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# Use of Slope and Feature Cues in Pigeon ( *Columba livia*) Goal-Searching Behavior

Daniele Nardi, Roseanne J. Mauch, Diana B. Klimas, and Verner P. Bingman

Reorientation is the ability to ground oneself in the environment, using an allocentric frame of reference, after having lost the sense of orientation. Among a plethora of spatial cues that can guide navigation and reorientation in human and nonhuman animals, much of the research has focused on visual cues—primarily the geometric shape of the environment and visual features ( Cheng & Newcombe, 2005). One type of spatial information that stands apart from these is terrain slope. Vertically extended, uniform, navigable surfaces provide allocentric information that can be used like a compass to establish a directional frame of reference (e.g., uphill can be likened to north, downhill to south, and so forth; Nardi, Newcombe, & Shipley, 2011). Importantly, however, a sloped environment has unique characteristics for reorientation and navigation. First, locomotion is generally more effortful compared to flat environments, and the energetic expenditure required to counteract the force of gravity potentially renders this cue very salient. Second, a slope can be perceived by multimodal sensory inputs (kinesthetic, vestibular, and visual); the redundancy of sensory cues associated with slope makes using this cue a different experience compared to other spatial cues.

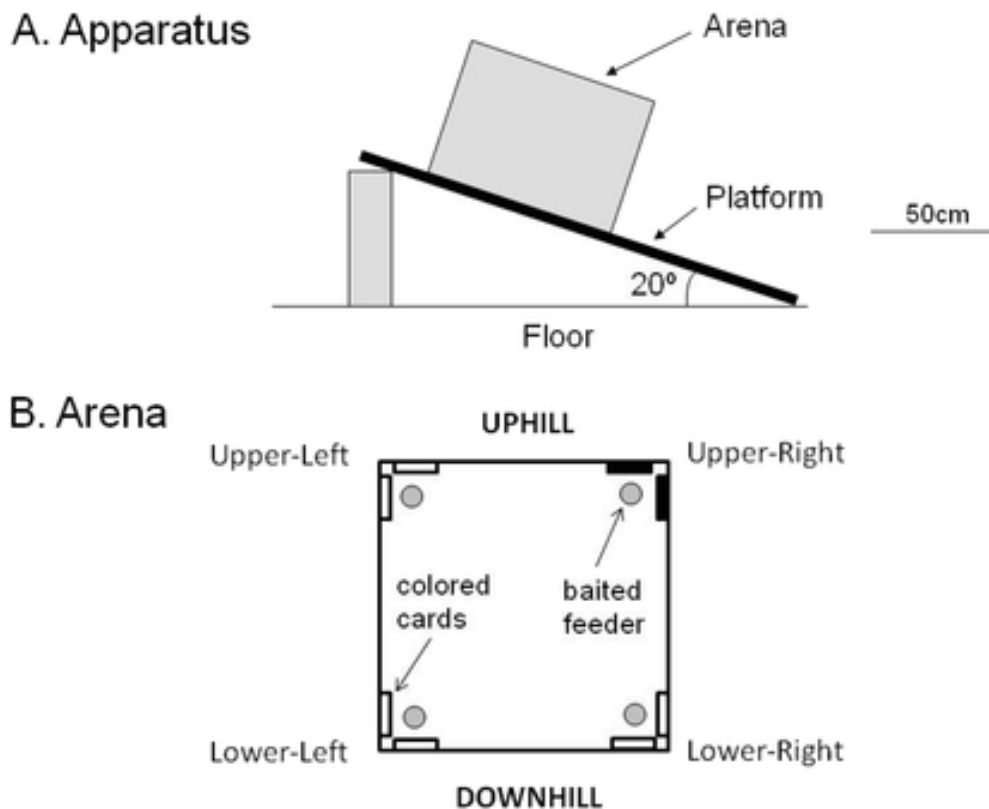
In one recent study, Nardi, Nitsch, and Bingman (2010) revealed the distinct properties of slope as a reorientation cue. Homing pigeons were trained to locate a reward in a fixed corner of an isosceles trapezoid arena; crucially, the arena was placed on a slope with multiple orientations. In these conditions, the shape of the arena determined consistently the reward, whereas the slope did not indicate in a predictable manner the position of the goal (in one orientation, the reward could have been uphill, and in another, it could have been downhill). Pigeons learned the task, and following probe tests surprisingly revealed that slope, despite being less informative, was actually driving search behavior. This result is reminiscent of that found in the groundbreaking study of Cheng in 1986, in which rats made systematic errors to the geometrically equivalent corners of a rectangular arena, showing that they were disregarding the more predictive cues (visual and olfactory feature cues), and instead were using the ambiguous geometry of the environment for reorientation. That study laid the foundation for the hypothesis of a geometric module—a unit of the brain dedicated to reorientation and selectively attuned to the geometry of the environment ( Cheng, 1986; Gallistel, 1990). Even though this hypothesis is now widely considered outdated (even by the same author who proposed it: see Cheng, 2008), and reorientation according to geometry has been recently shown to follow the general principles governing associative learning ( Rodriguez, Chamizo, & Mackintosh, 2011), this claim has been very influential in the field of reorientation in the past 25 years (for a review see Cheng & Newcombe, 2005; Twyman & Newcombe, 2010).

Similarly to the effect reported in Cheng's study (1986), in the study of Nardi et al. (2010), subjects were unresponsive to the best predictor (geometry in this case) and instead were using the ambiguous slope information to reorient. In summary, slope seems to be driving search behavior when its predictive value is equal to (Nardi & Bingman, 2009a, 2009b) or even lower (Nardi et al., 2010) than that of another available cue. In addition, a similar supremacy of vertical information in spatial tasks has recently been confirmed also in fish (Holbrook & Burt de Perera, 2011). It is therefore legitimate to wonder if there is a slope module for reorientation on vertically extended surfaces. According to Fodor's (1983) conceptualization of a module, and in line with claims of a geometric module (Cheng, 1986; Gallistel, 1990), a main assumption of a slope module for reorientation would be that slope gradient is a special property of space that guides reorientation irrespective of other task-relevant cues. Is this the case?

To answer this provocative question, we decided to carry out a goal location task, but instead of testing slope versus geometric cues, as in the previous studies, this time we examined slope versus feature cues. Pigeons were trained in a square arena and could locate the baited feeder using its position relative to the slope (e.g., upper-right corner) or its position relative to a distinctly colored pair of cards adjacent to the feeder (see Figure 1). An object marking the correct location acts as a beacon—a spatial cue that can be directly used to pin-point the goal—and is very salient (Chamizo, Manteiga, Rodrigo, & Mackintosh, 2006). If even when a beacon is available, behavior is strongly controlled by slope, then the case for a slope module governing reorientation in vertically extended environments would be more convincing; conversely, if pigeons now do not have a strong reliance on slope, the hypothesis of a slope module would be significantly weakened.

## **Method**

The experimental environment used was identical to that of Nardi and Bingman (2009a). It consisted of a square, wooden platform (183 × 183 cm, 10 cm thick) surrounded by circular curtains (see Figure 1). A square arena (112 × 112 cm, 61 cm high), with walls made of Styrofoam (4 cm thick), was placed on the platform. The test environment was illuminated by a 75 W light bulb attached to the ceiling above the center of the platform, next to a video camera (Philips LTC 350). Six experimentally naïve homing pigeons (*Columba livia*) were used as subjects.



**Figure 1.** (A) Schematic representation of the experimental environment viewed from the side. (B) Schematic representation of the arena viewed from above. The arena was placed on a 20° tilted platform, such that the baited feeder could be encoded based on its position relative to the slope (e.g., upper-right corner). The goal could also be identified by a pair of distinctly colored cards on the wall adjacent to the feeder. For half of the sample (  $n = 3$  ) the goal was in the upper-right corner (as represented in the figure); for the other half it was in the lower-left corner (  $n = 3$  ).

Training consisted of one session per day for 5 consecutive days; each session was composed of six reinforced trials. One side of the platform was placed on a wooden stage, such that the experimental environment was tilted with an inclination of 20° with respect to the floor (same inclination used in our previous studies; Figure 1). The elevated side of the platform changed from trial to trial, such that the slope gradient did not have a fixed azimuth relative to the room. A feeder (7.6 cm in diameter and 4.3 cm in height) was positioned in each of the four corners of the arena. Only one feeder (the goal) contained food covered by grit; the other three feeders were filled only with grit. For half of the birds, the goal feeder was placed in the upper-right corner (UR); for the other half it was placed in the lower-left corner (LL) (see Figure 1). Furthermore, two blue or yellow, laminated, square cards (15 cm  $\times$  2 each) were placed one on each side of a corner, just behind the feeder. The cards placed at the baited corner had a color different from the other three corners,

such that they could be used as a beacon to identify the goal. The distinct pair of cards were yellow for the pigeons trained to the LL corner (the other three pairs of cards were blue); conversely, the distinct pair of cards were blue for the pigeons trained to the UR corner. Pigeons can easily discriminate these two colors ( Strasser & Bingman, 1997). A bird was transported in a carrying cage inside the darkened experimental room and, before each trial, was slowly rotated on a swivel chair for 1 min (12 rpm) to prevent any use of inertial vector orientation; then it was placed inside the darkened arena, near the midpoint of one of the four sides. Once the light was turned on, the pigeon started searching for the goal. On each trial the pigeon started from a different side of the arena, in random order and counterbalanced across a session. This procedure was carried out to prevent birds from using response learning (locating the goal by always turning to the same side). 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. Between trials, pigeons were placed in a cage outside the experimental room; the approximate time between trials for each bird was 5–10 min.

After training, pigeons were taken through a testing phase. Testing consisted of one session per day for 7 consecutive days. Each session was composed of seven trials: five trials were reinforced and identical to training trials, and two trials were test trials and were not reinforced (all feeders filled with only grit). The unreinforced test trials ended once a pigeon pecked in one feeder. If a choice was not made in 5 min, the trial would be considered void; this occurred only for a total of six trials (out of all the 84 test trials). Test trials were administered on the third and sixth trial of a session. Three different types of test trials were carried out: Slope Test, Color Test, and Conflict Test. The test trial types were presented in random order, counterbalanced across subjects, with the constraint that the same test trial type could not be presented twice in the same session.

### **Slope Test**

The colored cards were removed from the arena, such that now the only spatial cue available was the slope. The purpose of this test was to assess if pigeons acquired a slope-based representation of the goal. This test type was carried out for a total of four trials per subject.

### **Color Test**

The arena now was placed horizontally on the floor, such that the only spatial cues available were the colored cards. The purpose of this test was to assess if pigeons acquired a feature-based representation of the goal. This test type was carried out for a total of four trials per subject.

## **Conflict Test**

The location of the distinct color cards was displaced with respect to training. The purpose of this test was to create a situation in which slope and feature cues dictated different correct locations and therefore to infer the preferred representational strategy used. If pigeons relied more heavily on slope information, we would expect choices to be mostly directed to the corner with the same position relative to the slope as during training (e.g., uphill on the right for the UR group; called “slope-correct” corner). Conversely, if pigeons relied more heavily on the color cards, we would expect them to search mostly at the corner with the (now displaced) distinct cards (“feature-correct” corner). For two trials, the distinct pair of cards were displaced horizontally relative to training; for two trials, they were displaced vertically, and for two trials, the distinct color cards were displaced diagonally. In sum, a total of six conflict trials were carried out per subject.

Means are always indicated  $\pm$  SEM.

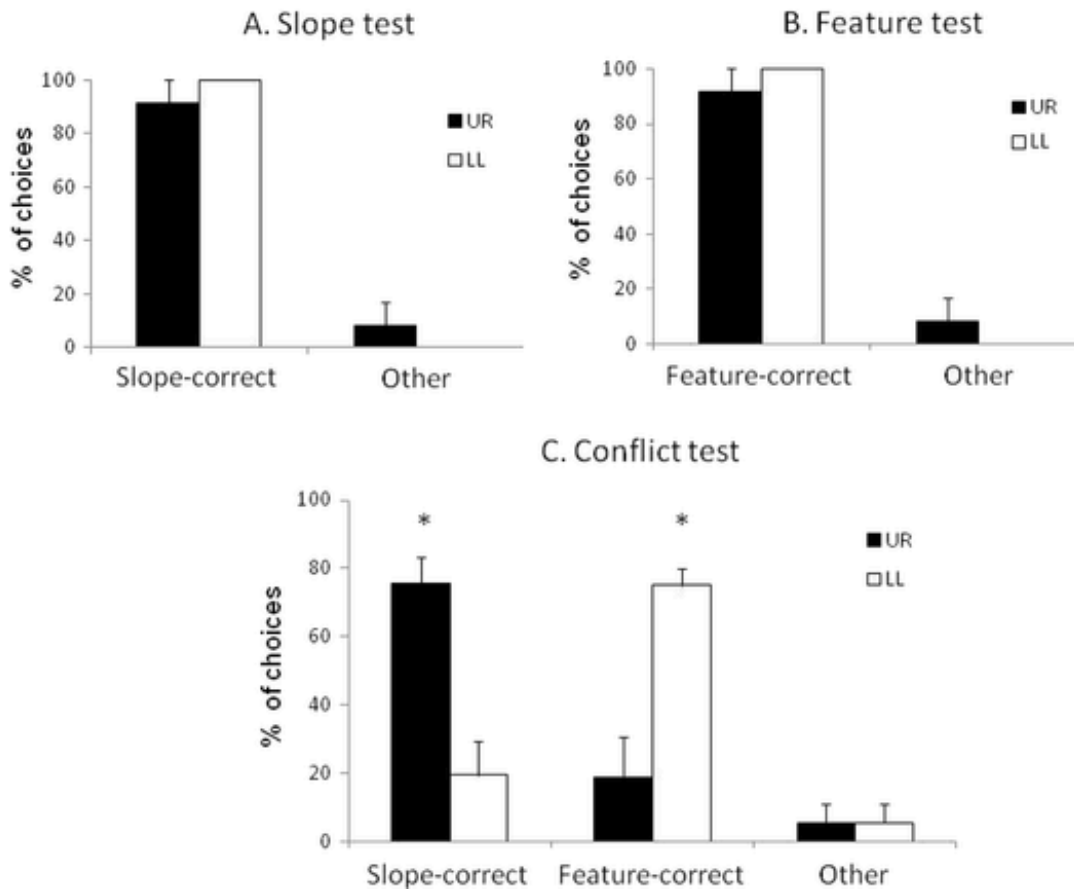
## **Results**

### **Training**

Considering the overall sample ( $n = 6$ ), the percentage of correct trials per session was significantly above chance (25% correct) starting from the first session,  $M = 53\% \pm 10$ ; one-sample  $t$  test,  $t(5) = 2.77$ ,  $p < .05$ , and then it increased monotonically throughout the sessions. In the last training session, the entire sample of pigeons performed at ceiling (six correct trials out of six). When breaking down the sample by training location, both the pigeons trained to the LL corner (LL group;  $n = 3$ ), and those trained to the UR corner (UR group;  $n = 3$ ) performed at chance in the first session only, LL: one-sample  $t$  test,  $t(2) = 4.25$ ,  $p > .05$ ; UR: one-sample  $t$  tests,  $t(2) = 3.21$ ,  $p > .05$ ; then they increased their performance monotonically throughout the sessions. The two groups performed differently only in the first training session, when the percentage of correct trials was significantly higher for the LL group ( $M = 72\% \pm 11$ ) than for the UR group,  $M = 33\% \pm 0$ ; Mann-Whitney,  $U = .0$ ,  $p < .05$ .

### **Slope Test**

When the feature cues were removed, pigeons as a group ( $n = 6$ ) were able to use the remaining cue (slope) as an orienting cue. They chose the corner in the trained location relative to the slope (“slope-correct” corner; e.g., uphill on the right for the UR group) almost at ceiling ( $M = 96\% \pm 4$ ). This was more than expected by chance (25% correct); one-sample  $t$  test,  $t(5) = 12.65$ ,  $p < .001$  (see Figure 2A). When breaking down the sample by training locations, there was no significant difference between the UR ( $n = 3$ ) and LL group ( $n = 3$ ) in performance, Mann-Whitney,  $U = 3.0$ ,  $p = .32$ .



**Figure 2.** Mean percentage of choices ( $\pm$ SEM) to each corner in the test trials. Black bars represent the group of pigeons trained to the upper-right corner (UR group;  $n = 3$ ), whereas white bars represent the group of pigeons trained to the lower-left corner (LL group;  $n = 3$ ). (A) In the Slope Test, only the slope cue was available (feature cues were removed). Overall, pigeons chose overwhelmingly the corner that matched the goal position relative to the slope gradient (“slope-correct” corner; e.g., uphill on the right for the UR group). There were no significant differences between the UR and the LL group. (B) In the Feature Test, only the feature cues were available (the arena was now placed horizontally). Overall, pigeons chose overwhelmingly the corner with the trained pair of cards (“feature-correct” corner). There were no significant differences between the UR and the LL group. (C) In the Conflict Test, slope and feature cues dictated two different correct corners. When not taking into account training location ( $n = 6$ ), choices were divided approximately equally to the slope-correct (48%) and to the feature-correct corner (47%). When the searches were broken down by training locations, the slope-correct corner was chosen significantly more by pigeons trained to the UR corner ( $n = 3$ ), whereas the feature-correct corner was chosen significantly more by pigeons trained to the LL corner ( $n = 3$ ).

### Feature Test

Similarly to the Slope Test, when the slope cue was removed by placing the arena on a flat surface, pigeons as a group ( $n = 6$ ) were able to use the remaining feature cues to reorient. They chose the feeder at the corner with the trained colored cards (“feature-correct” corner) almost at ceiling ( $M = 96\% \pm 4$ ); this choice preference was more than expected by chance (25% correct); one-sample  $t$  test,  $t(5) = 12.65$ ,  $p < .001$  (see Figure 2B). When breaking down the sample by training locations, there was no significant difference between the UR ( $n = 3$ ) and LL group ( $n = 3$ ) in performance, Mann–Whitney,  $U = 3.0$ ,  $p = .32$ .

### **Conflict Test**

When setting the two cues in conflict, choices were coded as slope-correct if they were directed to the trained corner according to the slope (e.g., uphill on the right for the UR group) or as feature-correct if directed to the trained corner according to the color cards. Considering pigeons as a group ( $n = 6$ ), overall searches were almost entirely ( $M = 94\% \pm 4$ ) directed at a location predicted by either of the spatial cues and were divided approximately equally between the slope-correct ( $M = 48\% \pm 14$ ) and the feature-correct corner,  $M = 47\% \pm 14$ ; one-sample  $t$  test,  $t(5) = .10$ ,  $p > .05$ . This performance was compared to that of Nardi and Bingman (2009a), in which pigeons—in an analogous conflict test—clearly chose the slope-correct corner over another potentially correct corner (geometric-correct in that case). Using Bayesian inference testing (Dienes, 2011; Gallistel, 2009; Rouder, Speckman, Sun, & Morey, 2009), we calculated the Bayes factor for the null hypothesis (that the slope-correct and feature-correct are chosen equally) versus the alternative hypothesis (that one corner is chosen more than the other). The alternative hypothesis was modeled on pigeons' behavior in Nardi and Bingman's study (2009a, Experiment 1), to have a prior mean and standard deviation. The analysis revealed a Bayes factor of 12.5 (Dienes, 2011) in favor of the null hypothesis, with weight = 1.10 (Gallistel, 2009); this magnitude is considered as providing “strong” evidence in favor of the null hypothesis (Jeffreys, 1961), which supports the conclusion that pigeons in the present experiment, as a group, chose the slope-correct and feature-correct corners equally.

However, when searches were broken down by training locations, a different pattern of choices emerged (see Figure 2C). The slope-correct corner was chosen significantly more by pigeons trained to the UR corner ( $n = 3$ ;  $M = 76\% \pm 8$ ) than by those trained to the LL corner ( $n = 3$ ;  $M = 19\% \pm 10$ ; Mann–Whitney,  $U = 0.0$ ,  $p < .05$ ), whereas the feature-correct corner was chosen significantly more by pigeons trained to the LL corner ( $M = 75\% \pm 5$ ) compared to those trained to the UR corner ( $M = 19\% \pm 12$ ; Mann–Whitney,  $U = 0.0$ ,  $p < .05$ ). Accordingly, the slope-correct corner was the only one chosen above chance (25% correct) by the UR group, one-sample  $t$  test,  $t(2) = 4.38$ ,  $p < .05$ , whereas the feature-correct corner was the only one chosen above chance by the LL group, one-sample  $t$  test,  $t(2) = 4.62$ ,  $p < .05$ . To further verify statistically this finding of unequal choice pattern between UR and LL groups, we performed an additional analysis using Bayesian inference testing (Dienes, 2011; Gallistel, 2009; Rouder et al., 2009). We calculated the Bayes factor for



the null hypothesis (that the slope-correct and the feature-correct corner are chosen equally) versus the alternative hypothesis (that one corner is chosen more than the other), for both the UR and LL groups separately. Again, the alternative hypothesis was modeled using Nardi and Bingman's study (2009a, Experiment 1). The analysis revealed a Bayes factor of 259.3 (Dienes, 2011) in favor of the alternative hypothesis for both groups, with weight = 2.41 (Gallistel, 2009); this magnitude is considered as providing “decisive” evidence in favor of the alternative hypothesis (Jeffreys, 1961). Therefore, the Bayesian analysis agrees with other tests in supporting the preference of each group for a different corner.

To ascertain that this training-location effect was not due to an inherent preference for the color yellow (at the LL corner) over blue (at the UR corner), we carried out a nondiscrimination, preference task. Four experimentally naïve pigeons were tested for two sessions of five trials each (a total of 10 trials per pigeon). One feeder was placed at the midpoint of the uphill side of the arena (next to the wall), and another feeder was placed at the midpoint of the downhill side (next to the wall). Both feeders were always baited. Adjacent to each feeder, on the wall of the arena, there was a colored card: yellow for one feeder and blue for the other feeder. These two colors were swapped pseudorandomly from trial to trial and counterbalanced between pigeons (in any one trial, for two birds the yellow card was uphill and for the other two birds it was downhill). Subjects started each trial from the center of the arena, with facing orientation pseudorandomized and counterbalanced. Pigeons ( $n = 4$ ) chose the feeder adjacent to the yellow card for an average of 4.0 trials (SEM = 0.4), and the feeder adjacent to the blue card for an average of 6.0 trials (SEM = 0.4). This choice distribution does not significantly deviate from an equal distribution between the two color cards, one-sample  $t$  test,  $t(3) = 2.45$ ,  $p > .05$ , and, if anything, it shows a slight, nonsignificant preference trend toward the color blue. This result, together with the fact that in the Feature Test, the two groups did not show any different preference for the feature-correct location, suggests that the pattern of behavior in the Conflict Test is not due to a different associative strength of color yellow and color blue.

## **Discussion**

The first main finding of this experiment is that, when not taking into account the training locations, pigeons solving a reorientation task with slope and feature cues do not preferentially rely on slope. On the contrary, when the two cues are set in conflict, they choose approximately equally the slope-correct and feature-correct location. In a series of studies using the same animal model, same inclination, similar apparatus, and analogous procedures (providing slope plus geometric cues; Nardi & Bingman, 2009a, 2009b; Nardi et al., 2010), slope was always shown to have overwhelming control over searching behavior. Such a dependence on one type of information for solving a task, even when that information is not the most effective, is a key premise for a module in Fodor's sense (1983). This is particularly interesting because, in the field of reorientation, an analogous strong reliance on a cue—the shape of the environment—led to the hypothesis of the existence of

another module: the geometric module ( Cheng, 1986; Gallistel, 1990; for recent views see: Cheng, 2008; Rodriguez et al., 2011; Twyman & Newcombe, 2010). In the present study, however, for the first time slope failed to dominate. This finding substantially weakens the modularity hypothesis: if slope is the cue that governs reorientation in slanted environments, then pigeons should use it in all circumstances—including when feature cues are available. Slope might still be modular to some degree (e.g., relatively to the integration with other cues), but this result strips modularity of its most notable attribute: that it guides behavior irrespective of other information. A more parsimonious and likely explanation for this set of results is based on the view that all spatial cues compete for associative strength in a reorientation task ( Miller & Shettleworth, 2007) and that cue salience, among other parameters, is a main factor in the weighting mechanism ( Newcombe & Huttenlocher, 2006). Slope has the characteristics of a very salient cue because of its distinct multimodal nature and of the effort involved with moving in the vertical dimension. This high salience can explain the greater weighting of slope when equally ( Nardi & Bingman, 2009a, 2009b) or even less ( Nardi et al., 2010) informative than geometry. But why would slope be more salient than geometry (previous studies) and not more salient than feature cues (present study)? The simplest possibility is related to the specific type of feature cues used: a distinctly colored pair of cards adjacent to the baited feeder. To solve the task, pigeons could have simply used a beaconing strategy, following the color that marked the reward. Because of its direct association to the goal, a beacon is a very salient spatial cue ( Chamizo et al., 2006). Therefore, slope might have dominated when tested with geometry, but when a beacon is available, the salience of the two cues could be much more comparable. This result is different from the one observed with fish in a 3-D search task ( Holbrook & Burt de Perera, 2011). In that study, the vertical information of the environment (a column of water) dominated over visual landmarks present at some distance from the water tank. However, it is possible that, if visual feature cues marking directly the goal location were used (as opposed to distant landmarks), reliance on vertical information would be decreased and balanced with feature cues.

The second major finding of this experiment is that, for the first time in our series of studies on slope, an effect of training location was found. Pigeons behaved differently in the conflict trials, based on whether the baited feeder was uphill or downhill. If the goal was uphill, subjects chose prevalently the slope-correct corner; if it was downhill, they chose prevalently the feature-correct corner. One plausible factor responsible for such a modulation of cue weighting is effort. The arena's side is about four pigeon-body lengths. Having to cover this order of distance for a total of 30 trials (i.e., training) can lead to different energetic expenditure based on whether the subject has to walk uphill or downhill. Although pigeons walk comfortably on a 20° slant, when they walk uphill they are actively “climbing,” and contrasting the force of gravity causes them to walk with a slower gait. Instead, when walking downhill, pigeons move quicker and with faster gait, because their movement is eased by the pull of gravity. Indeed, starting from the opposite side of the arena, latency to reach an uphill corner is on average longer than that for a

downhill corner (anecdotal observation). This confirms the intuitive notion that, on a moderate slant, walking uphill is a more effortful process than walking downhill. The differential energetic expenditure may not be crucial in a single trial, but when accumulating six trials over a session and repeating this for 5 days, there is a substantially greater cumulative energetic cost associated with reaching an uphill goal location compared to a downhill one. It is possible that this increased effort augmented the associative strength of slope, whereas with a downhill goal, such an enhancement did not occur. One might wonder why such an effect of training location did not emerge in previous reorientation studies on slope. As mentioned above, it is probably because the salience of slope is higher than that of geometry, but comparable to that of beacon feature, hitting a sweet spot for cue weighting that is sensitive to the effect of effort. There is growing evidence in support of how embodied constraints scale perception and how effort seems to play a key role in this (Gibson, 1979; Witt, Proffitt, & Epstein, 2010). For example, effort required for walking influences distance estimation (Proffitt, Stefanucci, Banton, & Epstein, 2003; Rieser, Pick, Ashmead, & Garing, 1995), and the physiological potential of an observer (including level of fatigue) affects the judgments of hill slant (Bhalla & Proffitt, 1999; but see Shaffer & Flint, 2011). It has also been shown that effort required to solve a foraging task alters the pattern of search behavior (Gilchrist, North, & Hood, 2001). To the best of our knowledge, the present experiment offers the first evidence identifying a role for effort in modulating the cue-weighting mechanism in a goal location task. This is probably due to the specific nature of the spatial cue used—slope, a surface property associated with the energetic cost of counteracting the force of gravity. When more effort is required to solve the task, slope—the cause of the increased energetic cost—becomes more salient and guides behavior. Future studies will have to examine more in depth this training-location effect on cue weighting, to ascertain the role of effort and whether there is a contribution of other factors not related to physiological potential.

In conclusion, the results of the present experiment, combined with our previous one (Nardi et al. 2010), allow us to infer that, when animals navigate in vertical spaces, features may be more important in guiding behavior than geometry. Our findings suggest more importantly that the types of cues animals use to guide navigation in three dimensions may differ, depending on whether they are going up or down. This possibility finds support also from a recent study on rats (Jovalekic, Hayman, Becares, et al., 2011). In a goal location task using a 3-D lattice maze, rats do not take a straight path (shortest path) toward an upward goal, but they do use a straight path toward a downward goal. Furthermore, when the direct path is blocked by a barrier (detour task), rats first cover the horizontal leg of the journey and only at the end they tend to do vertical movements. This sequence is prevailing only when reaching an upward goal (for a downward goal, the opposite order is equally frequent), and the authors proposed that this strategy may be due to temporal discounting of effort (deferring the more effortful leg of a journey: the upward leg). Relating this to pigeon's ecology—and birds' in general—the 3-D quality of flight may influence navigational cue use in unexpected ways; this would be worth of study.

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