons encoded a slope-based representation of the goal locations (the positions of the goal relative to the slope in the training orientations).

The findings of this study are in apparent contrast with views of associative learning that pose most emphasis on the predictive value of a stimulus for determining its associative strength. According to these views, because the geometric correct corner was the best predictor of the reward, geometry should have gained most associative strength and controlled behavior. Furthermore, an interpretation of the present data based on cue integration is very problematic. According to an adaptive combination view (Newcombe & Huttenlocher, 2006), cues are flexibly weighed based—among other factors—on their reliability. It would be expected that, if geometry was not guiding behavior when its' predictive value was the same as slope (Nardi & Bingman, 2009a), it should at least become the guiding cue when its predictive value was much higher than slope. However, pigeons' reliance—or better, lack of reliance—on geometry was unaffected by the diminished predictive value of slope. Under no test circumstances were pigeons relying on geometry when tested on a slanted floor. Intuitively, this does not fit into a flexible, adaptive integration of slope and geometry into a unified representation; conversely, it suggests that they are two modular representations guiding behavior (Cheng & Newcombe, 2005). It seems as if geometry guides behavior on a flat surface, but the presence of the slope inhibits geometric control and promotes relying on a slope-based goal representation (plus local cue). This is striking, especially if one thinks that geometry has been considered for about 25 years the primary cue guiding spatial orientation (Cheng, 1986; Gallistel, 1990; Hermer & Spelke, 1994, 1996; Wang & Spelke, 2002; but see also: Cheng, 2008; Cheng & Newcombe, 2005), but here it failed to control behavior even when three times more predictive than slope. It is worth noting that a parallel unresponsiveness to geometry was found testing rats in a kite-shaped pool with differently colored walls; geometry failed to control behavior even if it was the best predictor of the goal (Graham, Good, McGregor, & Pearce, 2006).

Furthermore, the present data do not support a view-based matching strategy for solving geometric-like tasks (Cheung, Sturzl, Zeil, & Cheng, 2008; Sheynikhovich, Chavarriaga, Strosslin, Arleo, & Gerstner, 2009; Sturzl, Cheung, Cheng, & Zeil, 2008). Walking and standing on a sloped floor, pigeons' head remains upright. Therefore, the view of the arena differs depending on whether the pigeon faces uphill, downhill, or sideways. Statically, the uphill and downhill walls of the arena undergo some foreshortening compared to the side walls; furthermore, the uphill wall appears higher than the downhill wall. Dynamically, because the floor is closer to the eyes when facing uphill, walking uphill provides more optic flow than walking downhill. Because of these slope-related visual cues, the geometric correct corner

might have looked very different during the training trials, as its position on the slope varied uphill and downhill. However, if we assume that pigeons were recognizing the goal corner based on a stored retinal image, then the view-based matching mechanism must have been able to withstand the abovementioned static and dynamic view effects. Therefore, even in the novel arena orientation on the slope, the geometric correct corner should have been preferred because visually correct.

It can be concluded that claiming a privileged use of geometric information or a pure view-based matching strategy for reorientation is insufficient when the environment has a vertical component. However, we do not wish to claim a special status for slope information, a sort of "slope module," implying an inherent primacy of the slope reference frame for reorientation without incorporation of more predictive cues. We believe that the results of the present study can be explained if it is assumed that slope is simply more salient than geometry.

Slope is a complex spatial cue that provides potentially redundant, multimodal sensory stimuli. A navigator can perceive a slope by the effort of moving uphill, downhill, or sideways (kinesthetic information), by the angles of the joints (proprioceptive information) and by the sense of balance (vestibular information). Furthermore, keeping the head upright, parallel to the force of gravity, the view of the slope changes depending on which side is being faced (uphill, downhill, sideways; visual information). Any combination of these sensory cues is theoretically sufficient to perceive a slope gradient. To date, it has been shown that slope information can be used for place learning even in the absence of visual cues (rats: Miniaci et al., 1999), or in the absence of proprioceptive and kinesthetic cues (humans: Restat et al., 2004). This suggests that each sensory cue associated with slope can gain associative strength and is potentially able to control behavior when dissociated. This multimodal redundancy is one of the reasons why slope information is uniquely salient.

A navigable, sloped surface is perceptually salient because movements with a vertical component are generally more effortful than horizontal movements. The cognitive salience of the vertical dimension is widespread in the animal kingdom, from bees (the symbolic use of the vertical axis in the waggle dance: Von Frisch, 1967) to humans (Carlson & Van Deman, 2008; Franklin & Tversky, 1990). In spatial learning there is evidence for a greater salience of a goal's vertical coordinate—compared to the horizontal ones—and for faster learning of a goal's location when the environment has a vertical component (slanted or vertical) compared to a flat environment (Grobéty & Schenk, 1992; Nardi & Bingman, 2009a; Restat et al., 2004).

Slopes are part of the topography of many natural environments, such as hills, dunes, and mountains. These terrain features are stable in time and not likely to be displaced, whereas other features of the environment can drastically change in the course of the day (different lighting between day and night) and of the seasons

(leafs change color and fall from trees, snow covers grass, rivers dry out in summer). As previously emphasized for geometric cues by Gallistel (1990), the permanent nature of terrain slope could be why it is an ecologically reliable source of information for navigating and locating a goal.

Finally, a higher salience of slope—a cue related to the vertical dimension and to gravity—can be explained by the ecological relevance verticality has for birds, as they routinely move in a three dimensional space. In particular, a geographical slant might be very salient for pigeons as they naturally feed on uneven ground and approach food by walking.

For all these reasons it can be assumed that, in the present study, slope was more salient than geometry. According to this, then slope's greater salience could counteract its lower predictive value, such that the goal's position relative to slope would capture more associative strength than geometry and guide behavior in the novel orientation. In this sense, it is possible that an associative model of spatial learning (e.g., Miller & Shettleworth, 2007) could account for the systematic error to the mirror image corner. Furthermore, salience is considered a parameter in the cue weighting mechanism also for an adaptive combination view (Newcombe & Huttenlocher, 2006). It is possible that slope and geometry actually are integrated in a unified representation, but the salience of slope is so great that geometry failed to control behavior even if it was a better predictor. If this is true, under some circumstances geometry should be able to guide goal searching on the slope. Future research could use a gentler inclination of the floor for testing, thus perhaps decreasing the salience of slope. If even in this condition animals do not rely on geometry, then a qualitative—rather than a quantitative—primacy for slope should be considered.

We conclude that slope information is a very salient spatial cue for pigeons, so salient that it can be one third as informative as geometry and still be the cue driving goal location behavior. This study suggests that spatial learning in the vertical dimension deserves more experimental attention, not only because it provides an animal with gravity-related sensory information, instead of only visual cues, but it also offers interesting—and surprising—insights into orientation mechanisms; animals, and birds in particular, do move in a three-dimensional, nonflat world.

We envision three lines of research to expand the present findings. First, as mentioned above, it should be examined if the current results can be replicated with different experimental parameters that could decrease the salience of slope (a gentler inclination) or increase the salience of geometry. Second, it would be interesting to test if a similar dominance of slope appears also with respect to visual feature cues—so far no study has investigated this relationship. Third, an interesting question to answer is whether the current results would similarly apply to other vertebrate groups, for which the vertical dimension is perhaps less ecologically relevant than in birds.

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