

Cue Salience Influences the Use of Height Cues in Reorientation in Pigeons (*Columba livia*)

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Although orienting ability has been examined with numerous types of cues, most research has focused only on cues from the horizontal plane. The current study investigated pigeons' use of wall height, a vertical cue, in an open-field task and compared it with their use of horizontal cues. Pigeons were trained to locate food in 2 diagonal corners of a rectangular enclosure with 2 opposite high walls as height cues. Before each trial, pigeons were rotated to disorient them. In training, pigeons could use either the horizontal cues from the rectangular enclosure or the height information from the walls to locate the food. In testing, the apparatus was modified to provide (a) horizontal cues only, (b) height cues only, and (c) both height and horizontal cues in conflict. In Experiment 1 the lower and high walls, respectively, were 40 and 80 cm, whereas in Experiment 2 they were made more perceptually salient by shortening them to 20 and 40 cm. Pigeons accurately located the goal corners with horizontal cues alone in both experiments, but they searched accurately with height cues alone only in Experiment 2. When the height cues conflicted with horizontal cues, pigeons preferred the horizontal cues over the height cues in Experiment 1 but not in Experiment 2, suggesting that perceptual salience influences the relative weighting of cues.

Keywords: adaptive combination theory, geometric module, height, pigeons, reorientation

Successful navigation is a complicated task that often starts with orientation in the environment (Ambosta, Reichert, & Kelly, 2013; Lubyk & Spetch, 2012). For an organism to reorient itself, it must recognize the available cues and use these to determine its heading. In recent years, many studies have shown that the geometric shape of a navigable environment with continuous surfaces is a salient orienting cue for a variety of species (for review, see Cheng, Huttenlocher, & Newcombe, 2013; Cheng & Newcombe, 2005). In the pioneering study of reorientation by geometry, Cheng found that rats used the geometric shape of a rectangular test arena to reorient whereas they sometimes ignored the feature information such as distinct visual patterns or odors (Cheng, 1986). This suggested a strong preference for the geometric information over features. Following studies found similar results in human children aged 1.5 to 2 years (Hermer & Spelke, 1996, 1994). To explain such blind reliance on geometry, the geometric module account was proposed, which suggests an innate and encapsulated cognitive module that is specialized in processing geometric information

in reorientation (Cheng, 1986; Hermer & Spelke, 1994, 1996). In the original study by Cheng (1986), the geometric information referred to the horizontal shape of the enclosure (i.e., rectangle) which has two components: horizontal distance between corners and right angle of the corners. Rearing studies in which animals were reared in a cylindrical environment have shown that some animals still can use the geometric shape of environment to reorient even without experience with these horizontal cues (Brown, Spetch, & Hurd, 2007; Chiandetti & Vallortigara, 2008). These results suggest that the ability to use geometry for reorientation may be innate, at least for some species.

However, other results have provided evidence that is inconsistent with the geometric module theory in that the geometric shape of the environment does not show absolute priority to feature cues (for review, see Twyman, Nardi, & Newcombe, 2013; Twyman & Newcombe, 2010). To reconcile these findings, an adaptive combination theory was proposed (Newcombe & Huttenlocher, 2006) which suggests that cue use is determined by the cue's salience, reliability, familiarity, and stability (see also Twyman, Nardi, et al., 2013). Therefore, the type of or fixed absolute properties of a cue does not solely determine whether it is given more consideration than other competing sources of information. If a cue is more salient than the geometric shape of the environment, it is more likely to be given precedence in the reorientation process. Some studies have shown that the rearing or initial training experience may be a moderating variable in cue salience (Brown et al., 2007; Kelly, Spetch, & Heth, 1998; Ratliff & Newcombe, 2008; Twyman, Newcombe, & Gould, 2013). These findings seem to violate the geometric module account and are consistent with adaptive combination theory.

Along with the ongoing debate between the two theories about the relative dominance of geometry in reorientation, different types

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and properties of cues have been examined (for review, see Cheng, Huttenlocher, & Newcombe, 2013; Cheng & Newcombe, 2005). However, most of the research has focused on horizontal cues (e.g., horizontal distance between two corners in a rectangular enclosure; angular amplitude of the horizontal corners of the enclosure). Given that mobile organisms can interact with three-dimensional environments in navigation, researchers have started to investigate cues in the third dimension—vertical cues—in reorientation. Vertical cues are derived from metric differences in the vertical plane and can have different forms. Some vertical features of the terrain such as a mountain's height or the slope of the ground, may provide reliable, stable information to guide three-dimensional navigation (Du, Spetch, & Mou, in press; Hu, Zhang, Wu, & Shao, 2015). A sloped plane (which provides both horizontal and vertical cues) provides orienting information through visual, proprioceptive and kinesthetic modalities, whereas the height of a mountain is typically perceived visually (Hu et al., 2015; Nardi, Newcombe, & Shipley, 2011). Although slope and height are two different types of cues, both contain a vertical component, and therefore both can be classified as providing vertical cues.

A few studies have examined the use of slope in reorientation. The ability to use slope alone to orient has now been shown in human adults, 8-to 10-year-old children, pigeons, and rats (Holmes, Nardi, Newcombe, & Weisberg, 2015; Miniaci, Scotto, & Bures, 1999; Nardi & Bingman, 2009; Nardi et al., 2011; Nardi, Nitsch, & Bingman, 2010). Recently, Hu et al. (2015) examined whether human children could use wall height to reorient. They found that both 3- and 4-year-olds could use horizontal geometry (i.e., the rectangular shape of the testing room) alone to reorient. However, only the 4-year-olds could use height cues alone to reorient. This finding suggests that height may be subordinate to the distance information provided by horizontal geometry. Recently, Du, Spetch, and Mou (in press) tested the use of height cues by human adults in virtual environments. Participants successfully used both the horizontal cues and the height alone to reorient. When the two types of cues were put in conflict, participants did not show preference for horizontal cues in either environment, although some evidence suggested that cue use was influenced by familiarity with the cues.

The studies by Hu et al. (2015) and by Du et al. (in press) indicate that older children and human adults can use height cues to reorient, but the generality of these findings to other animals remains to be tested. It is difficult to speculate on whether the use of height cues would be enhanced in a species, such as pigeons, for which navigation includes a substantial vertical component. On one hand, some evidence suggests that vertical cues are very important for species that navigate in a three-dimensional volumetric space. Hummingbirds, for example, can distinguish flowers by their relative height from the ground (Henderson, Hurly, & Healy, 2001, 2006), and fish have been found to give priority to vertical cues over horizontal cues in a navigation task (Holbrook & Burt de Perera, 2009). Rats have also been found to give priority to the vertical dimension of space in relocating a goal within a three-dimensional maze (Grobéty & Schenk, 1992; see also Flores-Abreu, Hurly, Ainge, & Healy, 2014). On the other hand, neuroscience research examining place cell and grid cell firing patterns in rats suggested that horizontal space is coded more precisely than vertical space (Hayman, Verriotes, Jovalekic, Fenton, & Jeffery,

2011). For pigeons, it is not clear that vertical cues would be particularly salient from the height at which they fly during navigation. Moreover, pigeons typically forage for food while walking on the ground, and research has suggested that pigeons are good at detecting the relative distance between walls in a rectangular enclosure (Kelly et al., 1998). Therefore, the extent to which pigeons would attend to visual height cues to get their bearings while foraging for food on a horizontal surface is unclear.

In the present study, we tested pigeons in an open-field reorientation task with vertical height cues. Similar to the design used for humans in Du et al. (in press), pigeons were trained in a rectangular enclosure with both horizontal cues (the rectangular shape) and vertical height cues (two opposite high walls) to learn two locations (two diagonal corners) that contained food. They were then tested in different enclosures which provided (a) only horizontal cues, (b) only height cues, or (c) both horizontal and height cues but the cues were in conflict (see Figure 1). We hypothesized that pigeons would encode horizontal cues and thus succeed in the horizontal only condition. But for the vertical height only and the conflict condition, we hypothesized that pigeons' might be more likely to use height cues only if the differences in

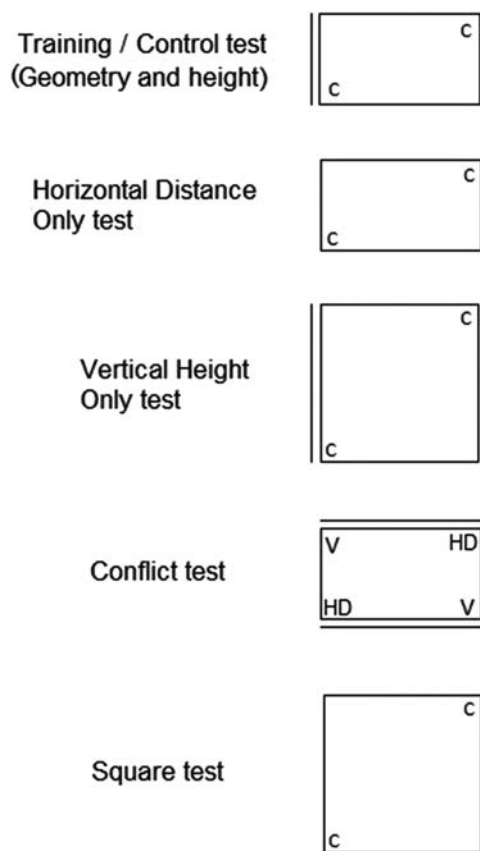


Figure 1. Top view schematic of the apparatuses. The double line indicates a high wall, and the single line indicates a lower wall. The letter C indicates a correct corner. In Conflict test, the letters HD indicate a corner that is correct according to horizontal distance and the letter V indicates a corner that is correct according to the vertical height cues. For simplicity, the correct corners are illustrated for the case in which the corners on the left to a short wall were correct.

height were visually salient from the perspective of foraging on the ground. In Experiment 1, all the walls were quite high so that the differences in wall height could be seen by looking up but would not be very salient from ground level. In Experiment 2, the wall heights were all shorter so that the difference in heights would be more noticeable from a ground level perspective.

Experiment 1

Method

Subjects. Seven adult pigeons (*Columba livia*) participated in Experiment 1. For the duration of the experiment, the birds were maintained at 85% of their free-feeding body weight and given free access to grit and water. Mazuri pellet food was provided as reinforcement during the experiment, in addition to receiving supplemental feedings following daily sessions to maintain body weight. The pigeons were housed in group cages (6–10 individuals) on a 12-hour light cycle with onset at 6 a.m. One bird (Bird 135) was excluded from data analysis because of its failure to maintain an accuracy criterion (80% or higher accuracy for 3 consecutive sessions) on training trials during the testing phase. Of the remaining six birds, one (Bird 44) had no prior open-field experience, two (Birds 46 and 47) had experience in open-field choice tasks that had no spatial learning component, and three (Birds 2, 85 and 943) had varied experimental histories including spatial reorientation tasks four years prior to this experiment. None had received any training that included use of vertical cues.

Apparatus. Five distinct apparatuses were used in the experiment (see Figure 1). Each one was constructed using uniformly white panels of Sintra board, held together by Velcro. The Training/Control apparatus was a 1.33 m $\times$ 0.67 m rectangle and the two 0.67 m walls were the high walls. The high walls were twice as high (0.8 m) as the shorter walls (0.4 m). The Horizontal Distance Only test apparatus maintained the same rectangular shape but all walls were 0.4 m high. The Vertical Height Only test apparatus was square shaped (1.33 m $\times$ 1.33 m) with walls maintaining different heights (i.e., two opposite walls were at 0.8 m high and the other two were at 0.4 m high). The Conflict test apparatus maintained the same shape as the training apparatus but with the high walls moved to the two long walls. Finally, the square test apparatus was a square arena with equal wall height of 0.4 m.

The apparatuses were enclosed in a square area, roughly 2 m $\times$ 2 m, draped with brown uniform fabric. A video camera was mounted above the area to observe the pigeon in the apparatus. The floor of the area was covered with approximately 4 cm of Aspen chip bedding. Four blue feeders (approximately 12 cm in diameter and 2 cm in height) were placed in each corner of the apparatus. Each feeder had two hollow spaces as food wells divided by a handle such that the food in the near food well of a feeder was visible to the pigeon from the center of the apparatus and food in the far well could not be seen unless the pigeon was standing over top of the feeder (see Figure 2).

General procedure. Before the current experiment, the birds were introduced to the blue feeders in individual cages. Once pigeons were familiar with the feeders, trials began in the apparatus. In each session, a pigeon was taken from the group cage, weighed, and carried to the testing area in a plastic carrying jug.

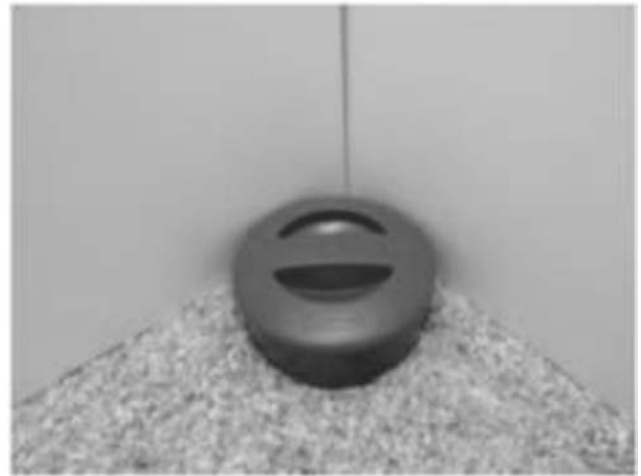


Figure 2. Blue feeders placed in each corner of the apparatus. The food in the near well was visible from a distance, whereas food in the far well was not. See the online article for the color version of this figure.

Before the first trial in each session and during each intertrial interval, with the room darkened, the pigeon was rotated in the jug at 30 rpm for 30 seconds. The pigeon was then placed in the center of a wall (randomized each trial) facing the center of the apparatus. Then the light was turned on to begin the trial. After completion, the room was again darkened to signal the end of the trial. The orientation of the apparatus within the testing area was rotated 90° clockwise every five trials. After all trials were completed for the day (one session), the pigeon was again weighed, fed, and taken back to the group cage. White noise was played during the experiment in the testing room to mask outside noises. Sessions were run five days per week at approximately the same time. Each session lasted for a maximum of 1 h.

Training procedure.

Phase 1. The training apparatus (see Figure 1) was used during all training phases and provided both horizontal cues and vertical height information that could be used to locate the two diagonal goal corners (counterbalanced across subjects). Feeders were placed in all corners, but only the two goal corners contained food: five food pellets were placed in both the near and far food wells of both goal feeders. Pigeons explored the apparatus until all pellets were eaten. Five trials were completed per session. This phase continued until all food was eaten in less than one minute for each trial in a single session.

Phase 2. Each of the two goal corners contained four food pellets, which were placed in the far food well of the feeders. The other two corners did not contain food. Pigeons could explore the area until all pellets were eaten. Ten trials were completed per day. This phase continued until the bird selected (by pecking) a goal corner with its first selection in 8 of 10 trials in one day. Phase 2 was run for at least three sessions, with the last two consecutive sessions meeting the criterion.

Phase 3. This phase continued exactly as Phase 2 except that four randomly selected trials out of 10 contained no food pellets. These were nonreinforcement training trials, with the remaining six being training trials as Phase 2. The purpose of the nonreinforcement trials was to adapt the pigeons to not always getting

food in preparation for testing. The first trial in each session was always a training trial and there was at least one training trial between each nonreinforcement trial. During the four nonreinforcement trials, the bird could explore the apparatus until two selections were made. Phase 3 was run for at least three sessions, with the last two consecutive sessions meeting the 80% correct criterion. Because of experimenter error, Bird 2 was only trained in Phase 3 for two sessions, but both sessions met the 80% correct criterion.

Test procedure.

Phase 4. This phase continued exactly as Phase 3 except that the nonreinforcement trials were replaced with test trials (with the remaining six being training trials in the training apparatus). One test trial remained a nonreinforcement training trial (Control test), and the other three used manipulated apparatuses (Horizontal Distance Only, Vertical Height Only, and Conflict; see Figure 1). The order of testing apparatus presentation was randomized. Between trials, the appropriate apparatus was assembled in the testing area. Training trials continued to be reinforced with food, but no food pellets were provided on any of the control or other test trials. Phase 4 continued for 10 sessions.

Phase 5. This phase continued exactly as Phase 4 except one test trial remained a nonreinforcement training trial (Control test), whereas the three other test trials used the square control apparatus (Square test). The Square test removed all orientation cues from the apparatus to check whether the pigeons' choice was influenced by any external cues. The order of testing apparatus presentation was randomized. Phase 5 continued for three sessions.

Data coding. Choice was operationalized as the pigeons approaching the feeder close enough that any part of the head passed above the feeder as seen from the overhead camera. The first two corner selections were recorded for individual bird for each trial. For the training trials, Control test, Horizontal Distance Only test, and Vertical Height Only test, the selections were scored as correct for the goal corner or the rotationally identical corner and as incorrect for either of the other two corners. Because there were no absolute correct corners in the Conflict tests, the choices in Conflict tests were coded in terms of the correct corners according to horizontal distance cues (HD corners). The choices in the Square test in Phase 5 were coded separately for the first and second half of the session (i.e., before and after the rotation of the apparatus). Choices were scored as correct if they were to the same corners in physical space as the correct corners on reinforced trials during that half of the session. The experimenter recorded the data after each trial on a score sheet. A correct choice was coded as 1 and an incorrect choice as 0. The recorded videos for each trial were then reviewed by another person to ensure accuracy of coding.

Results

All birds completed Training Phase 3 with accuracy higher than or equal to 0.8. However, Bird 135 did not maintain the required accuracy criterion during training trials of Phase 4 and hence its data were not included in the data analysis.

The proportion of first choices that were to correct corners was determined for each pigeon for each type of test and for the training (reinforced) trials in Phases 4 and 5. Independent *t* tests showed that the location of goal corners (long wall on left or right) had no influence on the choice proportions in each test (all *ps* >

.064). Figure 3 shows the average correct proportions for each test in Phase 4.

For training trials and each type of test, the choice proportions were compared with chance level (i.e., 0.5) by one-sample *t* test. Bonferroni's correction for multiple *t* tests was used if applicable (corrected $\alpha = .05/\text{number of } t \text{ tests}$).

In Phase 4, accuracy scores in training trials, Control tests, and Horizontal Distance Only tests were all significantly higher than chance level (all *ps* < .005 < corrected α , Cohen's *ds* > 2.96), indicating successful use of horizontal cues alone or horizontal and height cues together in choosing one of the two goal corners with their first choice. There was no significant difference between the accuracy in training trials ($M = 0.91$, $SD = 0.08$) and Control test ($M = 0.85$, $SD = 0.12$; $t(5) = 2.33$, $p = .068$, Cohen's $d = 1.36$), indicating that during the testing phase, the pigeons maintained accurate choice in the absence of food. Accuracy in the Vertical Height Only test was not different from chance level ($M = 0.63$, $SD = 0.19$; $t(5) = 1.75$, $p = .140$, Cohen's $d = 1.01$), indicating that the pigeons did not use height cues alone to successfully reorient.

In the Conflict test, the pigeons appeared to weigh horizontal cues more heavily than the vertical cues in that they selected one of the HD corners significantly more often than expected by chance ($M = 0.73$, $SD = 0.21$; $t(5) = 2.77$, $p = .040$, Cohen's $d = 1.60$). At the individual level, one of the six birds (Bird 47) chose HD corners less often than expected by chance, suggesting that the horizontal cues were not preferred by this bird. The other five birds each chose the HD corners more often than would be expected by chance.

In Phase 5, the birds again performed significantly above chance level on the training trials ($M = 0.86$, $SD = 0.11$; $t(5) = 8.28$, $p < .001$, Cohen's $d = 4.78$). Although accuracy was not significantly different from chance on the nonreinforcement Control test ($M = 0.72$, $SD = 0.25$; $t(5) = 2.17$, $p = .082$, Cohen's $d = 1.25$), there was no significant difference between the accuracy in the training

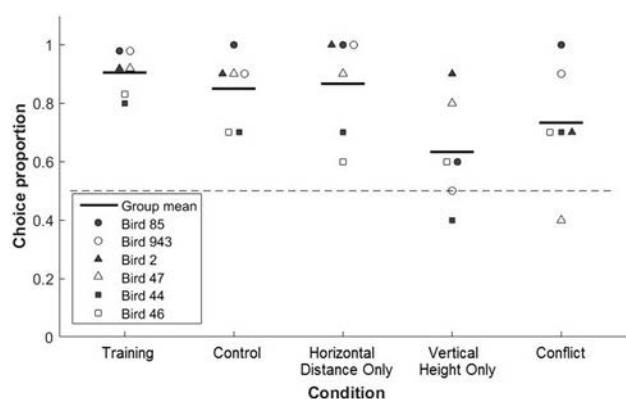


Figure 3. Choice proportions for individual birds and group means in training trials and each type of test in Testing Phase 4 in Experiment 1. Each dot represents an individual bird. For conflict tests, the choices were coded in terms of correct corners according to horizontal distance. The choice proportions in training trials, Control tests, Horizontal Distance Only, and Vertical Height Only tests show accuracy based on choices at correct corners. The dashed line indicates chance level (0.5). See the online article for the color version of this figure.

trials and the Control test, $t(5) = 1.89$, $p = .118$, Cohen's $d = 1.09$. In the Square test, the pigeons' choice proportions for corresponding correct corners on training trials were not above chance and in fact were slightly below chance (before rotation: $M = 0.31$, $SD = 0.19$; after rotation: $M = 0.38$, $SD = 0.27$), although the difference from chance was not significant in either case (both p s $> .051$ > corrected α , Cohen's d s < 1.47), indicating that external cues did not significantly bias pigeons' choice during the experiment.

Discussion

In Experiment 1, we found that pigeons learned to use horizontal cues to reorient successfully, which is consistent with previous findings (Kelly et al., 1998). However, the accuracy in the Vertical Height Only test indicated that the pigeons failed to learn the height cues. Furthermore, in the Conflict test, the horizontal cues were preferred by most of the birds, which indicates a heavier

weighting of horizontal cues over height cues. The results in Square test indicate that such findings were not caused by external influences.

Why did pigeons not encode the height cues to reorient? One possibility is that the height cues were not perceptually very salient from the pigeons' perspective. To examine this possibility, we simulated the experimental scene from a pigeon's view using the software SketchUp (Version 14.1.1282), where the height of the pigeon was set as 25 cm, a typical height for most of the subjects. As shown in Figure 4A, when a pigeon was standing at the center of the training apparatus and looking straight ahead at one corner, the height difference between walls is not very salient. We speculated that if the walls were lower, then the pigeons would more easily perceive the height difference without looking up, and thus the pigeons would be more likely to encode and use the height cues in reorientation. Figure 4B shows the view of an arena that maintains the same length and width but with all walls half as high

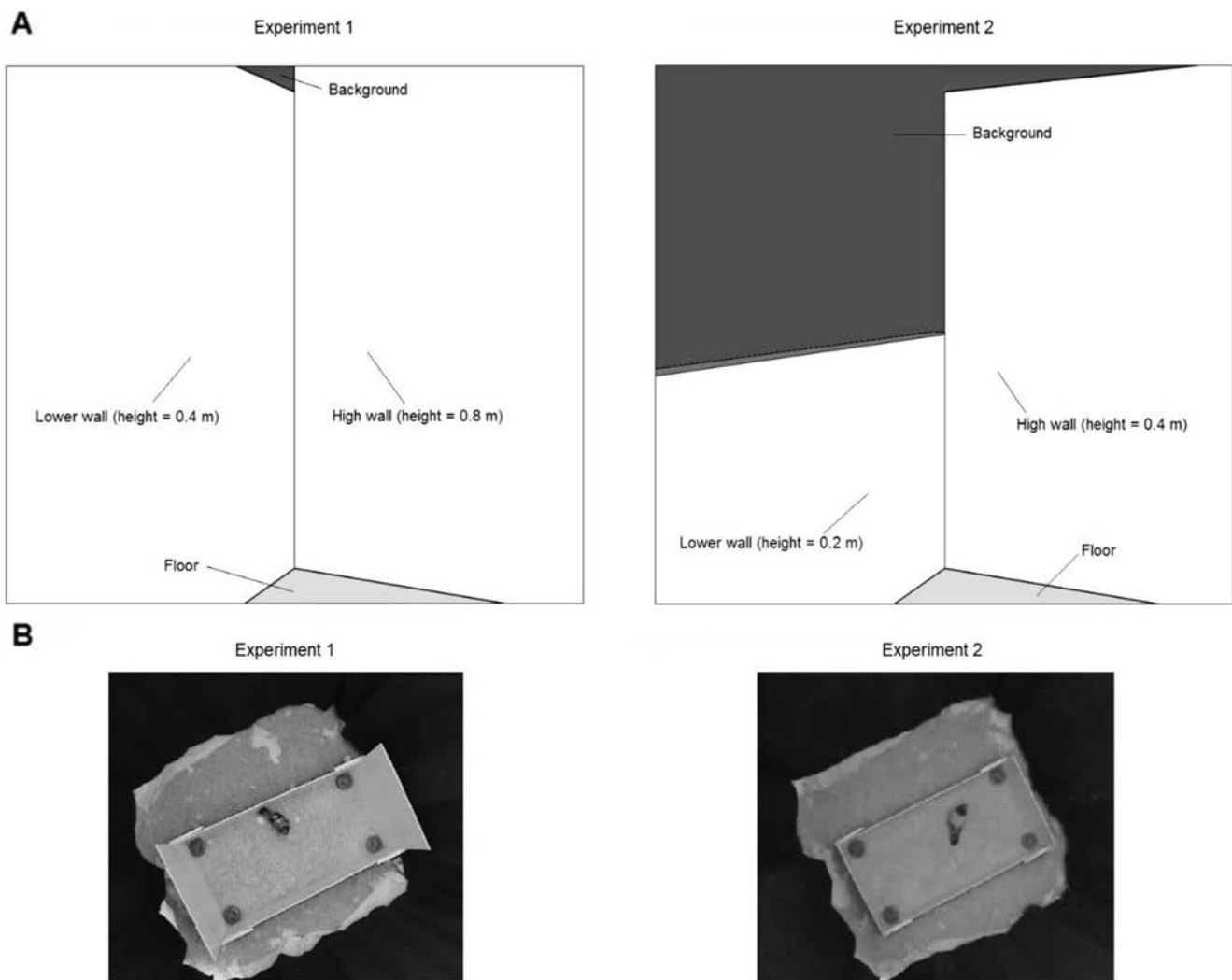


Figure 4. Comparisons of the apparatuses in two experiments. (A) Simulated scenes from a pigeon's view when it was standing at the center of the training apparatus and looking at one corner at 25 cm high. (B) Top-down views of the apparatuses. See the online article for the color version of this figure.

as in Experiment 1. To test our speculation, Experiment 2 was conducted with this modification of the wall height.

Experiment 2

The purpose of Experiment 2 was to investigate whether pigeons would use height cues to reorient when the wall heights were reduced to make the difference between them more noticeable.

Method

Subject. Nine adult pigeons (*Columba livia*) participated in Experiment 2. All birds were given free access to grit and water and they were maintained at 85% of their free-feeding body weight with the exception Bird 115, which was reduced to 80% of its free-feeding body weight during testing phases to increase its motivation to search for and eat food pellets during the experiment. Three birds were dropped from the experiment during training because of an experimental error in the training procedure, leaving six birds. Among these six birds, Birds 115 and 146 did not have any open-field experience, Birds 41, 51, and 62 had experience in open-field tasks without any spatial learning component, and Bird 63 participated in (but did not complete) two spatial open-field experiments (neither of which required reorientation) five years before this experiment.

Apparatus and procedure. The apparatuses used in the experiment maintained the same shape (same horizontal distance information) as those in Experiment 1. However, all walls were reduced to half of the height used in Experiment 1 so that the tall walls were 0.4 m high and the short walls were 0.2 m high. All other settings were identical to Experiment 1.

Results and Discussion

All six birds completed Training Phase 3 with accuracy higher than or equal to 90%. Choices were coded and confirmed as in Experiment 1. For Phase 4 and 5, independent *t* tests showed that the location of goal corners (long wall on left/right) had no influence on the choice proportions in each test (all *ps* > .115), indicating that the counterbalancing was successful.

The proportion of first choices that were to correct corners was determined for each pigeon for each type of test and for the training (reinforced) trials in Phase 4 and 5, and was compared with chance level (i.e., 0.5) by one-sample *t* tests. In Phase 4, the accuracy in training trials, Control, Horizontal Distance Only, and Vertical Height Only tests were all significantly higher than chance level (all *ps* < .002 < corrected α , Cohen's *ds* > 4.28; see Figure 5), indicating successful use of horizontal cues or height cues alone or together in choosing one of the two goal corners with their first choice. As in Experiment 1, there was no significant difference between the accuracy in training trials ($M = 0.94$, $SD = 0.02$) and Control test ($M = 0.97$, $SD = 0.05$; $t(5) = 0.99$, $p = .368$, Cohen's $d = 0.56$). For the Vertical Height Only test, all six pigeons showed the ability to use height alone to reorient; the accuracy of each pigeon was equal to or greater than 0.7. The success in using height cues alone to reorient differs from the results of Experiment 1, suggesting that our modification of the wall height of the apparatuses influenced pigeons' choice. With lower walls that pre-

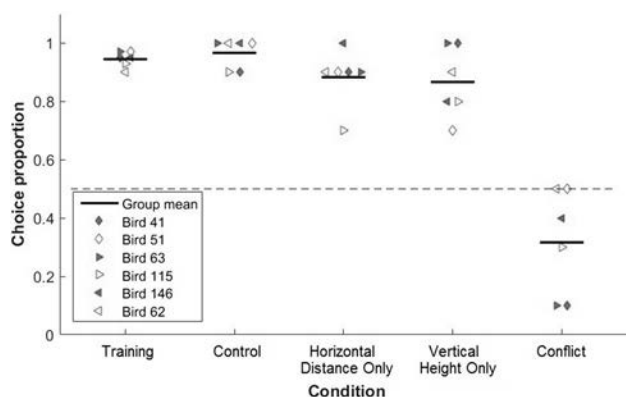


Figure 5. Choice proportions for individual birds and group means in training trials and each type of test in Testing Phase 4 in Experiment 2. Each dot represents an individual bird. For Conflict test, the choices were coded in terms of correct corners according to horizontal distance. The choice proportions in training trials, Control tests, Horizontal Distance Only, and Vertical Height Only tests show accuracy based on choices at correct corners. The dashed line indicates chance level (0.5). See the online article for the color version of this figure.

sumably made the difference in height more salient, the pigeons were able to use the wall height to reorient.

In the Conflict test, the proportion of choices to the HD corners was lower than chance level, although the difference failed to reach significance ($M = 0.32$, $SD = 0.18$; $t(5) = 2.45$, $p = .058$, Cohen's $d = 1.41$). At the individual level, four birds more often chose correct corners according to height. Thus, in contrast to the results of Experiment 1, the pigeons clearly showed no preference for using horizontal cues over height cues in Experiment 2. Consistent with our observations, an independent-sample *t* test comparing the proportions of choices to the HD corners in the Conflict test revealed a significant difference between the two experiments, $t(10) = 3.69$, $p = .004$, Cohen's $d = 2.13$). Thus, the relative weighting of the vertical and horizontal cues differed for pigeons in Experiment 2 compared with those in Experiment 1.

In Phase 5, the pigeons performed significantly above chance level both on the training (reinforced) trials ($M = 0.94$, $SD = 0.07$; $t(5) = 15.49$, $p < .001$, Cohen's $d = 8.94$) and in the Control test ($M = 0.89$, $SD = 0.17$; $t(5) = 5.53$, $p = .003$, Cohen's $d = 3.19$). The accuracy in training trials and Control test were not significantly different, $t(5) = 0.66$, $p = .536$, Cohen's $d = 0.38$. In the Square test, same as Experiment 1, the pigeons' choice proportions for corresponding correct corners on training trials were not different from chance, both before ($M = 0.41$, $SD = 0.33$) and after rotation ($M = 0.50$, $SD = 0.41$; both *ps* > .523, Cohen's *ds* < 0.40), indicating no interference from external cues.

Experiment 2 suggests that when the height cues are salient enough from pigeon's perspective, pigeons can use this type of cue to reorient. Furthermore, when the horizontal cues and height cues were presented in conflict, horizontal cues did not dominate over the height cues; in fact there was a tendency for height cues to be dominant.

General Discussion

The two experiments together showed that pigeons can orient using both horizontal cues and wall height as long as the height

cues are sufficiently salient. When the high walls were more than three times as high as a pigeon, pigeons did not appear to encode the height information. When the high walls were about one and half times as high as a pigeon and thus more easily perceived, the pigeons encoded the height information. In contrast, in both circumstances, pigeons successfully encoded horizontal cues, which is consistent with previous findings in pigeons as well as other animals and human children (for review, see Cheng, Huttenlocher, & Newcombe, 2013; Cheng & Newcombe, 2005). Such a result is not surprising. In the current study, the pigeons had to navigate on the horizontal plane and, on the other hand, pigeons have a wide field of view to perceive the horizontal shape of the arena. Therefore, they could encode the horizontal cues of the arena successfully.

When the horizontal and vertical cues were in conflict, however, the horizontal cues were not always preferred. Rather, the salience of cues appeared to influence how pigeons weighed the two types of cues. In the Conflict test of Experiment 1, when the walls were too high for pigeons, most pigeons relied on the horizontal cues. When the walls were lower, making the difference in height more noticeable, none of the pigeons showed a preference for horizontal cues and four out of six pigeons relied on height cues more often than horizontal cues, suggesting that the height cues were more salient. These findings seem consistent with the adaptive combination theory that the salience of a cue can influence its weighting (Newcombe & Huttenlocher, 2006; Twyman, Nardi, et al., 2013). The findings are also consistent with those in reorientation with height cues in human adults (Du et al., *in press*) and in navigation tasks with slope in rats (Miniaci et al., 1999). It can be speculated that despite the procedural differences, the failure in 3-year-old children in using height (Hu et al., 2015) might have been attributable to the particular height cues used being less salient than the horizontal geometry from the perspective of the children, rather than the fact that height cues were vertical cues.

Although we believe that the difference in use of height cues between Experiment 1 and Experiment 2 was most likely attributable to the change in absolute wall heights, it is possible that past experience of the pigeons could also have played a role, as the experimental histories of our birds varied. In particular, the two birds that showed the strongest control by horizontal cues in Experiment 1 had previous experience in a reorientation task with horizontal cues. However, past experience is unlikely to be the whole story because another pigeon from Experiment 1 that also had this experience showed similar choice to the birds that did not have this experience. It should be noted that an influence of past experience on use of cues to reorient would be consistent with the adaptive combination theory (Newcombe & Huttenlocher, 2006; Ratliff & Newcombe, 2008; Twyman, Nardi, et al., 2013).

Our findings from Experiment 2 showing that pigeons could use height cues to reorient are consistent with previous findings from reorientation tasks that pigeons readily encode slope information (Nardi & Bingman, 2009; Nardi et al., 2010), which includes a vertical component. However, although those studies showed that pigeons used slope over horizontal cues, we found that the vertical height cues were not preferred in all situations. It should be noted that in the current study, the pigeons did not fly and the goals were not located at different locations in vertical space. Thus, our vertical cues were purely visually perceived. In contrast, the slope cues in the previous studies provided multimodal information: the

inclination could be detected kinaesthetically, visually, or by differences in energy expenditure. When only visual information is available, such as in the case of our height cues, the salience of the visual information may be particularly critical. We speculate that if the pigeons perceived the height difference between walls by multiple modalities, they might encode height information more readily and give these height cues more weight. Further research could utilize an apparatus that requires the birds to fly to locations that differed in both dimensions, which would provide multimodal information.

Hummingbirds have been shown to prefer using vertical information to horizontal information to retrieve a rewarded location (Flores-Abreu et al., 2014), although the task used in that study did not involve reorientation. The hummingbirds flew to the rewarded locations, which provided multimodal vertical information. Our finding that even without vertical travel, pigeons could use height cues and even showed a nonsignificant tendency to choose according to height on the conflict tests in Experiment 2 is consistent with the importance of vertical information. Flores-Abreu et al. (2014) found that rats, as typical terrestrial animals, preferred using horizontal information to vertical information in the same task used for the hummingbirds. However, Grobéty and Schenk (1992) found that rats gave priority to the vertical over the horizontal dimension, which suggests that species may not be the only determining factor and that task characteristics and/or cue salience may also play a role in the relative dominance of vertical and horizontal information.

Recently, the relative priority of vertical cues to horizontal cues (e.g., horizontal geometry) in spatial navigation has been investigated with neuroscience techniques. Specifically, some neural studies on head direction cells and grid cells have suggested anisotropic representation of three-dimensional navigation (Jeffery, Jovalekic, Verriotes, & Hayman, 2013; Jeffery, Wilson, Casali, & Hayman, 2015). That is, information in the vertical dimension is represented differently in brain than information in the horizontal dimension. However, most of the supporting evidence has come from rodents and from free-foraging tasks. The present study provides new behavioral evidence in a different species and with a different task. We found that the priority given to horizontal and vertical information was malleable and appeared to depend on cue salience, which may not be consistent with the anisotropic account. Clearly, however, more comparative and neuroscience research with different tasks and species is needed to reach conclusions about the generality of the anisotropic account.

To our knowledge, this is the first study to test pigeons' ability to use height cues in a reorientation task. It provides evidence that when wall height is perceptually salient to pigeons, it is a reliable cue in reorientation and is not always dominated by horizontal cues. Our results suggest that the relative priority of cues in reorientation may be determined more by the salience of cues and potentially by the learning history, than by the dimension of space.

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