

Reorientation in diamond-shaped environments: encoding of features and angles in enclosures versus arrays by adult humans and pigeons (*Columbia livia*)

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Abstract Although geometric reorientation has been extensively studied in numerous species, most research has been conducted in enclosed environments and has focused on use of the geometric property of relative wall length. The current studies investigated how angular information is used by adult humans and pigeons to orient and find a goal in enclosures or arrays that did not provide relative wall length information. In enclosed conditions, the angles formed a diamond shape connected by walls, whereas in array conditions, free-standing angles defined the diamond shape. Adult humans and pigeons were trained to locate two geometrically equivalent corners, either the 60° or 120° angles. Blue feature panels were located in the goal corners so that participants could use either the features or the local angular information to orient. Subsequent tests in manipulated environments isolated the individual cues from training or placed them in conflict with one another. In both enclosed and array environments, humans and pigeons were able to orient when either the angles or the features from training were removed. On conflict tests, female, but not male, adult humans weighted features more heavily than angular geometry. For pigeons, angles were weighted more heavily than features for birds that were trained to go to acute corners, but no difference in weighting was seen for birds trained to go to obtuse corners. These conflict test results were not affected by environment type. A subsequent test with pigeons ruled out an interpretation based on exclusive use of a principal axis rather than angle. Overall, the results indicate that, for both

adult humans and pigeons, angular amplitude is a salient orientation cue in both enclosures and arrays of free-standing angles.

Keywords Geometry · Angles · Features · Reorientation · Enclosed environment · Array

Introduction

The ability to orient oneself in an environment is a crucial skill for establishing a frame of reference and navigating to a goal. Many properties of our surroundings can be used in the process of orientation. One such example is the geometry of an environment, defined as any property related to the overall shape. Other cues present which do not fall under this category are referred to as non-geometric, or featural, cues. These are cues such as color, texture, smell, etc. In a pioneer study, Cheng (1986) discovered that when rats attempted to re-locate food in one corner of a rectangular enclosure which contained a distinctly colored wall, they consistently made rotational errors and chose the corner that was geometrically equivalent to the correct corner as defined by the wall lengths. Cheng called this blind reliance on geometry despite the presence of more informative featural information a “purely geometric module” of spatial representation. Similar instances of reliance on geometry over featural information have been observed in young children (Hermer and Spelke 1994). However, rats are able to use featural information with extended training (Cheng 1986), or when geometry is uninformative or unreliable (Gibson et al. 2007). Similarly, children can also use features in larger environments (Learmonth et al. 2002; Learmonth et al. 2008), when features are pre-trained (Twyman et al. 2007),

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or when the features are incorporated into the geometric properties of the room (Wang et al. 1999; Lee and Spelke 2010). Featural information in some contexts can even facilitate the learning of geometric information (e.g., Graham et al. 2006; Kelly 2010; Horne and Pearce 2011), and in some species, salient featural information will override geometric information in a conflict situation (e.g., humans: Kelly and Bischof 2005, 2008; chickadees: Gray et al. 2005). Thus, preference for geometric or featural information varies by species and context, but all species studied to date have been able to encode the geometric properties of their environment (for a review see Cheng and Newcombe 2005).

Most research on geometric reorientation has used rectangular enclosures and has focused on the property of relative wall length. Recently, however, researchers have expanded the investigation of geometric reorientation to include non-rectangular enclosures in which the angular amplitudes of corners provide potentially informative cues, as well as non-enclosed environments composed of free-standing objects, angles, or walls. The results of such studies have been both variable and interesting. For example, Hupbach and Nadel (2005) tested children in a locomotor hide-and-seek task using a rhombic (i.e., diamond-shaped) enclosure which provided angular but not wall length information. Children under the age of four chose randomly and therefore showed no evidence of being able to use the angular information to orient. Children aged four and older chose both the correct corner and its rotational equivalent, indicating that they were able to successfully use the angular information to orient. The difficulty that young children exhibit in the encoding of local angular amplitudes, combined with evidence suggesting that children sometimes ignore informative *featural* cues in favor of less informative geometric cues (Hermer and Spelke 1994, but see Learmonth et al. 2002, 2008), has led some researchers to suggest that reorientation via geometry does not include the seemingly geometric attribute of angle (Spelke et al. 2010), or at least that “wall length is a more distinctive feature than size of angle” (Newcombe et al. 2010, p. 216).

Recent studies with birds, rats, and adult humans, however, have suggested that angular amplitude *can* provide a salient cue for reorientation, at least within enclosed environments. For example, when trained to find two geometrically equivalent corners of a parallelogram-shaped enclosure which provided both relative wall length and angular cues, both chicks (Tommasi and Polli 2004) and pigeons (Lubyk and Spetch 2012) chose the correct angular amplitudes when tested in a rhombic-shaped enclosure which removed the wall length information. These results indicated that both bird species had no trouble using the local angular information from

training when the relative wall length information was removed. Moreover, when wall length was placed in conflict with angular information, pigeons showed a preference for the angular information. For chicks in the Tommasi and Polli (2004) study, the results depended on the amplitude of the angles: They chose according to angular amplitude if they had been trained to locate the acute angles, but according to wall length information if they had been trained to locate obtuse angles. Interestingly, rats are also able to use either wall length or angular information when trained in a kite-shaped enclosure (Pearce et al. 2004).

Finally, several recent studies have shown the use of angular information by adult humans in virtual reorientation tasks. Bodily et al. (2011) found that adult humans trained in a trapezoid-shaped enclosure showed evidence of encoding angular information, although reliable principal axis information appeared to override the use of angles. This is interesting in light of similar research conducted by Lubyk et al. (2012), where adult humans also were able to use angular information when trained within a parallelogram-shaped enclosure, but they chose the correct angular locations over those designated by the principal axis in a conflict test. Both studies employed three-dimensional non-immersive techniques using a computer screen; nevertheless, it is important to note that research investigating potential differences between partial and full immersive reality has found no functional differences in spatial navigation (Kelly and Gibson 2007). However, one potential reason for the discrepant results between the studies is that in the Bodily et al.’s experiment, distinctly colored orbs which acted as featural information were present in the corners, whereas in the Lubyk et al.’s experiment, the only information present in training were the wall lengths, principal axis, and local angular information. This featural information in the corners of the environment potentially could have overshadowed the angular information by drawing participant attention at the corners to the orb rather than the angular amplitude, thus making the principal axis more salient than the angles. Unfortunately, Bodily et al. did not include the distinctly colored orbs in any of the testing environments, so it is impossible to fully understand the role their presence may have played in training. Other recent studies have also confirmed the encoding of angular information by adult humans within enclosed environments (e.g., Sturz and Bodily 2011).

Although there is clear evidence that both pigeons and adult humans encode angular information and can use this information to locate a goal within enclosed environments, it is not clear whether the encoding of angular information depends on whether the angles are part of the overall geometry of an enclosure or instead are free-standing

objects. Some studies suggest that use of angular information to reorient may be easier when the angles are part of the global shape of an enclosure. Lee et al. (2012) tested 2-year-old children in various rectangular- and diamond-shaped environments created by continuous surfaces or arrays of free-standing angles or walls. Interestingly, despite being able to orient easily in the enclosed continuous surface environments, the children were unable to orient when only free-standing angles at the corners created an array. However, orientation could be accomplished if truncated walls were placed between the object locations. Overall, the study concluded that 2-year-old children could use surface distances and directions to reorient, but were unable to use local angular information. Similarly, Gouteux and Spelke (2001) found that young children were unable to use the global rectangular shape formed by an array of four identical objects to orient, but were able to orient when truncated walls joined the four potential goal locations. These studies suggest that, at least in children, there may be something unique about the presence of continuous surfaces in the encoding of a global shape. In studies with adult humans, Reichert and Kelly (2011) found that males used the distinct angular information provided by a rectangular array composed of free-standing angles to orient, but females did not. However, the failure of females to use angular information to orient did not appear to be due to a failure to discriminate the angles, because in a subsequent study in which reorientation was not necessary, participants of both sexes easily discriminated between the two angular amplitudes when placed next to one another, as opposed to in an array (Reichert and Kelly 2012).

There is also evidence suggesting that separate cognitive and neural processes may be at work in enclosed environments compared to those composed of arrays (e.g., Doeller et al. 2008) and that surfaces or boundaries may be processed differently than free-standing landmarks (Lever et al. 2002; Lee and Spelke 2010). Recently, Sutton et al. (2012) conducted a study with adult humans examining neural activity during reorientation in various types of environments. Using functional magnetic resonance imaging (fMRI), the authors found that despite the behavioral responses for the various environments being similar, different areas of the brain were activated in the enclosures as compared to the arrays formed by discrete free-standing objects. In addition, some behavioral studies have shown that both human (Reichert and Kelly 2011) and non-human animals (Vallortigara et al. 1990; Spetch et al. 1997; Pecchia and Vallortigara 2010) tend to favor local cues present over the global shape formed by an array (for a review see Lew 2011). Despite this evidence suggesting separate neural processes, this dichotomy has been questioned by some researchers (see Gibson et al. 2007; Pecchia and Vallortigara 2012; Sutton 2009). Overall, more

research is needed comparing the orientation processes used in enclosures and arrays.

Another unanswered question about the use of angular information to reorient is whether the encoding of angular information is readily overshadowed by salient featural information. Specifically, both pigeons and adult humans seem to encode the geometry of a rectangular enclosure even if a salient feature is present; this encoding of geometry is revealed by removal of the feature and/or procedures such as verbal shadowing that interfere with the conjoining of featural and geometric information (e.g., Hermer and Spelke 1994). In other words, encoding of the geometric shape of an enclosure based on relative wall length seems to be automatic and occurs even if a salient and more informative featural cue is present; this has led to suggestions that the encoding of geometry may be encapsulated and obligatory (Cheng 1986; Spelke et al. 2010). Although there is now considerable evidence against the suggestion of a fully encapsulated geometric module (see Twyman and Newcombe 2010), both pigeons and adult humans seem to encode the geometric shape of an enclosure despite the presence of a salient feature. Thus, an interesting question is whether angular information, unlike global shape, is susceptible to overshadowing by a featural cue.

Our research used a small-scale orientation task to address two main questions: (1) Does the encoding of angular information depend on whether the angles are part of an enclosure or array; and (2) will angular information encoding in enclosures and arrays still occur despite the presence of salient feature cues? Experiment 1 addressed these questions in adult humans and Experiment 2 addressed these questions in pigeons. In both experiments, we trained the subjects to locate two geometrically equivalent corners in either a diamond-shaped enclosure or a diamond-shaped array. Importantly, blue panels were always located in the two trained corners so that either the features (i.e., blue panels) or the local angular amplitudes (i.e., 60° or 120°) could be used for orientation and navigation to the goal. Relative wall length was not an informative cue in training, as all walls had identical dimensions. Following training, subjects were tested in three manipulated environments which matched the environment type from training (i.e., either enclosed or array). The adult humans in Experiment 1 were trained and tested in only *one* environment type (i.e., between-subjects design). However, for the pigeons in Experiment 2, following completion of testing in the first environment type, they were re-trained to locate the same goal corners in the other environment type and then tested again with the manipulated arrays in this new environment type.

In both experiments, testing included manipulated environments in which: (a) the angular information was

removed; (b) the features were removed; or (c) the features were rotated to place them in conflict with the angular information. In the conflict tests, subjects were forced to choose between corners that matched the training angle and corners that matched the feature from training. This manipulation allowed us to examine how the feature and angle cues from training were weighted when placed in competition and provided us with a means to examine whether angular information was potentially encoded as a type of feature, rather than geometry. If the local angular information was encoded as a feature, the cue competition when the blue panels and angles were placed in conflict would be between *two* types of features (i.e., the angles and the panels). Alternatively, if the angular information was treated as geometric, the results would resemble the typical competition and preference effects shown between geometry and features in this type of task. Specifically, human males tend to rely more heavily on geometric information in a conflict situation, while females prefer to use featural information (Astur et al. 1998; MacFadden et al. 2003; Saucier et al. 2003; Kelly and Bischof 2005; Andersen et al. 2012). Therefore, the results of Experiments 1 and 2 could potentially inform us about whether adult humans and pigeons treated angular information as featural or as geometric information.

Experiment 1

In Experiment 1, adult humans were trained in a fully immersive three-dimensional environment to locate two geometrically equivalent corners of either a diamond-shaped enclosure or array. In testing, participants were

placed in three manipulated environments to determine which cues had been encoded from training and how they were weighted with respect to one another.

Methods

Participants

Participants were 94 undergraduate students from the University of Alberta, 49 males and 45 females, who received class credit for their participation. Ages ranged from 18 to 36 years with a mean of 20 years. Participants were divided into two groups so that half received the array environments and the other half the enclosed environments. Within each environment, goal corners were counterbalanced to be either acute (60°) or obtuse (120°).

Environments and stimuli

Training and testing environments were created using Vizard software (WorldViz, Santa Barbara, CA) and incorporated into the virtual environment via an nVisor SX60 head-mounted display (HMD, NVIS, Inc. Virginia). Screen resolution within the display was $1,280 \times 1,024$ pixels. Participants' visual orientation was tracked by an InterSense (Massachusetts) IS-900 motion tracking system. Range of view from the participants' point of view within the virtual environment was similar to real-world range. For training, both the enclosed diamond and diamond-shaped array were 6.45×6.45 m with a wall height of 4.30 m. Blue feature panels, which were only located in the two correct corners, were 1.50 m wide and extended from the floor to the top of the walls. In the diamond-shaped

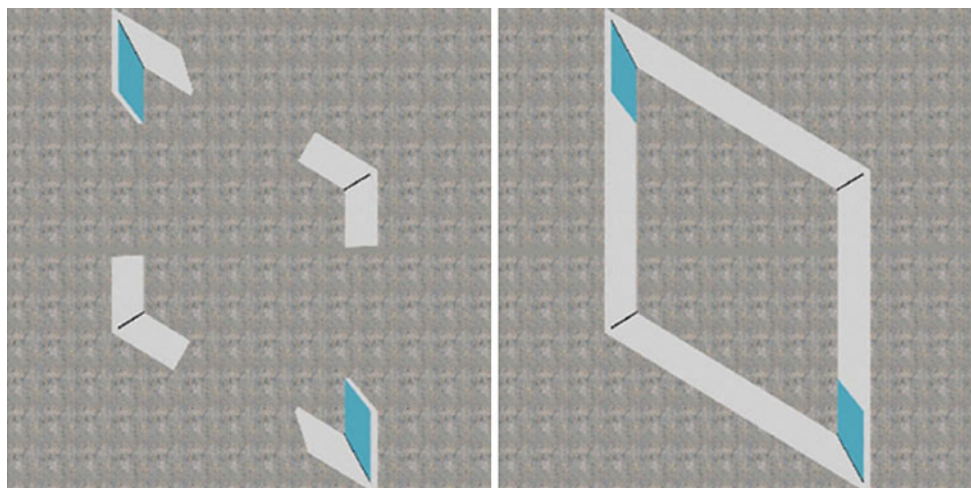


Fig. 1 Top-down views of the array (left) and enclosed (right) training environments. Both are examples of groups where the acute (60°) corners were correct. For participants who were trained to locate

the obtuse (120°) corners, the blue feature panels were instead located in the opposite obtuse corners

array, each arm of the free-standing angles was 1.50 m wide (see Fig. 1). Dimensions of the test environments were identical to training (see Fig. 2).

General procedures

Participants were run individually using a virtual reality headset, which allowed them to physically turn to face any direction in the virtual environment. Before starting the experiment, the participant was informed that their goal was to determine, in each new environment, which corner was the *correct* corner. The participant always appeared in the center of the diamond-shaped environment and was permitted to turn to face any direction before making a choice. Corner selection was accomplished via a handset containing a trigger button, which from the participant's perspective within the virtual environment was a long blue wand. Immediately following a corner choice, feedback was presented both visually in the virtual environment, as well as acoustically through speakers in the headset. Feedback was: (1) positive, where a gold coin appeared accompanied by a *ding* sound; (2) negative, where an X appeared accompanied by an unpleasant jarring noise; or (3) uninformative, where an *OK* appeared accompanied by a neutral *click*, meant only to inform that participant that their choice was logged. The type of feedback received

depended both on the participant's corner choice (i.e., correct vs. incorrect) and the stage of the experiment (i.e., in the second half of training sometimes uninformative feedback was given). Following feedback, the environment faded and after a 2-s inter-trial interval, in which the environment was completely black, the participant re-appeared in the same training environment facing a new randomly determined orientation.

Training The experiment began with a practice trial, in which the participant selected each of the four corners and received informative feedback (i.e., “correct” feedback from the two correct corners which contained the blue feature panels and “incorrect” feedback from the other two corners). Goal corners were counterbalanced across both the enclosed and array groups so that half of the participants were trained to locate the acute (60°) corners and the other half were trained to locate the obtuse (120°) corners. The blue feature panels always were located in the two correct corners. Following the practice trial, training was organized into blocks of five trials each. In the first of training, participants were always given informative feedback regarding their choice (i.e., “correct” or “incorrect” visual feedback with simultaneous sound; see above). In order to move to the second phase of training, participants had to choose one of their two correct corners on four of the five trials in one block. If participants did not meet this

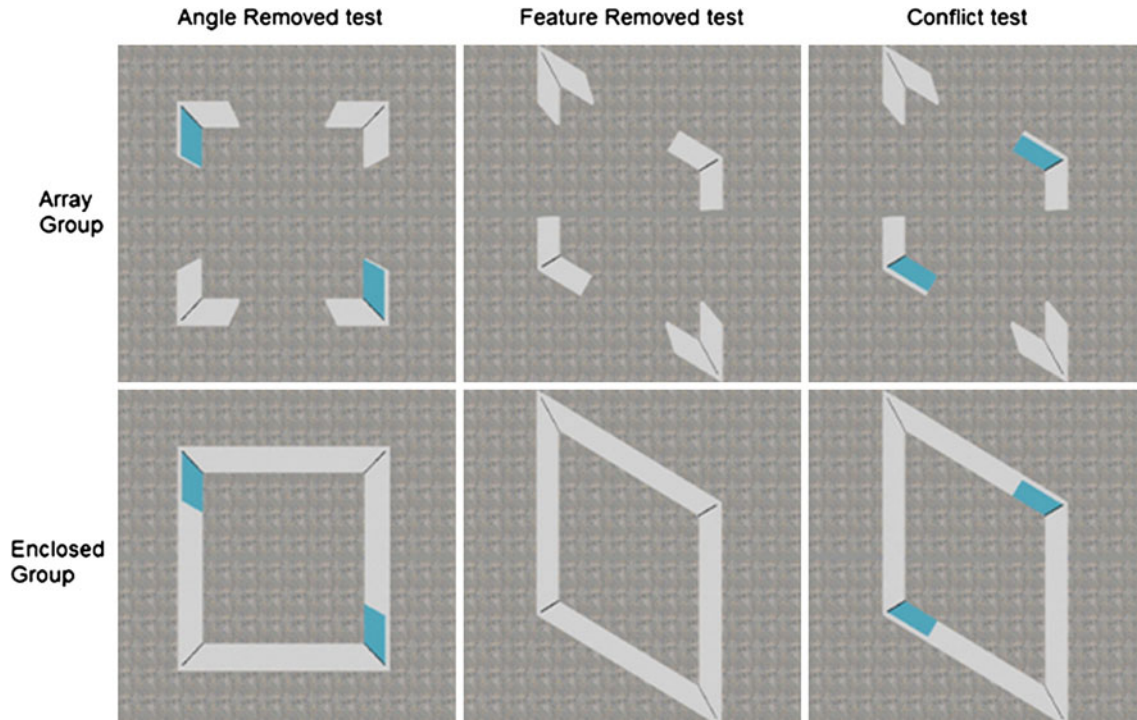


Fig. 2 Top-down views of the three manipulated test environments for both the array and enclosed environments. All are examples of groups where the acute (60°) corners were correct. For participants who were trained to locate the obtuse (120°) corners, the blue feature

panels were instead located in the opposite obtuse corners (with the exception of the Feature Removed test which did not contain blue feature panels)

criterion, they repeated another block of five trials, and so on until they passed. The second phase of training was identical to the first, with the exception that on three of the five trials (randomly determined), participants received the uninformative feedback regarding their choice, regardless of whether it was correct or incorrect. The criterion to pass the second phase was the same as the first: four of five trials correct in one block.

Testing In testing, participants saw three manipulated environments which matched their training environment type (i.e., they were either continuous surfaced enclosed environments or environments created by free-standing angles). The tests were: (1) a square environment which maintained the blue feature panels in two opposing corners but removed the informative angular information (see Fig. 2, left column); (2) a diamond-shaped environment identical to training but with the blue feature panels removed (see Fig. 2, middle column); and (3) a diamond-shaped environment with the blue panels shifted so that they were located in the previously non-reinforced angular locations from training (see Fig. 2, right column). All test trial choices resulted in uninformative feedback. Control trials identical to the participant's training environment were dispersed between the test trials, but were followed by uninformative feedback; these were later used to assess whether a participant remembered their initial correct corners, and only participants who scored a minimum of 80 % correct were included in analysis. Testing was presented in five blocks of four trials each (i.e., a total of 20 test trials), irrespective of participant accuracy. Each block contained one control trial, and one of each type of test trial, all randomized for order of presentation.

Results

Nine males and 5 females failed to meet the requirement in the control trials and were not included in final analyses. The final pool of participants consisted of 40 males and 40 females. Within each sex, assignment to environments was counterbalanced so that all four combinations of environment (i.e., enclosed or array) and correct angle (i.e., acute or obtuse) had 10 male and 10 female participants. Participants in both environments learned the task easily, most requiring only one block of trials in each phase of training to pass to testing. Univariate analyses of variance (ANOVA) were used to examine participants' performance in each of the test conditions across the factors of Sex (male or female), Environment (array or enclosed), and Goal Corners (acute or obtuse). All alpha levels were set to .05.

Results from the square Angle Removed test showed a significant interaction between Environment and Goal Corners ($F(1, 80) = 4.20, p < .05, \eta_p^2 = .05$; see Fig. 3).

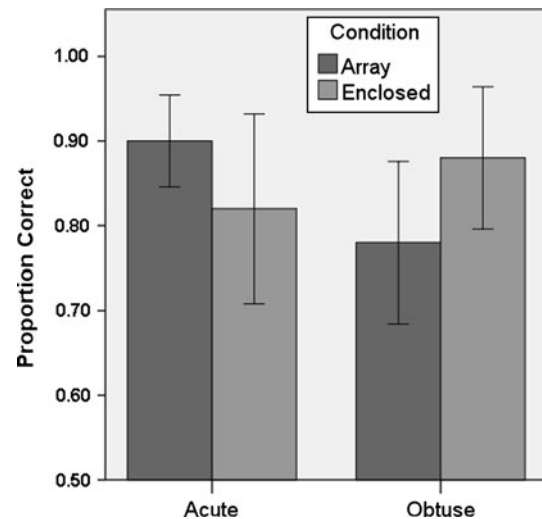


Fig. 3 Proportion of correct choices to corners with blue feature panels, as a function of Environment type and Goal Corner on Angle Removed test. Participants in the array environment (*dark*) were significantly more accurate in choosing the correct feature if the goal had been in the acute (60°) corners, whereas participants in the enclosed environment (*light*) were significantly more accurate when the goal had been in the obtuse (120°) corners. Error bars represent standard error of the mean

This interaction was driven by higher accuracy for participants trained to locate the acute corners in array environment and higher accuracy for participants trained to locate obtuse corners in the enclosed environment. Importantly, all groups chose their correct corners significantly more often than expected by chance (.50; array acute: $M = .90, SD = .12, t(19) = 14.74, p < .001$; array obtuse: $M = .78, SD = .21, t(19) = 5.85, p < .001$; enclosed acute: $M = .82, SD = .25, t(19) = 5.71, p < .001$; enclosed obtuse: $M = .88, SD = .19, t(19) = 9.04, p < .001$).

Results of the Feature Removed test, in which the blue feature panels were removed from the diamond environment, showed a main effect of both Sex ($F(1, 80) = 6.86, p = .01, \eta_p^2 = .09$; see Fig. 4, top) and environment ($F(1, 80) = 6.86, p = .01, \eta_p^2 = .09$; see Fig. 4, bottom). Although both males and females performed significantly better than chance (.50; male: $M = .87, SD = .19, t(39) = 12.00, p < .001$; female: $M = .73, SD = .28, t(39) = 5.37, p < .001$), males in both the array and enclosed environments performed significantly better than females. In addition, participants in the array were significantly more accurate at locating their goal corners than those in the enclosed, although participants in both conditions performed better than chance (.50) (array: $M = .87, SD = .19, t(39) = 12.33, p < .001$; enclosed: $M = .74, SD = .28, t(39) = 5.30, p < .001$).

In the Conflict test, where participants had to choose *either* the correct angular amplitude from training *or* the

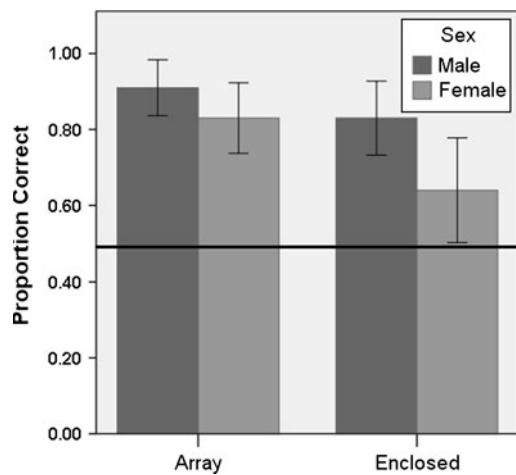


Fig. 4 Proportion of correct choices to trained angular amplitudes on the Feature Removed test by Sex and Environment Type. Error bars represent standard error of the mean. The horizontal line indicates chance level (.50)

blue features that were previously associated with the correct corners, there was a main effect of Sex ($F(1, 80) = 10.30, p < .005, \eta_p^2 = .13$): Females weighted the blue feature panels significantly heavier than expected by chance (.50; $M = .73, SD = .35; t(39) = 4.03, p < .001$), while males as a whole did not select either the features or correct angles at a rate that significantly differed from chance (Feature: $M = .45, SD = .40$; angle: $M = .55, SD = .40; t(39) = .70, p = .49$). This sex effect did not interact significantly with environment type or goal corner.

Discussion

In contrast to most studies examining the role of geometry in reorientation, which commonly have paired informative relative wall length information with uninformative angular information (e.g., right angles) in enclosed environments, here we removed the wall length information and added informative angular information *and* features in both enclosures and arrays. In the square Angle Removed test, there was a significant interaction between environment type and goal Corners. Specifically, in the array environment, participants who were trained to locate the acute corners performed significantly better than those who were trained to locate the obtuse corners. Interestingly, the opposite was true for the enclosed environment: participants trained to locate the obtuse corners of the diamond-shaped enclosure outperformed those who were trained to find the acute corners when features were the only available cue. These findings suggest in the array environment, the blue feature panels were more salient when located in acute corners, but in the enclosed environment they were more salient when located in the obtuse corners. To the

best of our knowledge, this is the first demonstration of feature salience changing as a function of both environment type and angular amplitude. Although we do not have a good explanation for this pattern of results, one possibility is that the salience of the different angular amplitudes may have varied between enclosures and arrays, and angular amplitude may have partially overshadowed featural cues.

In the diamond-shaped Feature Removed test, irrespective of Environment and Goal Corner, males were more accurate than females at locating their trained goal corners when the blue feature panels were removed. This suggests that males encoded the angular properties to a greater extent than the females in training. However, females still performed above chance in this test, which indicates that they *did* encode the geometry of the local angles to a sufficient extent to use it to locate their goal corners. This finding, particularly for the array environment, is interesting because it differs from that of Reichert and Kelly (2011), in which females were not able to use the local angular amplitudes of free-standing angles which formed an array. However, in the Reichert and Kelly study, there were no features present in either training or testing; therefore, it is possible that in the current experiment, the presence of the blue feature panels in the goal corners facilitated the learning of the local geometry. This enhancement of geometry by features has previously been shown to occur in non-human animals (Clark's nutcrackers: Kelly 2010; Rats: Graham et al. 2006; Horne and Pearce 2011). However, to the best of our knowledge, this is the first time it has been shown to occur in adult humans.

In the Feature Removed test, participants in the array environment overall were significantly better at locating their goal corners than those in the enclosed environment. This strong encoding of angular information from free-standing arrays is also interesting in light of the Reichert and Kelly (2011) study in which only males showed evidence of encoding the distinct angular amplitudes of four free-standing angles. The current study differs from these findings in that participants who were trained and tested in the array environment actually *outperformed* those in the enclosed environment when they were required to locate their goal corners without the presence of the blue feature panels. However, interestingly, Reichert and Kelly (2012) found that both males and females readily discriminated between the two angular amplitudes when placed side-by-side, despite females not being able to use the local angles when they were arranged in an array configuration (Reichert and Kelly 2011). This finding suggests that the reorientation process played a key factor in females' inability to distinguish the two amplitudes from one another in the 2011 study. In the current study, participants were not actively disoriented between trials, but were

passively disoriented by the room appearing in a new randomly facing orientation prior to each trial. However, we do not believe that this accounts for females' ability to use the local angular amplitudes successfully. Gouteux and Spelke (2001) found that young children were able to successfully reorient in an isosceles-shaped environment when they were allowed to spin around with their eyes open instead of closed. This indicated that being able to self-track the environment's rotation was a key aspect in staying oriented. However, in the current experiment, the virtual environment was rotated during a brief inter-trial interval, during which time the participant experienced only darkness. The room then re-appeared in a new orientation, which prevented the participants from tracking the motion as it occurred. Additionally, previous research conducted with domestic chicks has found that there is no difference in outcome between active disorientation (i.e., the subject spinning) and passive disorientation (i.e., the environment spinning) in these types of spatial tasks (Chiandetti and Vallortigara 2010).

Our finding that participants in the array environment outperformed those in the enclosed environment in the diamond-shaped Feature Removed test is also interesting in light of the previously discussed findings of Lee et al. (2012), in which young children could successfully orient in a diamond-shaped enclosure, but *not* a diamond-shaped array created by four free-standing angles. Additionally, when the angular information of the corners was removed, and only truncated walls joining the goal locations were present, the children were able to orient. These results suggested that the children used the walls, but not the angles, to assess distance and direction information. In the current study, the better performance on the Feature Removed test in the array group than in the enclosed group suggests that by adulthood, humans not only become able to extract geometric information from free-standing angles without the contribution of extended surfaces, but the encoding of angular information may even be more impervious to overshadowing by a feature. One potential explanation for these results is that the participants in the array group mentally completed the diamond shape in order to orient and navigate. In this case, the free-standing angles could have caused the angular amplitudes to be more salient than those in the enclosed group.

In the Conflict test, in which the blue feature panels were shifted to incorrect angular locations, females relied on the features more than the correct angles when making their choices, whereas males responded at chance level. Furthermore, there was no significant effect of environment type (i.e., enclosed or array) in participants' choices in the Conflict test. Some recent studies have proposed that due to the differing visual salience of different amplitudes (i.e., a

30° angle *looks* very different than a 100° angle), angles may be encoded as independent features rather than as geometric information that is integrated into the overall shape of the environment (Spelke et al. 2010; Sturz et al. 2012). However, the sex difference found in our study is similar to a common sex effect found in studies examining spatial reorientation in enclosed environments which contain both geometric and featural information: men tend to rely more heavily on geometric information, whereas women primarily rely on featural information (Astur et al. 1998; MacFadden et al. 2003; Saucier et al. 2003; Kelly and Bischof 2005; Lourenco et al. 2011; Andersen et al. 2012). It is important to emphasize that women *are* able to encode the geometric properties of their environments, such as was shown in the Feature Removed test (see also Kelly and Bischof 2008); it simply appears that features serve as a primary source of information for reorientation in females. It has been proposed that this sex-specific specialization of orientation and navigation involving different cues has evolved from ancient hunting and gathering roles (Eals and Silverman 1994); specifically, males need to navigate long distances for hunting, while females require more local object-specific skills for gathering. However, irrespective of evolutionary influences, the fact that a preference for the blue feature panel over the angular amplitude was shown by females and not by males in our study suggests that the angular amplitudes were likely encoded as geometric information, rather than as additional features. This goes against result suggestions that angles may be encoded similarly to features by adult humans (Sturz et al. 2012). Overall, the results of Experiment 1 are interesting because they show that adults, unlike children, have no problem extracting information from angles without the presence of extended surfaces.

Experiment 2

In Experiment 2, pigeons took part in a task similar to that of the adult humans in Experiment 1. They were trained to locate two geometrically equivalent corners of either a diamond-shaped enclosure or an array created by four free-standing angles. The arena was scaled to be roughly the same relative size to the pigeons as the virtual environment was to the humans in Experiment 1. Following training, pigeons were tested in three manipulated environments to determine which cues were encoded in training and how they were weighted with respect to one another. Following testing, pigeons were then re-trained and re-tested in the *other* environment type. This allowed us to examine how the previous experience and order of environment presentation affected their learning.

General methods

Subjects

The subjects were eight adult pigeons (*Columba livia*; four Homing and four Silver King), all naive to open field geometry studies. Birds were kept on a 12:12 h light:dark cycle with light onset at 6 AM. Birds were housed individually in metal cages and kept at 85 % of their free feeding weight on a diet of Kee Tee pigeon pellets and vitamin supplement. Water and grit were available ad libitum.

Apparatus

All apparatus used for training and testing were constructed of Sintra, a lightweight material of polyvinyl chloride (PVC) compressed between two sheets. For the enclosed environments, all apparatus had the same wall dimensions (85 cm × 85 cm; 60 cm height) and corner angular amplitudes (60° and 120°; see Fig. 5, right; Fig. 6, bottom row). For the array environments, each of the arms of the free-standing angles was 20 cm wide and 60 cm high and when placed together created an array with global dimensions similar to those of the enclosed group (82 cm × 82 cm). The angular amplitudes in both the enclosures and arrays were the same (60° and 120°; see Fig. 5, left; Fig. 6, top row). In order to prevent the pigeons from escaping the experimental arena, the arrays were placed within a large circular enclosure approximately 130 cm in diameter. For both the array and enclosed group, the blue feature panels were located on one side of each of the correct corners. In all apparatus, approximately 3 cm of aspen chip bedding lined the floor. Small porcelain containers (7 cm diameter × 4 cm height) covered with a thin sheet of paper towel and

secured with an elastic band were attached to the floor with Velcro at a distance of 10 cm from each of the four corners in the later stages of training and in testing. All containers contained approximately 1 cm of grit, and during training, the two reinforced corners contained four Kee Tee pigeon pellets as a reward. A white translucent curtain hung from the ceiling around the apparatus to block out external visual cues. Four 40-W fluorescent bulbs illuminated the apparatus from the outside of the curtains. Four noise machines were located around the apparatus which played white noise and blocked out external auditory cues.

General procedures

Pigeons received one experimental session per day consisting of ten trials. Prior to being placed in the arena, the pigeon was rotated in a small holding container at a rate of 12 rpm for 30 s. With the lights extinguished, the pigeon was then placed in the arena in the center of one of the walls (randomly determined) facing the center of the arena. In the array environment, subjects were placed in the equivalent space between the free-standing angles facing inward. Light onset signaled the start of the trial and, in all phases except Habituation, the subject had a maximum of 5 min to select a corner by pecking through the paper towel. In training, the subject was given an additional minute to make a second corner selection in order to receive additional reinforcement. In testing, only one corner choice was allowed as all test trials were non-reinforced. The lights were extinguished to signal the end of the trial and the bird was returned to the holding container. The orientation of the apparatus was shifted to face a new direction at random intervals throughout the experimental session to prevent the birds from orienting based on external cues.

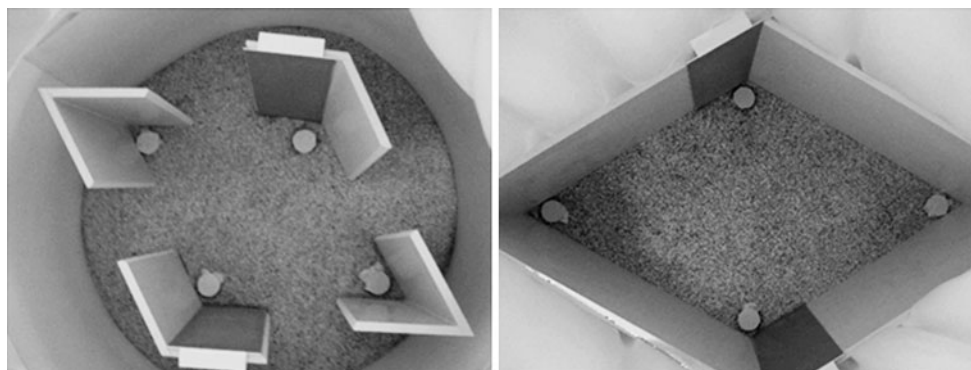


Fig. 5 Top-down views of training enclosures for both the array (*left*) and enclosed (*right*) groups. Both are examples in which the obtuse (120°) corners were correct in training. For birds trained to locate the

acute (60°) corners, the blue feature panels were located in the two opposite acute corners

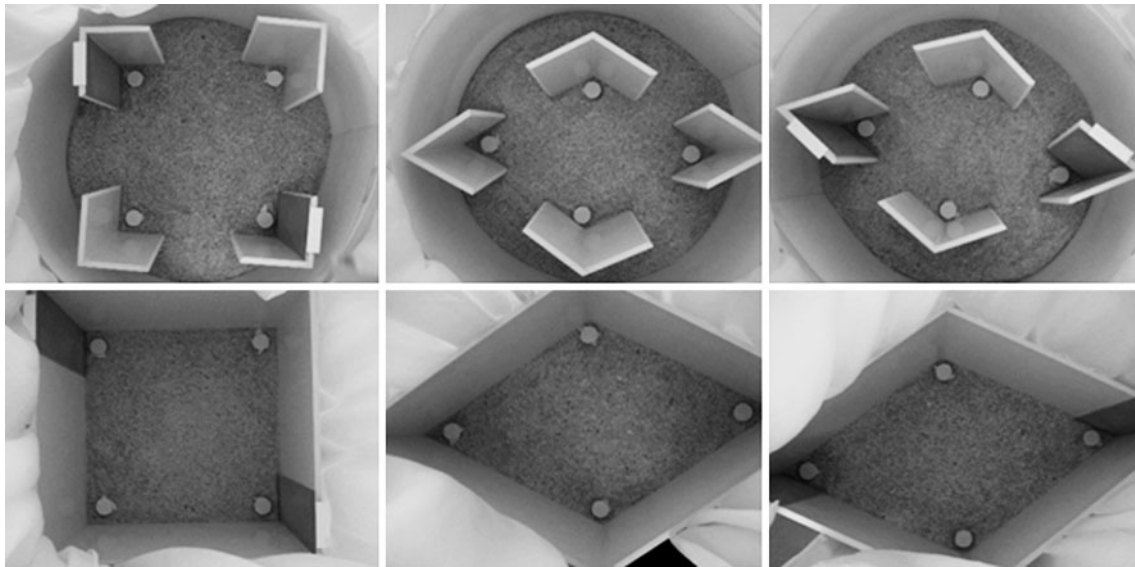


Fig. 6 Top-down views of test enclosures for both the array (*top row*) and enclosed (*bottom row*) groups: Angle Removed (*left column*), Feature Removed (*middle column*), and Conflict (*right column*). All are examples in which the obtuse (120°) corners were correct in training

Part I: initial training and testing

Procedures

Training Training was divided into three phases which all took place in the training apparatus. Half of the birds were assigned to the array group and were initially trained in the diamond array (see Fig. 5, left), while the other half were assigned to the enclosed group and were first trained in the diamond enclosure (see Fig. 5, right). Within each group, half were trained to locate the acute (60°) corners and the other half the obtuse (120°) corners. The first phase (Habituation) was designed to allow the pigeon to become comfortable in the arena and to learn which two corners contained the food rewards. A container full of grit was secured in each of the four corners, but no paper towel was present. The two correct corners each contained 15 food pellets on top of the grit. The blue feature panels were located in the two correct corners throughout all phases of training. The pigeon was given a maximum of 20 min per trial to locate and consume all 30 pellets and up to five trials were given per session. Habituation continued until the pigeon consumed all 30 pellets in less than 1 min for four consecutive trials in 1 day.

In the second phase of training, a small square of paper towel was introduced to all four containers. The paper towel coverage was gradually increased so that it eventually completely covered the containers and was secured with an elastic band. The amount of grit present in the containers was also slowly decreased over trials. In this phase and all remaining phases, only four food pellets served as reinforcement in each of the two correct corners,

and daily experimental sessions consisted of ten trials. Phase 2 continued until the pigeon directed its first choice on eight of the ten trials to one of the two correct corners. Phase 3 was identical to the end of Phase 2 except that only six of the ten trials contained food in the correct corners (i.e., four of the ten trials were non-reinforced). The non-reinforced trials were randomly situated between the reinforced trials, but never occurred back-to-back. A pigeon passed into testing when it completed two consecutive sessions in a row with a minimum score of eight out of ten correct.

Testing Testing took place in three manipulated arenas that matched the training environment type (i.e., birds trained in the array were tested in arrays). All test trials were non-reinforced. The three types of tests were the same as in Experiment 1. On Angle Removed tests (see Fig. 6, left column), the informative angular information from training was replaced with uninformative right angles. On Feature Removed tests (see Fig. 6, center column), the angular information was identical to training, but the blue feature panels were removed. On Conflict tests (see Fig. 6, right column), the blue feature panels were shifted to the incorrect angular amplitudes from training, placing the features and angles in direct conflict with one another.

Each daily test session consisted of: (1) six baseline trials, conducted as reinforced training trials in the training arena; (2) three non-reinforced test trials, one of each type; and (3) one control trial, conducted as a non-reinforced training trial. The order of trials was randomized across days, but was controlled so that there were never two non-reinforced trials (i.e., test or control) in a row. Corner choices were operationally defined as pecking through the

paper towel (as confirmed from the overhead camera and a break through the paper towel). Testing continued until the pigeon completed (i.e., made a choice in) eight trials in each of the test and control conditions. This required a minimum of eight sessions (i.e., days), but took longer if pigeons failed to make a choice on some trials.

Results

Data were compiled for analysis by converting each individual pigeon's number of correct and incorrect choices into proportions. All birds completed training with perfect or near perfect accuracy to their correct corners, as defined by both the angular amplitudes and blue feature panels. All pigeons achieved perfect accuracy in the control trials during testing (i.e., they selected one of the two trained corners on every trial), indicating that they remembered their trained goal corners throughout testing.

On the Angle Removed test, which paired the blue feature panels with uninformative right angles, all birds had perfect or near perfect accuracy, indicating that the birds clearly encoded the blue features and were able to successfully use them even when the environment was void of the angular amplitudes they were paired with in training.

On the Feature Removed test, all birds performed significantly above chance level (.50; $M = .94$, $SD = .13$, $t(7) = 9.43$, $p < .001$), indicating that they had also encoded the angular information from training. Univariate analyses of variance (ANOVA) revealed no significant effects of either Goal Corner (i.e., acute or obtuse) or Environment (i.e., array or enclosed) on corner choice.

In the Conflict test, in which pigeons had to select *either* the correct angular location from training *or* the corner associated with the blue feature panel, the ANOVA revealed a main effect of Goal Corner ($F(1,7) = 31.22$, $p < .01$, $\eta_p^2 = .89$): birds that were trained to go to the obtuse (120°) corners did not differ from chance (.50) in their choices to the blue feature panel ($M = .54$, $SD = .28$, $t(3) = .25$, $p = .82$). However, birds that were trained to go to the acute (60°) corners chose the blue feature panel significantly *less* than would be expected by chance, choosing the correct angular information instead ($M = .07$, $SD = .08$, $t(3) = -11.60$, $p < .001$). As in the other tests, there was no significant effect of Environment.

Part II: re-training and re-testing

Procedures

Re-training Following successful completion of Experiment 1, pigeons were re-trained in the other environment

(i.e., array or enclosure). Birds' correct corners stayed the same from previous training (i.e., acute or obtuse), and the blue feature panels were still located in the correct corners. Birds were first given one session with five reinforced trials in the old training environment and five reinforced trials in the new training environment, presented in random order. Once pigeons chose correctly on their first choice at four out of five trials in each environment, they were given a second phase of re-training in which all ten trials were in the new environment type. Once pigeons chose correctly on at least eight of the ten trials in 1 day, they proceeded to the last phase of re-training, which was the same as the second except that four of the ten trials were non-reinforced. Birds progressed to re-testing when they scored eight out of ten trials correct in one session.

Re-testing Re-testing in the new environment type followed the same procedures used in the first testing phase. Re-testing continued until birds made a choice on eight Control trials and eight of each of the Angle Removed, Feature Removed, and Conflict tests (see Fig. 6, left, center, and right columns, respectively).

Results

Pigeons quickly learned to locate their goal corners in the new environment. In testing, all birds maintained perfect accuracy to their trained goal corners in the Control test, demonstrating that they remembered their correct corners from training.

In the square Angle Removed test, birds again had near perfect accuracy to the blue feature panels. In the Feature Removed test, birds chose the trained goal corners significantly more often than chance (.50; $M = .76$, $SD = .32$, $t(7) = 2.33$, $p = .05$), and an ANOVA revealed no significant effects of Goal Corner (i.e., acute or obtuse) or Environment (i.e., array or enclosed). Interestingly, in the Conflict test, birds chose the corner associated with the blue feature panel significantly more than chance (.50; $M = .78$, $SD = .26$, $t(7) = 3.03$, $p < .05$). As in Part I testing, there was no significant effect of Environment; however, unlike Part I, there was no effect of Goal Corners (i.e., acute or obtuse) on the Conflict test; after re-training in a new environment, angular amplitude no longer affected whether pigeons preferred the featural or angular cues.

Discussion

In training, both features and angles were informative so learning either one would have been sufficient to complete the task. In both initial testing and in re-testing in the new environment, pigeons chose the correct corner significantly above chance in both the Angle Removed and Feature Removed tests, irrespective of environment (i.e., array or

enclosed); this shows that both cues were sufficiently encoded in training to allow successful reorientation and location of the goal corners. This is not surprising for the enclosed environment in light of the wealth of research which has shown that both human and non-human animals can encode angular information in enclosed environments, even when other informative cues such as relative wall length are present (Tommasi and Polli 2004; Lubyk and Spetch 2012; Lubyk et al. 2012; but see Sturz and Bodily 2011). However, the fact that the environment type did *not* affect the encoding of local angular information is interesting, especially in light of evidence that young children use the wall (i.e., boundary) information rather than the local angular information to orient in similar diamond-shaped environments (Lee et al. 2012). The similar and above-chance performance by pigeons in both the array and enclosed environments in the Feature Removed test suggests that pigeons do not depend on directional cues derived from wall boundaries for orientation. Clearly, despite the presence of informative features in training, pigeons, like the humans in Experiment 1, readily extracted the angular information provided by the corners in both the array and enclosure.

Interestingly, the Part 1 conflict test showed an effect of trained goal corner: pigeons that were trained to locate the obtuse (120°) corners of the enclosure or array did not consistently prefer either the correct angular location or the blue feature panel, whereas birds that were trained to locate the acute (60°) corners showed a strong preference to the correct angular location over the blue feature panel. This is interesting because an effect of amplitude on angle salience was not found in a previous study with pigeons that were trained in a parallelogram-shaped enclosure using the same 60° and 120° angles (Lubyk and Spetch 2012); pigeons in that study weighted the correct angular locations heavier than other salient geometric information, irrespective of goal corner amplitude. However, the Lubyk and Spetch training did not provide salient featural information. One possibility is that the featural information present in the current experiment facilitated the encoding of the angular amplitudes and enhanced the difference in salience between acute and obtuse angles (see Graham et al. 2006; Kelly 2010; Horne and Pearce 2011). Effects of amplitude on angle salience were also found in studies conducted with chicks in enclosures (Tommasi and Polli 2004) and adult humans with arrays of angles (Reichert and Kelly 2011). As in the current study, the smaller angles (60° vs. 120° for the chicks and 50° vs. 75° for the adult humans) appeared to be more salient.

Although greater salience of the acute angles over the obtuse angles provides a reasonable interpretation for the effect of goal corner, another possibility is that the angular information was equally salient in both the acute and

obtuse corners, but the visual salience of the blue feature panel differed; specifically, the blue features may have been *less* salient in the acute corners because the visible surface area of the features were smaller. Pigeons tended to approach the angles in the arena head-on in order to make a choice; this would have resulted in the subjective visibility of the blue panel to be significantly reduced in the acute corners as compared to the obtuse and could have caused the acute-trained pigeons to therefore rely more on the angular information.

Part 2 examined pigeons' performance in the same test conditions as Part 1, but reversed the environment type. Although performance in the Angle Removed and Feature Removed tests remained similar to those of Part 1, the Conflict test results differed. Specifically, birds in both the array and enclosed environments now weighted the blue features significantly heavier than the correct angular locations. This change in preference to the featural cue, irrespective of goal corner or environment type, could reflect the extended exposure to the blue feature panel. This would be consistent with previous research which has shown that with increased amounts of training, features tend to become dominant over other informative sources of environmental information (see Ratliff and Newcombe 2007; Twyman et al. 2007).

Experiment 3

One potential weakness of the above two experiments is that due to the overall shape of the diamond-shaped enclosure and array, there is a principal axis which runs down the centroid of the space (for more information on principal axes see Cheng 2005). Due to this presence, choice of the correct angular location could therefore be driven by the principal axis rather than the local angular amplitude. We think this possibility is unlikely, however, due to findings in similar studies conducted with both adult humans and pigeons in parallelogram-shaped environments (Lubyk et al. 2012; Lubyk and Spetch 2012, respectively), which found that local angular amplitudes were weighted heavier than principal axis information, despite both being encoded in training. Nevertheless, in order to rule out this potential alternative explanation to our results, additional test manipulations conducted with pigeons are reported here in Experiment 3.

This experiment was designed to confirm that choice of the correct angles reflected attention to angular information and were not instead based on exclusive use of principal axis information. Four of the pigeons from Experiment 2 were re-trained to locate their geometrically equivalent goal corners in the array environment. Only the array environment was used because the free-standing angles

allowed manipulation of angles in any configuration. The birds were tested without informative featural information in manipulated environments that preserved only either the principal axis from training or the angular information from training. A third test preserved both angles and the principal axis and served as a control to ensure that the birds' accuracy in the absence of features was not diminished relative to their performance in Experiment 2.

Methods

Subjects

The subjects were four of the original eight adult pigeons (*C. livia*; two Homing and two Silver King) that participated in Experiment 2, run approximately 6 months after their Experiment 2 completion date. One of the birds participated in a non-related spatial operant task in the time between Experiments 2 and 3. The pigeons were counter-balanced across their original groups so that two (one acute, one obtuse) had initially been trained in the enclosed environment first, while the other two (again one acute, one obtuse) had been trained in the array environment first.

Apparatus

The re-training apparatus was identical to the Experiment 2 array training arena (see Fig. 5, left). The test arrays were created using various configurations of the 60°, 90°, and 120° free-standing angles used in Experiment 2. On initial test trials, all blue feature panels were removed from the test arrays in order to isolate either the principal axis or angular information. However, all but one of the pigeons quickly stopped responding on these tests, presumably because the absence of the features was associated with non-reinforcement. We therefore restarted testing with an altered protocol, which provided blue feature panels in all four corners; this still rendered the featural information uninformative in terms of which corner was correct, but provided a cue associated with reinforcement at all corners in order to increase motivation to choose.

For the Principal Axis Only test (see Fig. 7, left), the free-standing angles were located in the same positions as in the training environment, but uninformative 90° right angles replaced the 60° and 120° angles. The Angle Only test arena (see Fig. 7, middle) equated the distances between all four angles' apexes to that of the distance between the two acute (60°) corners in training (approximately 82 cm across). The Angles + Principal Axis test (see Fig. 7, right) was the same as the Feature Removed test in Experiment 2, except that all four corners had blue feature panels and served to ensure that accuracy in an

arena which contained both a principal axis and local angular information did not decrease relative to Experiment 2.

Procedures

Training All birds were re-familiarized with their goal corners in the array environment. Containers covered with paper towels were present in all corners but only the two trained corners, which also contained the blue feature panel, held a food reward of four pellets each. As before, in order to progress to partial reinforcement, the pigeon had to complete 2 consecutive days with a minimum score of eight out of ten correct. They then had to achieve at least eight out of ten correct in 1 day of partial reinforcement in order to progress to testing.

Testing Testing took place in manipulated arrays designed to examine whether pigeons had encoded and could individually use both the local angular amplitudes and the principal axis. Blue feature panels were located in all corners and hence were uninformative. For the Principal Axis Only test (see Fig. 7, left), the informative angular amplitudes from training were replaced with right angles. This isolated the principal axis and allowed us to examine whether the pigeons could orient and find their trained goal corners without the informative angular amplitudes. If so, the acute (i.e., 60°) trained birds would choose the right angles located at either end of the principal axis, whereas the obtuse (i.e., 120°) trained birds would choose the right angles at either end of the short axis.

For the crucial Angle Only test (see Fig. 7, middle), the distances between the free-standing angles were equated to remove the principal axis as a cue. If the pigeons were able to use the local angles independently, they would still choose their trained angles (i.e., acute or obtuse), despite all angles being spaced apart equally. The Principal Axis + Angles test (see Fig. 7, right) provided both principal axis and angular information and served as a control to ensure that pigeons would continue to respond accurately in the absence of *informative* featural information as they had in Experiment 2.

Each daily test session consisted of six reinforced baseline trials within the training array, three non-reinforced test trials (one of each type), and one non-reinforced control (i.e., training) trial. As before, the order of trials was randomized across days, but was controlled so that two non-reinforced trials (i.e., test or control) never occurred in a row. Testing continued until the pigeon completed (i.e., made a choice in) eight trials in each of the test and control conditions.

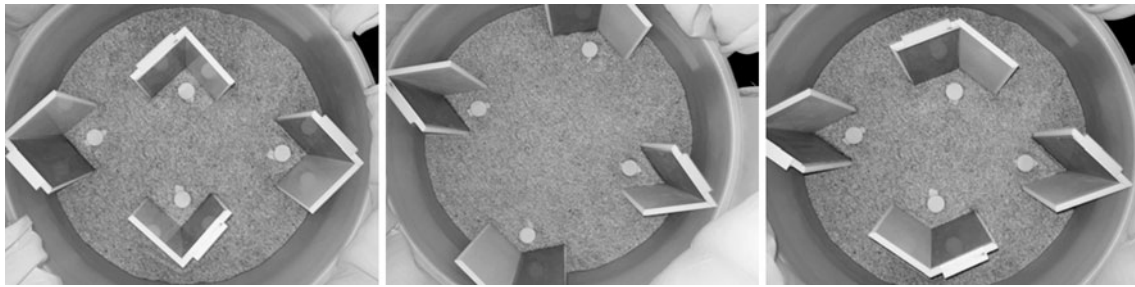


Fig. 7 Top-down views of test enclosures for Experiment 3: Principal Axis Only (*left*), Angles Only (*middle*), and Principal Axis + Angles (*right*). Note that in all three test conditions the blue feature panels are

present in all four corners, thus rendering the information useless for location of the trained corners

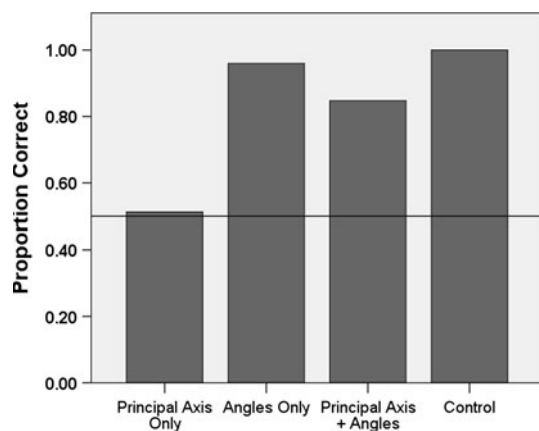


Fig. 8 Mean proportion of correct choices made by pigeons to the tests in Experiment 3. Data are collapsed across environment type (i.e., array and enclosure) as well as goal corner (i.e., acute and obtuse) because of the lack of significant differences found between the groups. The *horizontal line* indicates chance level (.50)

Results

All birds easily re-learned their goal corners, meeting the criterion to move on in the minimum number of sessions in both phases of training (i.e., full reinforcement and partial reinforcement). On the Principal Axis + Angle test, overall performance was significantly higher than would be expected by chance (.50; $M = .85$, $SD = .16$, $t(3) = 4.47$, $p < .05$; see Fig. 8). This test was also used as a control to ensure that performance in the task did not suffer as a result of the time elapsed between Experiments 2 and 3. It also served to ensure that our protocol adjustment regarding having blue features on all four angles in testing (to eliminate the usefulness of the feature while still driving motivation to choose) yielded the same results as the equivalent test in Experiment 2 (i.e., the Feature Removed test, which contained no feature panels). A paired-sample t test comparing the birds' accuracy to the correct corners in Experiment 2 (i.e., no feature panels; see Fig. 6, center column, top row) and 3 (i.e., four feature panels; see Fig. 7, right) revealed no significant difference in performance

between the two (Experiment 2, no feature panels: $M = 1.00$, $SD = 0$; Experiment 3, all four feature panels: $M = 0.85$, $SD = .16$; $t(3) = 1.96$, $p = .15$).

On the Principal Axis Only test, overall performance did not differ from chance (.50; $M = .51$, $SD = .12$, $t(3) = .21$, $p = .85$; see Fig. 8) and none of the pigeons were correct on more than five out of the eight trials. On the Angle Only test, one of the birds failed to discriminate between the local angles in the absence of a reliable principal axis, choosing the incorrect corners more often than the correct ones (two out of eight correct). The remaining three birds, however, had extremely high accuracy to the correct local angles, with two directing all eight of their choices to the correct corners, and one directing seven choices to the correct corners. Therefore, although the overall performance was not above chance, three of the four birds were significantly more accurate than chance according to a binomial test (.50; $p < .05$). No statistical analyses were conducted on the Control trials, which were conducted as non-reinforced baseline trials, as performance in these trials was at ceiling for all subjects.

Discussion

The results for the Experiment 3 Principal Axis Only test are interesting because they showed that, surprisingly, pigeons were not able to locate their trained goal corners based solely on the principal axis information provided by the array configuration. This result is in line with findings in both domestic chicks (Tommasi and Polli 2004) and pigeons (Lubyk and Spetch 2012), in which subjects weighted the correct angular locations from training heavier than the locations associated with the principal axis. However, in those experiments, birds were able to locate their correct corners when tested in a rectangular environment which maintained the same wall length proportions and principal axis from training. These findings, combined with our current results, suggest that in those studies, the wall length information may have been crucial to successful orientation, as no wall length or distance

information was present in the current test condition in which the spaces between the angles were equated.

The main goal of Experiment 3 was to explore whether pigeons could encode the local angular amplitudes in testing when they were not confounded by the principal axis information. The results of the current Angle Only test show that three of the four pigeons had no trouble extracting the local angular information from the free-standing angles in the absence of both informative featural information and a reliable principal axis (the fourth pigeon did not respond accurately according to either the principal axis or angular information when tested alone). These results suggest that in Experiment 2, pigeons were in fact using the angular amplitudes when the features were removed and *not* relying instead on the principal axis; the results of the Principal Axis Only test, in which birds were not able to orient based on the principal axis alone, further supports this conclusion. In order to completely rule out the principal axis as a confounding factor for the adult human experiment, though, future studies should conduct similar tests with humans in order to isolate the principal axis and angle information.

General discussion

There are three interesting conclusions suggested by our results. First, and perhaps most surprisingly, both adult humans and pigeons oriented and located correct corners just as easily in diamond-shaped arrays composed of free-standing angles as in diamond-shaped enclosures in which walls connected the angles. For both species, the accurate performance on the square Angle Removed tests indicated that the featural information provided at the correct corners was encoded, whereas the accurate performance on the Feature Removed tests indicated that orientation did not depend on this featural information. That is, the presence of informative features did not prevent the encoding of angular information. Thus, angles seem to provide a salient cue for both adult humans and pigeons, and angular information was used both within enclosed environments and arrays. In fact, humans performed more accurately on Feature Removed tests in the array environment than in the enclosed environment, suggesting that angular information may have been even more salient in the arrays. This attention to angular geometry is consistent with our previous studies (Lubyk et al. 2012) but is surprising in light of suggestions that angles provide a weak geometric cue (e.g., Newcombe et al. 2010).

Second, the results for adult humans revealed sex differences in the weighting of features and angles that mirror those seen in the encoding of features and geometry based on relative wall length. Specifically, although significantly oriented, females were less accurate than males when the

featural information was removed, and they showed higher weighting of features on conflict tests compared to males. These results are consistent with results from previous studies (Astur et al. 1998; Kelly and Bischof 2005; Andersen et al. 2012) which have suggested that females are more likely to attend to local landmarks, whereas males attend more to the geometry of the environment. The similar sex difference found here suggests that, contrary to recent suggestions (Newcombe et al. 2010; Spelke et al. 2010; Sturz et al. 2012), angular information was likely processed as a geometric cue rather than as local feature. Unfortunately, we could not investigate potential sex effects in pigeons because of the small number of subjects and because the sex was not known for all pigeons in our study.

Third, we observed some differences between the group trained to go to acute angles and the group trained to go to obtuse angles. For humans, this difference was revealed only as an interaction between training angle and environment type on the Angle Removed test. For pigeons, however, a main effect of training angle appeared on the first set of conflict tests, with acute-trained pigeons showing a much higher preference for angular information than obtuse-trained pigeons. This result is consistent with findings by Tommasi and Polli (2004), where domestic chicks trained to go to acute corners of a parallelogram were more likely to choose angle over wall length information on conflict tests, whereas the opposite was true for chicks trained to go to obtuse corners. Together, these results suggest that in some situations, acute angles may be more salient than obtuse angles.

Finally, although this research was not designed to provide a direct comparison between the performance of humans and pigeons, it is clear that both species were consistent in encoding angular geometry in both arrays and enclosures. This suggests that, irrespective of how it is encoded, angular information is a salient part of the geometry of an environment. However, crucial questions still remain regarding *how* angular information is processed by both pigeons and humans in enclosed environments and arrays. For instance, it is not known whether it is the actual divergence of the arms from the apex (i.e., how angle is measured mathematically) that is encoded, or simply the resulting *distance* between the outermost points of the angle. The goal of the current experiments was to explore *whether* local angular information could be readily extracted from environments and used for orientation; our results do not distinguish between the two possible ways of using the angles. To our knowledge, this has not been examined in either humans or non-human animals and is an important next step in fully understanding exactly how the angular information present in environments is used.

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