University of Alberta

The role of geometric and non-geometric environmental cues in reorientation:
Pigeons’ and humans’ use of relative wall lengths, angular information, and features

by

Danielle Mary Lubyk

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Abstract

The purpose of the following studies was to explore how humans and pigeons encode and use the geometric and featural information of their environments to orient and navigate. Chapters 1 and 2 examine the use of angular amplitude and relative wall length information in parallelogram-shaped enclosures by humans and pigeons. Results show that both species readily encode both cues in training and are able to use them individually to orient, but the angular information of the corners is weighted heavier than the relative wall lengths. Chapters 3 and 4 build upon these findings, using diamond-shaped enclosures and arrays to examine how orientation via angular amplitudes and features compare in the two environment types. Results indicate that both humans and pigeons can orient using either cue. However, the relative salience of the featural and angular information differs by species, environment type, and the amplitude of the goal angles.

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the blue feature panel and the correct angular location equally often. Error bars reflect the standard error of the mean.

General Introduction

The Study of Comparative Cognition

Cognition is the mental process of gaining knowledge and understanding of the surrounding world through thought, experience, memory, and the senses. Often these mental processes are incorrectly attributed to being unique only to humans; however, nonhuman animals also exhibit behavioral flexibility and learning which reflects the existence of advanced cognition. Indeed, it is quite common for pet owners, nature lovers, etc. to subjectively attribute human-like emotions or qualities such as love, guilt, curiosity, or memory to nonhuman animals through their personal observations. However, mere anecdotal evidence of such cognition does not withstand the scrutiny of scientific inquiry. For example, in the early twentieth century, motivated by the recent writings of Charles Darwin on animal intelligence, a German mathematician claimed that his horse, Clever Hans, was able to solve complex arithmetic problems, tell time, keep track of the days of the week, differentiate musical tones, and even read. Clever Hans and his owner travelled around Germany exhibiting his talents. However, when Hans' astounding abilities were put to the test, it was discovered that he in fact was responding to the involuntary reactions and body language of his trainer, rather than actually completing the tasks mentally (Pfungst, 1911). It is for this reason that comparative cognition, the study of the cognitive processes of human and non-human animals (Shettleworth, 2010), provides a scientific approach to the study of the generality of cognition in the animal kingdom. The majority of the advanced methods that exist today, which are used to scientifically study and explore animal cognition, are due to the early paradigms developed by Ivan Pavlov and Edward Thorndike, who pioneered the studies of associative and behavioral learning.

While the pure observation of behavior is a necessary first step in understanding and studying animal cognition, is it not alone sufficient; answering complex questions about the nature of cognition requires objective and empirical experiments which isolate potential variables. Morgan's Canon states that in comparative cognition the simplest explanation is most likely the correct one; therefore psychologists should always interpret the available information with the same level of contemplation and thought as the evidence requires. Keeping this principle in mind, the science of comparative cognition explores the mental processes of attention, perception, memory, timing, spatial cognition, tool use, problem solving, and social cognition, to name a few (for a complete overview, see Shettleworth, 2010). By studying these complex processes in human and nonhuman animals, we are able to gain insight into the evolution of these cognitive processes, as well as of the species themselves. While all of these processes are worthwhile to study, and themselves occupy a large body of literature, for the purpose of the following thesis, the focus herein will be solely the study of spatial cognition in human and nonhuman animals.

Spatial Cognition

For many animals, survival is based largely on the organism's ability to move around in order to locate food sources, shelter, or conspecifics. This ability to be mobile and navigate is often taken for granted when studying the ecology and behavior of a particular species. However, there is a premium on the ability to orient in a given environment and efficiently navigate to a goal location; randomly wandering around until the goal is found, would, for several species, substantially increase the risk of being predated, getting lost, or not obtaining the necessary resources in the required time. For instance, starlings *(Sturnus vulgaris)* spend the majority of their time foraging for food to bring back to the nest for their young, often making as many as 400 round trips to and from their nest daily (Kacelnik, 1984). For such animals, the cost of inefficient navigation would be substantial.

Animals use a variety of environmental cues and processes to determine their orientation and subsequently navigate to a goal. However, these processes vary by species and context. Animals that use the sun to orient and determine heading are said to possess a *sun compass,* meaning they use the relative position of the sun over the earth to direct their movement home after foraging (e.g., sea turtles: Mott & Salmon, 2011; arctic birds: Alerstam, Gudmundsson, Green, & Hedenstrom, 2001; pigeons: Gagliardo, Vallortigara, Nardi, & Bingman, 2005; monarch butterflies: Zhu, Sauman, Yuan, Casselman, Emery-Le, Emery, & Reppert, 2008). Many insects, such as ants, also use the sun's polarized light (Wehner & Müller, 2006). *Dead reckoning* (or *path integration*), where an internal record of the direction of travel away from the start point is recorded and repeatedly updated, has also been studied in several insect species, including ants (Buehlmann, Hansson, & Knaden, 2012) and bees (Kirchner & Braun, 1994).

Cues for orientation which are more relevant in avian and mammalian species, including humans, are the *featural* properties of the environment. Featural information can be any distinct cue present in the environment, such as colour, shape, or smell, which aids in the orientation process. A distinct feature can serve as a *beacon*, a proximal cue that is directly associated or close to a given goal location. For instance, several species of birds use distinct sounds or informative visual cues such as surrounding objects to return to their nests. Featural cues which aid in orientation but are not directly associated with a goal location are referred to as *distal* cues. In the classic demonstration of proximal and distal cue use by Morris (1981), rats in one group were trained to swim to a visible platform in a circular tank full of water. Irrespective of the platform's location within the tank, the proximal cue of the platform became a beacon, and the rats easily located it. However, for another group, the platform was located slightly below the water's surface, and the rats had to use the distal cues present in the room outside of the tank to locate the platform. This experiment demonstrated animals' ability to adapt in a given situation and to use either type of cue to orient and navigate to a goal location.

In addition to featural information, the *geometric* information present in an environment also serves as informative cues for orientation. Geometric information is any cue based on the global shape of the environment (Cheng, 2005). This includes, among others, such properties as wall length, metric information, angles, and relational distances. Cheng (1986) coined the term "geometric module", referring to an *exclusive* reliance on an environment's geometry despite the presence of other informative cues, following his interesting discovery in rats. Rats were trained to locate a food reward in one corner of a rectangular enclosure which provided the geometric cue of relative wall length (i.e., where orientation can be achieved by using the differing wall lengths based on an animal's subjective position, such as a longer wall on right and a shorter wall on left). Adjacent to the food reward was a distinctly coloured wall (a feature), which, if used in combination with the relative wall length relationships, would always lead the rat to the correct corner. However, Cheng found that instead, rats ignored the distinctive featural information and searched exclusively in the two geometrically equivalent corners which had the same relative wall length information. In subsequent tests, Cheng learned that rats *could* learn to use the featural information present, but it remained that their default was to use purely the geometry of the environment to orient. Cheng called this blind reliance on geometry the "geometric module." This module has since been called into question in favour of more parsimonious explanations of orientation (see Cheng, 2008; Twyman & Newcombe, 2010). However, it nevertheless provided the foundation for the study of geometric cue use in human and nonhuman animals, which is still widely prevalent today.

Despite the current doubt of the geometric module, a very relevant type of information which sources from an environment's geometry is the *principal axis of space,* which runs through the centroid (i.e., center of mass) of any enclosed space. Mechanically, the principal axis minimizes the amount of wobble when the space is rotated around it (for a more detailed overview see Cheng, 2005). Many studies examining orientation and navigation in both human and nonhuman animals argue that principal axes are the most primitive and commonly used source of geometric information. However, because a single principal axis only exists if the space has a non-equilateral shape (e.g., a rectangle as opposed to a square), the principal axis information is often confounded with other types of salient geometry such as relative wall length information. However, it is still the case that principal axis information remains a distinct contender in the spatial orientation literature, and many researchers focus on it as a main facilitator of geometric orientation (see Bodily, Eastman, & Sturz, 2011; Sturz & Bodily, 2011; Sturz, Gurley, & Bodily, 2011).

Since Cheng’s (1986) pioneer study with rats, all animals studied to date have been shown to be able to orient based on the geometric properties of their environment (for a review see Cheng & Newcombe, 2005), though the hierarchical weighting of these cues with others, such as features, varies by both species and context.

Model Avian Species

Birds have long been used as models of human spatial cognition because of the similarity in brain function with regard to spatial memory between the two. The majority of studies examining the encoding of spatial cues, however, have focused on the domestic chick *(Gallus gallus)* and homing pigeon *(Columba livia).* These two avian species provide a unique perspective on the study of spatial cognition for several reasons: First, chicks are precocial, meaning they are relatively mature and mobile from the time they hatch. This enables them to be the subject of study very early on in their life, and manipulations of cue and sensory availability allow researchers to examine which aspects of cognition are innate and which are learned (for a review see Vallortigara, Regolin, Chiandetti, & Rugani, 2010). Pigeons, on the other hand, are altricial, meaning they are immature when they hatch and are completely reliant on their parents for care several weeks. Therefore, these two species give a unique perspective on the role of development in the acquisition and use of spatial knowledge, and is why they are often directly compared in the spatial literature (e.g., Kelly, Chiandetti, & Vallortigara, 2010; Wilzeck & Kelly, 2011). Second, the lifestyles and main modes of locomotion in the two species are very different; chickens have been domesticated for egg and meat production and are ground-dwelling birds, while pigeons have been bred over centuries for homing long distances. These differences allow researchers to examine the effects of lifestyle and mode of travel. Lastly, although chickens and pigeons are both members of the avian class, they have not shared a common ancestor for nearly 100 million years (Hackett et al., 2008), which allows for the study of the evolution of spatial abilities. For the following studies, however, the pigeon (*Columba livia;* Homing and Silver King strains) is the model avian species, and will be compared to adult humans with respect to the encoding of environmental information for orientation and navigation.

Current Studies

Since Cheng's (1986) pioneer study of geometry, a wealth of experiments examining spatial orientation via geometry and features have been published in a variety of species. Recently, one type of environmental cue which has been receiving a lot of attention is the cue of angular amplitude. The angular information created by conjoined walls has long been assumed to belong under the umbrella category of geometric information, due to the inherent geometric aspect of angles: they have measurable numeric amplitude and together create the global geometric shape of the environment. However, recent literature conducted with humans and domestic chicks, which will be discussed in the forthcoming chapters, has called this into question. The following studies examine spatial orientation and navigation in pigeons and humans with respect to various environmental cues. Chapter 1 examines orientation and small-scale navigation in pigeons in a parallelogram-shaped enclosure which provides the cues of relative wall length, angular amplitude, and a principal axis of symmetry. Subsequent transformational tests (Cheng & Spetch, 1988) place the cues present in training either in isolation or in conflict with one another to determine which were encoded and which are weighted more heavily. Chapter 2 asks the same questions but in humans, using a non-immersive three-dimensional environmental which participants navigate through on a computer screen. Previous research into the generality of spatial processes in real versus virtual environments has shown that both environment types provide comparable results and therefore virtual environments provide a valid source of information on real-world navigation (see Klatzky, Loomis, Beall, Chance, & Golledge, 1998; Sturz, Bodily, Katz, & Kelly, 2009).

Chapters 3 and 4 build on the findings of Chapters 1 and 2 and examine the use of angle and feature information in humans and pigeons, respectively. Pigeons are trained in either a small scale diamond-shaped enclosure or an equal-sized environment created by an array of freestanding angles. Both environment types contain salient feature information which can also be used to locate the goal. Subsequent tests in both environments which use an overshadowing procedure to determine whether pigeons weight both the angular and feature information equally, as well as to explore the possibility that angles may be encoded as features, rather than geometry. Humans receive the same experimental paradigm, except in a fully-immersive three-dimensional virtual environment which is scaled to be the same relative size as the environments that the pigeons experience.

Overall, the following chapters provide detailed investigations into how both pigeons and humans represent and use the geometric and featural properties of their environment to orient and navigate to a goal location.

Bibliography

Alerstam, T., Gudmundsson, G., Green, M., & Hedenstrom (2001). Migration along orthodromic sun compass routes by arctic birds. *Science*, *291*, 300-303. doi:10.1126/science.291.5502.300

Bodily, K. D., Eastman, C. K., & Sturz, B. R. (2011). Neither by global nor local cues alone: evidence for a unified orientation process. *Animal Cognition*, *14*, 665-674. doi:10.1007/s10071-011-0401-x

Buehlmann, C., Hansson, B. S., & Knaden, M. (2012). Path integration controls nest-plume following in desert ants. *Current Biology, 22,* 645-649. doi: 10.1016/j.cub.2012.02.029

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23,* 149-178. doi:10.1016/0010-0277(86)90041-7

Cheng, K. (2005). Reflections on geometry and navigation. *Connection Science*, *17*, 5-21. doi:10.1080/09540090500138077

Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Science, 12,* 355-361. doi:10.1016/j.tics.2008.06.004

Cheng, K. & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review, 12,* 1–23. doi:10.3758/BF03196346

Cheng, K. & Spetch, M. L. (1988). Mechanisms of landmark use in mammals and birds. In: Healy S. (Ed) Spatial representation in animals. Oxford University Press, Oxford, pp 1-17.

Hackett, S. J., Kimbali, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., Chojnowski, J. L., Cox, W. A., Han, K., Harshman, J., Huddleston, J., Huddleston, C. J., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Steadman, D. W. & Witt, C. (2008) A phylogenomic study of birds reveals their evolutionary history. *Science, 320,* 1763–1768.

Gagliardo, A., Vallortigara, G., Nardi, D., & Bingman, V. P. (2005). A lateralized avian hippocampus: preferential role of the left hippocampal formation in homing pigeon sun compass-based spatial learning. *The European Journal of Neuroscience*, *22*, 2549-2559. doi:10.1111/j.1460-9568.2005.04444.x

Kacelnik, A. (1984). Central place foraging in starlings *(Sturnus vulgaris).* I. Patch residence time. *Journal of Animal Ecology, 53*, 283-299. doi:10.2307/4357

Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2010). Re-orienting in space: Do animals use global or local geometry strategies? *Biology Letters, 7,* 372-375. doi:10.1098/rsbl.2010.1024

Kirchner, W. H., & Braun, U. (1994). Dancing honey-bees indicate the location of food sources using path integration rather than cognitive maps. *Animal Behaviour, 48, 1437-1441.* doi:10.1006/anbe.1994.1379

Klatzky, R. L., Loomis, J. M., Beall, A. C., Chance, S. S., & Golledge, R. G. (1998). Spatial updating of self-position and orientation during real, imagined, and virtual locomotion. *Psychological Science, 9,* 293–298. doi:10.1111/1467-9280.00058

Morris, R. G. M. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation, 12,* 239-260.

Mott, C. R., & Salmon, M. (2011). Sun Compass orientation by juvenile green sea turtles *(Chelonia mydas), Chelonian Conservation and Biology, 10,* 73-81.

Pfungst, O. (1911). *Clever Hans (The horse of Mr. von Osten): A contribution to experimental animal and human psychology* (Trans. C. L. Rahn). New York: Henry Holt.

Shettleworth, S. J. (2010). *Cognition, Evolution, and Behavior.* New York, NY: Oxford University Press.

Sturz, B. R., & Bodily, K. D. (2011). Is surface-based orientation influenced by a proportional relationship of shape parameters? *Psychonomic Bulletin & Review*, *18*, 848-854. doi:10.3758/s13423-011-0111-z

Sturz, B. R., Bodily, K. D., Katz, J. S., & Kelly, D. (2009). Evidence against integration of spatial maps in humans: generality across real and virtual environments. *Animal Cognition*, *12*, 237-247. doi:10.1007/s10071-008-0182-z

Sturz, B. R., Gurley, T., & Bodily, K. D. (2011). Orientation in trapezoid-shaped enclosures: implications for theoretical accounts of geometry learning. *Journal of Experimental Psychology Animal Behavior Processes*, *37*, 246-253. doi:10.1037/a0021215

Twyman, A. & Newcombe, N. S. (2010). Five reasons to doubt the existence of a geometric module. *Cognitive Science, 34,* 1315-1356. doi:10.1111/j.1551-6709.2009.01081.x

Vallortigara, G., Regolin, L., Chiandetti, C., & Rugani, R. (2010). Rudiments of mind: insights through the chick model on number and space cognition in animals. *Comparative Cognition and Behavior Reviews, 5,* 78-99. doi:10.3819/ccbr.2010.50004

Wehner, R. & Müller, M. (2006). The significance of direct sunlight and polarized skylight in the ant's celestial system of navigation. *Proceedings of the National Academy of Sciences USA, 103,* 12575-12579. doi: 10.1073/pnas.0604430103

Wilzeck, C. & Kelly, D. M. (2011, March). The influence of age and gender on the visual side-bias in pigeons *(Columba livia).* In A. Blaisdell (Chair), *Attention and Associative Processes.* Symposium conducted at the Annual International Conference on Comparative Cognition, Melbourne Beach, FL.

Zhu, H., Sauman, I., Yuan, Q., Casselman, A., Emery-Le, M., Emery, P., & Reppert, S. M. (2008). Cryptochromes define a novel circadian clock mechanism in monarch butterflies that may underlie sun compass navigation. *PLoS Biology*, *6*, e4. doi:10.1371/journal.pbio.0060004

Chapter 1:

Pigeons' Use of Angular, Wall Length, and Principal Axis Information in an Open-Field Environment[1]

Introduction

Successful orientation in an environment is often an essential first step in navigating to a goal location, such as a shelter or food source, and thus is crucial for survival. However, not all sources of environmental information are reliable all of the time. For example, remembering that a food source is next to a tall lush tree may not be informative a few weeks later when the leaves have fallen and the tree is bare. For this reason, animals are equipped with the cognitive skills to use various sources of environmental information to orient and navigate (see Able, 1991).

One recently studied type of cue used by many animals to orient in small spaces is geometric information, which includes angles, wall lengths, the overall shape of an environment, and the spatial relationship between objects. Research in comparative cognition has demonstrated that locating a target in an enclosed space depends heavily on the geometry provided by the environment. This was first observed in a foundational study by Cheng (1986) in which he demonstrated that rats, when trained to locate food in one corner of a rectangular enclosure, made repeated rotational errors (choice of the geometrically equivalent but

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[1] *A version of this chapter has been published. Lubyk & Spetch 2012. Finding the best angle: pigeons (Columba livia) weight angular information more heavily than relative wall length in an open-field geometry task. Animal Cognition. 15: 305-312.*

opposite corner) despite the presence of a distinctly colored wall adjacent to the food source. Cheng called this blind reliance on geometry a “purely geometric module”, because the rats ignored the feature and used only the geometry of the enclosure to reorient. This geometric module has also been demonstrated in young prelinguistic children (Hermer & Spelke, 1994). Children witnessed the hiding of a toy in one corner of a rectangular room and then, after disorientation, were asked to find the toy. Children made repeated rotational errors during their search despite the presence of a distinct visual feature that could be used to differentiate between the corners.

These rotational errors do not reflect an inability to encode features of the environment. In fact, Gibson et al. (2007) showed that rats were able to use the features of their environment to find a goal location when the previously learned geometry was uninformative. Similarly, children can encode the featural properties of a room if the features are embedded into the geometry via three-dimensional bulges in the walls (Wang et al., 1999), or if the children are pre-trained with features (Twyman et al., 2007). Thus, the strong reliance on geometry despite the presence of more informative features seems to reflect a hierarchy in which geometric information takes precedence.

Although preference for geometric or non-geometric information varies, all species tested to date have been shown to be able to use the geometry of their environment to reorient (e.g., rhesus monkeys: Gouteux et al., 2001; pigeons: Kelly et al., 1998; Kelly & Spetch, 2001; chicks: Vallortigara et al., 1990; Vallortigara et al., 2004; fish: Sovrano et al., 2002, 2003, 2007; Vargas et al., 2004; Brown et al., 2007; ants: Wystrach & Beugnon, 2009; for reviews see Cheng & Newcombe, 2005; Kelly & Spetch, 2012). Recent studies on geometric encoding have significantly expanded our knowledge on how animals encode and use the geometry of their environments in several ways, including the encoding of relative versus absolute metrics (e.g., Tommasi & Vallortigara, 2000; Kelly & Spetch, 2001; Gray et al., 2004; Gray & Spetch, 2006; Wilzeck et al., 2009), and local versus global cues (e.g., Della Chiesa et al., 2006a, 2006b).

In the study most relevant to the current research, Tommasi and Polli (2004) trained domestic chicks *(Gallus gallus)* to locate food in two geometrically equivalent corners of a parallelogram-shaped enclosure, in which either the local geometry (angular amplitude of the corners) or global geometry (relative wall lengths) was alone sufficient to locate the goal corners. Transformational tests which forced the chicks to use only either the angular amplitude or relative wall length revealed the chicks’ ability to use either of these geometric cues successfully in isolation. However, a conflict test that placed the two cues in direct competition with one another revealed an interesting effect of previous experience: chicks initially trained to locate acute corners preferred the same angular location (i.e., the acute corners) in the conflict test, whereas chicks initially trained to locate food in the *obtuse* corners preferred the location defined by the correct relative wall lengths (i.e., also the acute corners). This study was the first to attempt to isolate the presentation of two distinct types of geometric properties in the domestic chick.

In a similar study, Hupbach and Nadel (2005) tested young children in a rhombus-shaped environment that only provided angular cues for orientation and found that children did *not* distinguish between the unique amplitudes of the corners until the age of four, suggesting an early inability to encode the local geometry of the angles. Sturz et al. (2011) trained adult participants in a virtual environment to select two geometrically equivalent corners of a rectangular-shaped environment. They were then tested in eight unique trapezoid-shaped environments. Interestingly, performance during these tests indicated that participants were making selections based on the global geometry of the environment (i.e., a principal axis) and not local geometry (i.e., angular amplitude of corners), which differs from Tommasi and Polli's (2004) findings in chicks (but see Cheng & Gallistel, 2005). In another very recent study, Reichert and Kelly (2011) trained adult humans to find a goal hidden in front of one of four L-shaped objects that differed in local angle (50^o or 75^o) and were arranged to form a rectangle. Single cue and conflict tests failed to provide evidence that participants encoded the global geometry provided by the rectangular arrangement of objects, and only the male participants showed significant evidence of encoding the local angular information from the objects.

Although there have been several studies on pigeons' use of geometry for orientation and small-scale navigation (see Cheng et al., 2006 for a review), we are not aware of any studies that have investigated their use of the local geometric properties of angle and wall length. Examining how pigeons compare to chicks in their response to manipulations of local geometry is particularly interesting given the recent research suggesting the possibility of fundamental differences in the ways these two commonly-used avian species encode and represent geometry (Wilzeck et al., 2009).

The current experiment was conducted in a similar fashion to that of Tommasi and Polli (2004). Pigeons were trained to locate food in two geometrically equivalent corners of a parallelogram-shaped training enclosure. Because there were no distinct featural cues present, both diagonally-opposite corners contained identical geometric information. Birds were counterbalanced so that half were trained to go to the acute (60°) corners and half to the obtuse (120°) corners. Due to the shape of the enclosure, either angular amplitude (angle created by the converging of the two walls on either side) or relative wall lengths (combination of long and short walls on either left or right side of angle) could be used to orient and navigate to the goal.

Once the pigeons had learned to go to their reinforced locations (herein referred to as the “goal corners”), transformational tests (Cheng & Spetch 1988) in rectangular, rhombus, and reverse parallelogram-shaped enclosures were carried out to determine if the birds had encoded both types of local geometry, as well as which type of information was dominant. The goals of the current study were a) to determine if pigeons could use two types of geometric properties, angles and wall lengths, in an isolated fashion in testing despite being presented as integrated properties in training, b) to explore the possibility of an ordered hierarchy for geometric cue preference through the conflict test, and c) to compare the current findings to those of the domestic chick in order to determine whether cross-species similarities exist with respect to the encoding of geometric properties for orientation and navigation.

Method

Subjects

The subjects were five male and three female adult pigeons (*Columba livia;* 4 Silver King and 4 Homing), all experimentally-naïve in open field geometry tasks. Homing pigeons had prior outdoor flying experience whereas Silver King pigeons did not. All birds were kept at 85 percent of their free feeding body weight on a diet of Key Tee pigeon pellets. Birds were housed in large individual metal cages (42 cm height x 47 cm width x 42 cm depth) and kept on a 12 hour light-dark cycle with light onset at 7:00am. Grit and water were provided *ad libitum.*

Apparatus

The apparatus used during training was a parallelogram-shaped enclosure (140 cm length x 70 cm width x 60 cm height; see Figure 1-1, top left) constructed of uniformly white Sintra, a lightweight material of polyvinyl chloride (PVC) compressed between two rigid sheets. The angular amplitudes of the two acute corners of the enclosure (formed by a long wall on the left and a short wall on the right) were 60°, while the angular amplitudes of the two obtuse corners of the enclosure (formed by a short wall on the left and a long wall on the right) were 120°. The floor of the enclosure was covered with approximately 4 cm of aspen chip bedding. In each corner a small white ceramic container (4 cm high, 7 cm diameter) was adhered to the ground with Velcro. Each container was layered with a small amount of grit. Except during preliminary shaping, each container was covered with a small square of paper towel secured with an elastic band. On reinforced trials the containers in both goal corners contained food. On non-reinforced trials and test trials, all containers were empty. Uniformly white translucent curtains hung around the experimental enclosure, which was placed on 12 cm high castors so its orientation could be changed across trials. The experimental room was lit by four 40 watt fluorescent light bulbs hidden behind a translucent plastic diffuser located approximately 2.2 m above the top of the arena. To block any visual cues on the ceiling a white translucent curtain also covered the entire ceiling of the experimental room except for a hole for the camera lens.

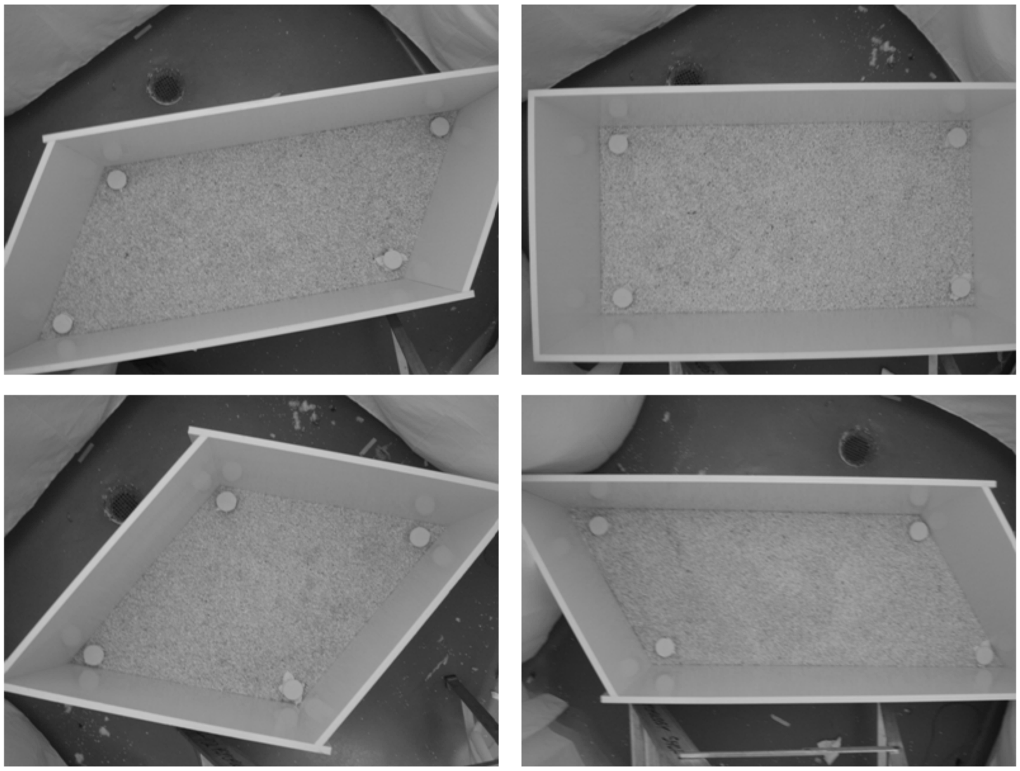

Figure 1-1. Top–down views of the parallelogram training enclosure (*top left*) and the rectangular (*top right*), rhombus (*bottom left*), and reverse parallelogram (*bottom right*) test enclosures.

The testing enclosures were constructed with the same materials as the training enclosure, except they were the following shapes: a rectangular-shaped enclosure (140 cm length x 70 cm width x 60 cm height; see Figure 1-1, top right), a rhombus-shaped enclosure (85 cm sides x 60 cm height; see Figure 1-1, bottom left) with the same angular dimensions as the training enclosure, and a reverse parallelogram-shaped enclosure (140 cm length x 70 cm width x 60 cm height; see Figure 1-1, bottom right), in which the angular amplitudes were now located in the opposite corners than in the training enclosure.

Procedure

Four pigeons were randomly assigned to each of the two training conditions, which were defined by their goal corners: four birds were trained to go to acute corners and four to obtuse corners. Each bird received one session per day, which consisted of ten individual trials. Birds were passively disoriented in the dark before each trial by being placed in a metal holding box and slowly rotated for one minute at a speed of 12 rpm. They were then placed in the enclosure facing a randomly chosen wall. The beginning of the trial was signaled by the light onset. In shaping, birds had a maximum of five minutes to select a container and consume the food before the lights were extinguished and the trial ended. If a choice was made in under five minutes, birds were given an additional minute in which they could choose a second container, which provided them with additional reinforcement if correct. The same protocol was in place during testing, except that none of the containers held food. The enclosure was also rotated every five trials to a randomly selected orientation to discourage the birds from using extraneous cues to orient.

Shaping

Initial shaping procedures began in each bird’s home cage. The birds were fed from the experimental food container in their home cage, with a small square of paper towel loosely placed over half of the container. Over several days, the paper towel was adjusted until it completely covered the food container, at which time it was secured with an elastic band. Initially, a large hole in the paper towel allowed birds to readily view and access the food. The size of the hole was then gradually decreased until no hole remained and the birds were required to peck through the paper towel to access their food. Once the bird was readily pecking through the paper towel, it began in the experiment.

Birds were first habituated to the parallelogram-shaped training enclosure by receiving a maximum of four trials of 20 minutes each per day to explore the enclosure and discover food in the two goal corners. Each of the four corners of the enclosure contained identical containers, but only the bird’s goal corners (i.e., 60° corners for acute birds and 120° corners for obtuse birds) held food. Containers were filled to the top with grit to make the food inside easily visible. No paper towel was present. Once a bird found and consumed the food from both goal corners in less than one minute for two consecutive trials it was moved to shaping. Initially the paper towel loosely sat over the containers. Next it was secured with an elastic band but with a large hole in the center, as in the birds' home-cage training. Across several days the size of the hole and the amount of grit in the containers were reduced until there was no hole in the paper towel and only a small amount of grit lined the bottom of the container. Once the bird reached this point, it was then required to complete one full session (i.e., ten trials) of shaping with a minimum of 80 percent accuracy (defined as a first choice being to either goal corner) in order to progress to the next phase of training.

Upon successful completion of reinforced shaping, birds began non-reinforced shaping, which prepared them for the subsequent non-reinforced test trials. The conditions of non-reinforced shaping were equivalent to those of the previous shaping, with all containers completely covered and containing only a small amount of grit, except now only 60 percent of trials contained reinforcement (i.e., four of the ten trials did not contain food in the goal corners). A minimum accuracy of 80 percent of choices to the goal corners over two consecutive sessions was required for progression to testing.

Testing

Each test session was composed of ten individual trials. Five of these were reinforced baseline trials in the training enclosure, two were non-reinforced control trials in the training enclosure, and three were non-reinforced test trials-one in each new test enclosure (rhombus, rectangle and reverse parallelogram).

The rectangular-shaped enclosure removed the angular information but maintained the proper wall lengths from training (see Figure 1-1, top right). If birds encoded the relative wall lengths of the training environment (e.g., long wall on the left and short wall on the right, in the case of birds trained to go to the acute corners), they should choose corners that maintained the trained wall length relationships. The rhombus-shaped enclosure (see Figure 1-1, bottom left), removed the wall length information but maintained the angular information. If birds had encoded the angular amplitude of their goal corners (e.g., 60°), they should choose the corners with correct angles despite the absence of the relative wall length information. The reverse parallelogram-shaped enclosure paired previously reinforced angular locations with unreinforced wall length locations and vice versa (see Figure 1-1, bottom right) and therefore provided a conflict test to determine which type of cue the pigeons preferred. If birds placed a higher priority on the angular information, they would continue to go to the angles they went to in training, even though these angles were now at incorrect wall length locations. Conversely, if they placed a higher priority on relative wall lengths, they would continue to go to the corners that maintained the same short-long wall relationship from training.

Trial type (i.e., baseline, control, or test) was determined in a pseudo-random fashion by counterbalancing order of presentation of test trials and ensuring that control and baseline trials were spaced approximately equally across each session. Individual trials lasted until the birds made two choices or for a maximum of five minutes, whichever occurred first. Although birds were allowed to make two choices in testing in order to maintain consistency from training, only the first choice in each trial was scored and used for all reported results. The testing phase of the experiment continued until birds successfully completed (i.e., made at least one choice) five trials of each of the test conditions (i.e., rectangle, rhombus, and reverse-parallelogram) as well as five control trials.

Results

Both groups of pigeons readily learned to choose their two geometrically equivalent goal corners (see Acute: Figure 1-2, top; Obtuse: Figure 1-2, bottom). There was no effect of Training Condition on total number of training days required, including training to peck through the paper towel (Acute: M=8.50, SD=1.73, Obtuse: M=6.75, SD=1.26; t_6=1.64, P=.15), or the number of days required to complete training once the birds learned to peck (Acute: M=3.75, SD=1.50, Obtuse: M=3.25, SD=.50; t_6=.63, P=.55). Accuracy to the birds' goal corners on the last two sessions of training (i.e., once the birds learned to peck through the paper towel) also revealed no significant effect of Training Condition (Acute or Obtuse), t_6=.63, P=.55. As well, all birds' accuracies to their goal corners were significantly above chance (50%), t_7=21.30, P<.0001.

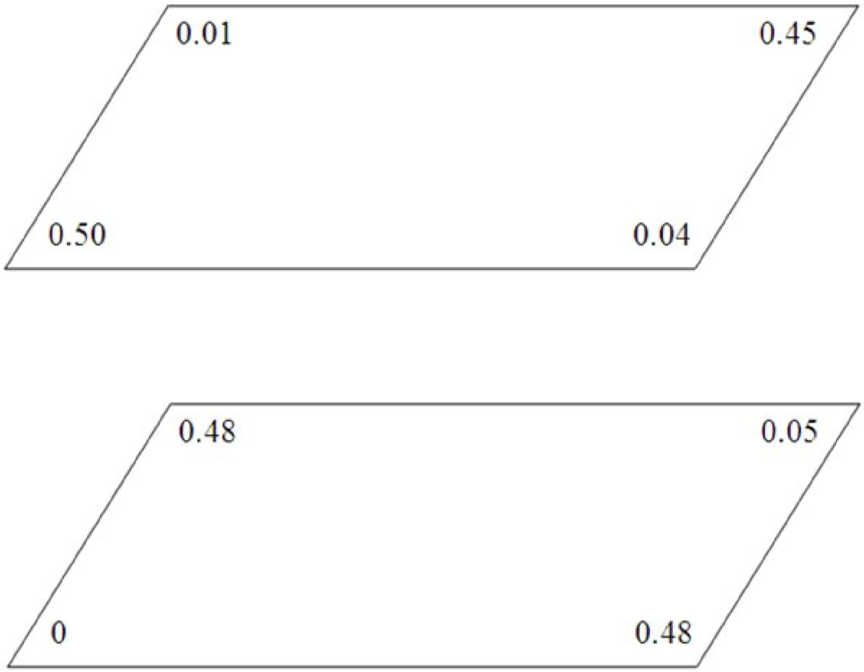

Figure 1-2. Proportion of choices to each of the four corners in training for the acute (60°) birds (*top*) and the obtuse (120°) birds (*bottom*). Proportions are rounded to two decimal places.

During testing, birds' accuracy in the training enclosure, as demonstrated by the Control trials, remained extremely high. In order to compare performance across the Control, Rectangle and Rhombus tests, a repeated measures analysis of variance with Training Condition (levels: Acute and Obtuse) as a between factor and Test (levels: Control, Rectangle, and Rhombus) as a within factor was carried out. Results revealed no interaction of Training Condition and Test ($F_{2,12}$=.49, P=.62), as well as no effect of Training Condition ($F_{1,6}$=.24, P=.64) on performance. However, there was a main effect of Test ($F_{1,6}$=11.44, *P*=.01). Post hoc pairwise comparisons (Tukey Test) revealed that birds' accuracy in the Control test (*M*=.97, *SD*=.05) was significantly higher than in the Rectangle test (*M*=.84, *SD*=.09) but was not significantly higher than in the Rhombus test (*M*=.87, *SD*=.10). Accuracy did not differ significantly between the Rectangle and Rhombus tests (see Figure 1-3).

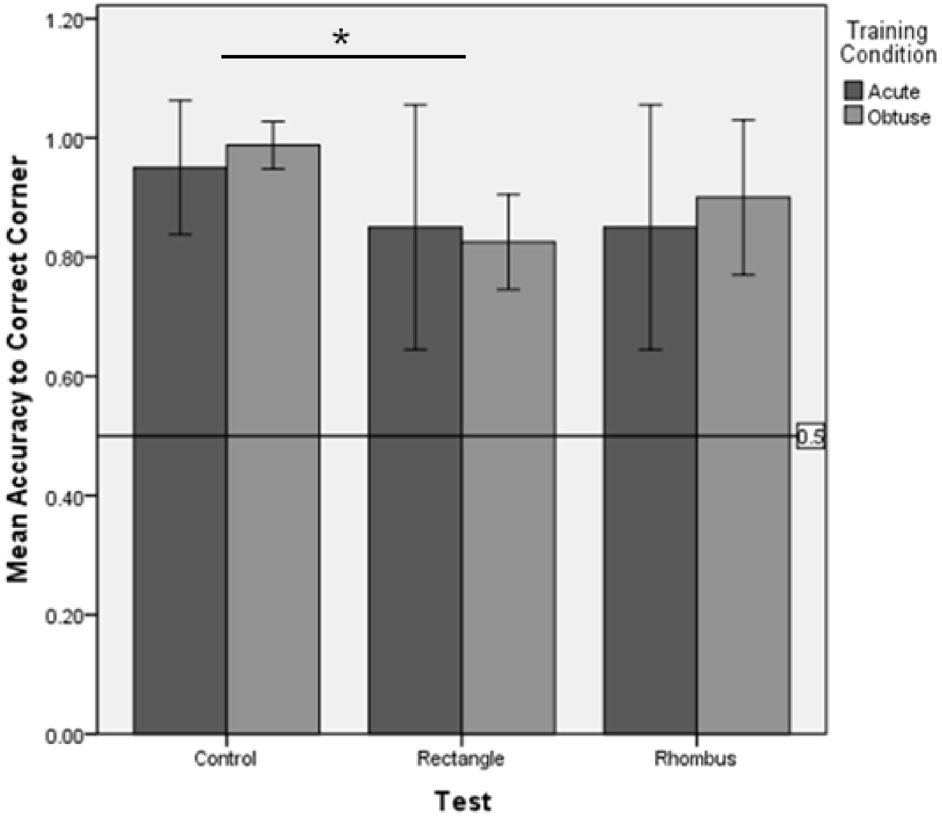

Figure 1-3. Mean proportion of choices to goal corners for acute and obtuse birds in each test condition. Error bars represent standard error of the mean. Chance level is .50

A detailed examination of results in the rectangular enclosure (see Acute: Figure 1-4, top; Obtuse: 1-5, top) clearly shows that pigeons in both training conditions chose correctly based purely on the relationships between the relative wall lengths. Specifically, pigeons in the acute group split the majority of their choices between the two geometrically equivalent corners that were intersected by a long wall on the left and a short wall on the right, whereas pigeons in the obtuse group mainly split their choices between the two corners that had a short wall on the left and a long wall on the right. An independent samples *t*-test confirmed that birds chose their correct corners at a rate significantly higher than that expected by chance (50%), $t_7=10.42$, $P<.001$.

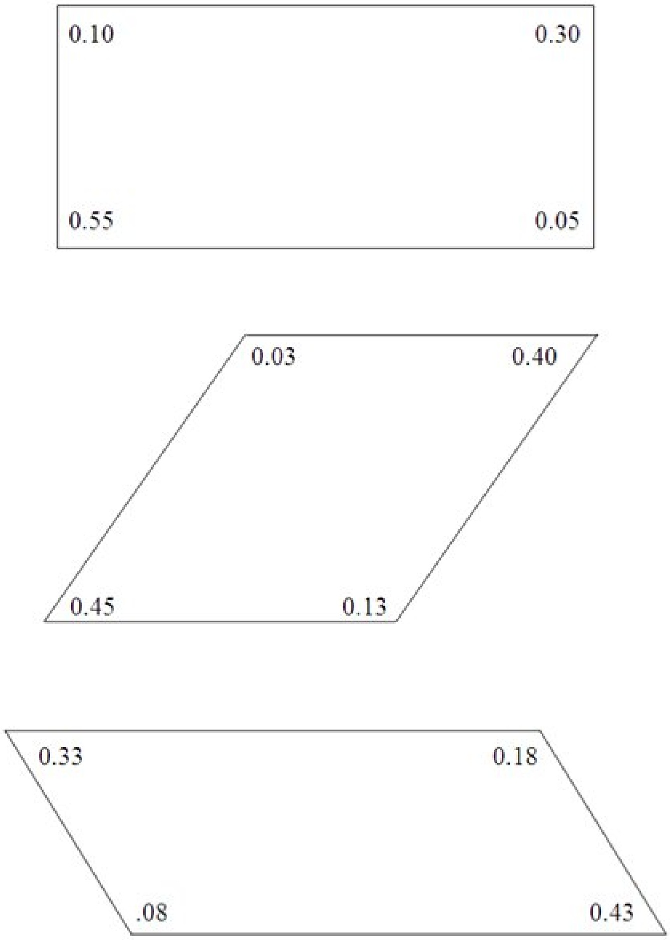

Figure 1-4. Proportion of acute birds' (*n* = 4) choices to each of the four corners in the rectangular (*top*), rhombus (*middle*), and reverse parallelogram (*bottom*) test enclosures. Proportions are rounded to two decimal places.

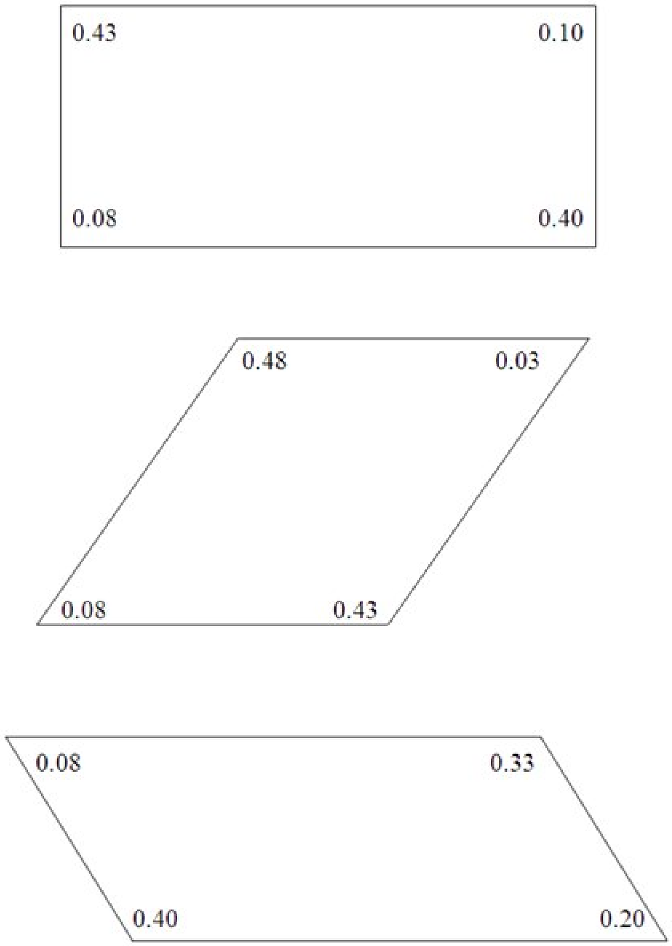

Figure 1-5. Proportion of obtuse birds' (*n* = 4) choices to each of the four corners in the rectangular (*top*), rhombus (*middle*), and reverse parallelogram (*bottom*) test enclosures. Proportions are rounded to two decimal places.

Similarly, testing results in the rhombus-shaped enclosure (see Acute: Figure 1-4, middle; Obtuse: 1-5, middle) clearly indicate that pigeons successfully navigated to their correct corners despite the angular amplitudes of the corners being the only geometric property available. Specifically, pigeons in the acute group split the majority of their choices between the two corners with a 60° angle, whereas pigeons in the obtuse group mainly split their choices between the two corners with a 120° angle. This occurred at a rate significantly higher than expected by chance (50%), t_7=10.25, P<.001.

On Conflict tests in the reverse parallelogram, pigeons in both groups primarily chose the corners with the previously reinforced angles rather than the corners with the previously reinforced wall lengths (see Acute: Figure 1-4, bottom; Obtuse: 1-5, bottom). A between-group *t*-test on choice of the corners with the correct angles revealed no difference between groups (t_6=.16, P=.88), and therefore the data were collapsed. A one-sample *t*-test confirmed that the pigeons chose the corners associated with the correct angular information significantly more often than expected by the 50% chance level (t_7=3.37, P=.012). Specifically, pigeons in the acute group primarily split their choices between the 60° corners and birds in the obtuse group primarily split their choices between the 120° corners, even though these corners were now adjacent to incorrect relative wall lengths.

A repeated measures analysis of variance revealed no effect of strain (Homing or Silver King; $F_{1,5}$=1.65, P=.26) or sex (Male or Female; $F_{1,5}$= 2.47, P=.18) on performance in the Control, Rectangle, and Rhombus tests. Independent samples *t*-tests also showed no effect of strain (t_6=1.85, P=.11) or sex (t_6=1.56, P=.17) on birds' preferences in the reverse parallelogram Conflict test.

Discussion

The current experiment clearly showed that pigeons can orient using both wall length and angular amplitude. To our knowledge, this is the first study to separately test pigeons' use of these two local geometric properties of an enclosed environment for reorientation. Pigeons readily learned to find a goal location in the parallelogram which provided both types of local cues, a result that is not surprising given the many previous demonstrations that pigeons readily orient in rectangular-shaped enclosures which provide only wall length information (e.g., Kelly et al., 1998; Kelly & Spetch, 2001). Despite the redundancy of the two local cues in training, the pigeons clearly encoded both, as evidenced by their high accuracy in both the Rectangle and Rhombus enclosures. This is particularly interesting because it suggests that the cues were not encoded exclusively as an integrated or configural geometric property, but instead were encoded as separable cues that individually supported highly accurate orientation. This strategy for encoding geometric information may make sense if one considers the natural outdoor spaces in which pigeons evolved. For example, angular amplitude, such as that provided by a crevice in a cliff, and length of an extended surface, such as that provided by a row of trees, may often represent separate sources of geometric information.

These results, that pigeons are able to encode the two types of geometry separately, are similar to those of Tommasi and Polli (2004) in the domestic chick, suggesting a possible species similarity in the way the two birds encode and use different types of geometric cues. The finding that pigeons readily encode and employ angular information separately from wall length information is also very interesting because of studies showing that children under the age of four are highly sensitive to relative wall length information in rectangular rooms (e.g., Hermer & Spelke, 1994), yet seem unable to distinguish between unique angular amplitudes for the purposes of orientation (Hupbach & Nadel, 2005).

In the reverse parallelogram Conflict test, where birds were forced to choose between the correct location defined by either angular amplitude or relative wall length, pigeons in both groups chose the locations that preserved the correct angular information. These results differ from findings in the domestic chick; Tommasi and Polli (2004) found that in chicks, the corners that were weighed heavier in the Conflict test were dependent on initial training: chicks whose goal corners in training were acute still chose the acute corners in the Conflict test, while chicks whose goal corners were obtuse chose the acute corners as well in the Conflict test. Tommasi and Polli suggested that differences in the visual salience of acute and obtuse corners might underlie this difference between groups (i.e., due to the degree of the angle, chicks standing in a 60° acute corner would experience being “surrounded” by the walls to a much larger extent than chicks standing in a 120° obtuse corner). Thus, angular information might have been more salient than relative wall lengths for the acute group but less salient than relative wall lengths for the obtuse groups. Our findings that pigeons in the acute and obtuse groups learned at equal rates and showed similar preference for angular information on Conflict tests suggest that, unlike chicks, pigeons did not find acute corners more salient than obtuse corners.

The inconsistent findings between pigeons and chicks in the Conflict test could reflect inherent species or developmental differences regarding the weighting of geometric properties. Chicks and pigeons differ from each other in a number of ways other than species. Chicks are precocial, meaning they are relatively self-sufficient and mobile from the time of hatching, while pigeons are altricial, or dependent on their parents for nourishment and protection for a certain length of time after hatching. In addition, chickens' only mode of locomotion is walking, while pigeons are able to fly long distances. However, both species conduct their foraging while walking on the ground, and thus must be able to make use of the immediate environmental information in order to orient and navigate short distances. Further research is needed to determine the source of the difference between pigeon and chicks in weighting of geometric properties.

A further interesting finding of the current study is that the results do not seem to support the existing literature on small-scale spatial navigation via principal axes, in which an animal follows the main axis that runs through the centroid (i.e., center of mass) of the space, then turns to either the left or right at the end, depending on the goal's location. The use of principal axes has been suggested as a main strategy of small-scale navigation in several species. For example, Pearce et al. (2004) demonstrated that when rats were first trained to locate a submerged platform in a rectangular pool, then tested in a pool that rearranged the walls to be kite-shaped, rats more often chose the corners associated with the correct wall lengths from training as well as the corner formed by the apex of the kite. The authors interpreted this as a reliance on local geometry created by the corners. Cheng and Gallistel (2005), however, argue that the rats' behavior in the kite-shaped pool instead reflect a reliance on a principal axis running down the length of the space. This reliance on a principal axis would account for the rats' choice of both the corner that matched the local geometry of training *and* the corner at the apex of the kite, which matched neither the correct angle nor the correct wall length relationship from training. This interpretation of the results is also in line with the conclusions drawn by Sturz et al. (2011) in their experiment with adult humans in the trapezoid-shaped virtual environments. However, results from the current experiment do not support a principal axis strategy of navigation. For example, if birds in the acute group used a principal axis to remember the correct corner in training, they would have learned to travel down the length of the space and then turn left, which would bring them to the acute corner. However, in the reverse parallelogram Conflict test, navigation via that same strategy would have caused them to choose the obtuse corner. Birds in the obtuse group also did not respond in accordance with a principal axis strategy in the reverse parallelogram. The current findings are more in line with recent results by Kelly et al. (2010). They found that when both chicks and pigeons were trained to locate two geometrically equivalent corners of a rectangular-shaped enclosure, and then were tested in an L-shaped enclosure, neither species demonstrated behavior that reflected the use of a principal axis.

Although the encoding of geometry for orientation has been shown to be extremely general across species (for reviews see Cheng & Newcombe, 2005; Kelly and Spetch, 2012), it is possible that fundamental species differences may exist in specific ways in which geometry is encoded and represented in the brain. For example, Wilzeck et al. (2009) demonstrated that pigeons show a different pattern of geometric encoding than chicks relative to the way the two hemispheres represent information. More investigation is necessary in order to determine if chicks and pigeons are using similar strategies of spatial information processing but with different hierarchal preferences, or if the several million years of separate evolutionary paths followed by these two species has led to distinctly different ways of encoding geometric information.

Bibliography

Able, K. P. (1991). Common themes and variations in animal orientation systems. *American Zooligist, 31,* 157-167. Retrieved from http://icb.oxfordjournals.org/

Brown, A. A., Spetch, M. L., & Hurd, P. L. (2007). Growing in circles, rearing environment alters spatial navigation in fish. *Psychological Science, 18,* 569-573. doi:10.1111/j.1467-9280.2007.01941.x

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. Cognition, 23, 149-178. doi:10.1016/0010-0277(86)90041-7

Cheng, K., Spetch, M. L., Kelly, D. M., Bingman, V. P. (2006). Small-scale spatial cognition in pigeons. Behavioral Processes 72, 115-127. doi:10.1016/j.beproc.2005.11.018

Cheng, K. & Gallistel, C. R. (2005). Shape parameters explain data from spatial transformations: Comment on Pearce et al. (2004) and Tommasi and Polli (2004). *Journal of Experimental Psychology Animal Behavioral Processes, 31,* 254-259. doi:10.1037/0097-7403.31.2.254

Cheng, K. & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review, 12,* 1–23. doi:10.3758/BF03196346

Cheng, K. & Spetch, M. L. (1988). Mechanisms of landmark use in mammals and birds. In: Healy S (Ed) Spatial representation in animals. Oxford University Press, Oxford, pp 1-17.

Della Chiesa, A., Speranza, M., Tommasi, L., & Vallortigara, G. (2006a). Spatial cognition based on geometry and landmarks in the domestic chick *(Gallus gallus). Behavioral Brain Research, 175,* 119–127

Della Chiesa, A., Pecchia, T., Tommasi, L., & Vallortigara, G. (2006b). Multiple landmarks, the encoding of environmental geometry and the spatial logistics of a dual brain. *Animal Cognition, 9,* 281–293.

Gibson, B. M., Wilks, T. J., & Kelly, D. M. (2007). Rats (*Rattus norvegicus*) encode the shape of an array of discrete objects. *Journal of Comparative Psychology, 121,* 130-144. doi:10.1037/0735-7036.121.2.130

Gouteux, S., Thinus-Blanc, C., & Vauclair, J. (2001). Rhesus monkeys use geometric and nongeometric information during a reorientation task. *Journal of Experimental Psychology General, 130,* 505-519. doi:10.1037/0096-3445.130.3.505

Gray, E. & Spetch, M. L. (2006). Pigeons encode absolute distance but relational direction from landmarks and walls. *Journal of Experimental Psychology Animal Behavioral Processes, 32,* 474-480. doi:10.1037/0097-7403.32.4.474

Gray, E., Spetch, M. L., Kelly, D. M., & Nguyen, A. (2004). Searching in the center: Pigeons encode relative distance from walls of an enclosure. *Journal of Comparative Psychology, 118,* 113-117. doi:10.1037/0735-7036.118.1.113

Hermer, L. & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Letters to Nature, 370,* 57-59. doi:10.1038/370057a0

Hupbach, A. & Nadel, L. (2005). Reorientation in a rhombic environment: No evidence for an encapsulated geometric module. *Cognitive Development, 20,* 279-302. doi:10.1016/j.cogdev.2005.04.003

Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2010). Re-orienting in space: Do animals use global or local geometry strategies? Biology Letters, 7, 372-375. doi:10.1098/rsbl.2010.1024

Kelly, D. M., Spetch, M. L., & Heth, C. D. (1998). Pigeons' *(Columba livia)* encoding of geometric and featural properties of a spatial environment. *Journal of Comparative Psychology, 112,* 259–269. doi:10.1037/0735-7036.112.3.259

Kelly, D. M. & Spetch, M. L (2001). Pigeons encode relative geometry. *Journal of Experimental Psychology Animal Behavioral Processes, 27,* 417–422. doi:10.1037/0097-7403.27.4.417

Kelly, D. M. & Spetch, M. L (2012). Comparative Spatial Cognition: Encoding of Geometric Information from Surfaces and Landmark Arrays. In E. Wasserman and T. Zentall (Eds), *Handbook of Comparative Cognition.* Oxford University Press.

Pearce, J. M., Good, M. A., Jones, P. M., & McGregor, A. (2004). Transfer of spatial behavior between different environments: Implications for theories of spatial learning and for the role of the hippocampus in spatial learning. *Journal of Experimental Psychology Animal Behavior Processes, 30,* 135-147. doi:10.1037/0097-7403.30.2.135

Reichert, J. F. & Kelly, D. M. (2011a). Use of local and global geometry from object arrays by adult humans. *Behavioral Processes, 86,* 196-205. doi:10.1016/j.beproc.2010.11.008

Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2002). Modularity and spatial orientation in a simple mind: Encoding of geometric and nongeometric properties of a spatial environment by fish. *Cognition, 85,* B51–B59. doi:10.1016/S0010-0277(02)00110-5

Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2003). Modularity as a fish *(Xenotoca eiseni)* views it: Conjoining geometric and nongeometric information for spatial reorientation. *Journal of Experimental Psychology Animal Behavior Processes, 29,* 199–210. doi:10.1037/0097-7403.29.3.199

Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2007). How fish do geometry in large and in small spaces. *Animal Cognition, 10,* 47–54.

Sturz, B. R., Gurley, T., & Bodily, K. D. (2011). Orientation in trapezoid-shaped enclosures: Implications for theoretical accounts of geometry learning. *Journal of Experimental Psychology Animal Behavior Processes, 37,* 246-253. doi: 10.1037/a0021215

Tommasi, L & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick *(Gallus gallus). Animal Cognition, 7,* 53-59. doi:10.1007/s10071-003-0182-y

Tommasi, L. & Vallortigara, G. (2000). Searching for the center: Spatial cognition in the domestic chick. *Journal of Experimental Psychology*

Animal Behavior Processes, 26, 477-486. doi:10.1037/0097-7403.26.4.477

Twyman, A., Friedman, A., & Spetch, M. L. (2007). Penetrating the geometric module: Catalyzing children's use of landmarks. *Developmental Psychology, 43,* 1523–1530. doi:10.1037/0012-1649.43.6.1523

Vallortigara, G., Pagni, P., & Sovrano, V. A. (2004). Separate geometric and non-geometric modules for spatial representation: Evidence from a lopsided animal brain. *Journal of Cognitive Neuroscience, 16,* 390-400. doi:10.1162/089892904322926737

Vallortigara, G., Zanforlin, M., & Pasti, G. (1990). Geometric modules in animals' spatial representations: A test with chicks *(Gallus gallus domesticus). Journal of Comparative Psychology, 104,* 248–254. doi:10.1037/0735-7036.104.3.248

Vargas, J. P., López, J. C., Salas, C., & Thinus-Blanc, C. (2004). Encoding of geometric and featural information by goldfish *(Carassius auratus). Journal of Comparative Psychology,* 118, 206-216. doi:10.1037/0735-7036.118.2.206

Wang, R. F., Hermer, L., & Spelke, E. S. (1999). Mechanisms of reorientation and object localization by children: A comparison with rats. *Behavioral Neuroscience, 113,* 475–485. doi:10.1037/0735-7044.113.3.475

Wilzeck, C., Prior, H., & Kelly, D. M. (2009). Geometry and landmark representation by pigeons: Evidence for species differences in the hemispheric organization of spatial information processing? *European*

Journal of Neuroscience, 29, 813-822. doi:10.1111/j.1460-9568.2009.06626.x

Wystrach, A. & Beugnon, G. (2009). Ants learn geometry and features. Current Biology, 19, 61-66. doi:10.1016/j.cub.2008.11.054

Chapter 2:

Adult Humans' Use of Angular, Wall Length, and Principal Axis Information in a 3D Virtual Environment[2]

Introduction

Humans and other animals often need to orient in their environment. One widely used cue for orientation is the geometry of the environment, which includes angles, wall lengths, the overall shape or principal axes of the environment, and the spatial relationships between objects. In Cheng's (1986) foundational study, rats located food in one corner of a rectangular enclosure and then were disoriented. Although a visually distinct feature could serve as a reliable beacon, rats frequently made rotational errors after disorientation, searching in both the correct corner and its rotational equivalent. This blind reliance on geometry of the enclosure, despite the presence of an informative feature, was called a "purely geometric module" (p. 149). Reliance on geometric information despite the presence of more informative features has also been demonstrated in young children (Hermer & Spelke, 1994), although children *can* use landmarks for reorientation in larger environments (Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, Sheridan, & Jones, 2008) or after a few training trials (Twyman, Friedman, & Spetch, 2007).

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[2] *A version of this chapter has been published. Lubyk, Dupuis, Gutiérrez, & Spetch 2012. Geometric orientation by humans: angles weigh in. Psychonomic Bulletin & Review. 19: 436-442.*

Use of geometry for orientation has been demonstrated in several species (for a review see Cheng & Newcombe, 2005). However, most studies have used rectangular enclosures in which geometry is provided by wall length relationships. The angular amplitude of corners, a type of local geometry, does not differ in a rectangular enclosure so cannot provide an orientation cue. A few recent studies have investigated encoding of angles using non-rectangular environments. Tommasi and Polli (2004) trained domestic chicks to locate geometrically equivalent corners of a parallelogram-shaped enclosure. Tests in manipulated environments demonstrated that chicks encoded both the angular amplitude of the corners and the relative wall lengths. However, when these geometric properties were placed in conflict, chicks trained to choose the smaller (i.e., acute) corners weighted angles more heavily than wall lengths, whereas chicks trained to locate the larger (i.e., obtuse) corners weighted the wall lengths heavier. In a similar task, Lubyk and Spetch (2011) found no effect of training angle in pigeons: Pigeons weighted angles heavier than relative wall lengths whether they had been trained to locate acute or obtuse corners. Finally, Jones, Pearce, Davies, Good, and McGregor (2007) demonstrated that rats can use angular amplitudes or wall length relationships to orient in a kite-shaped arena.

A minimal number studies have examined use of angles for orientation in humans. Hupbach and Nadel (2005) found that children could not use the angles in a rhombic-shaped room to reorient until the age of four. Well before that age, children can readily use the geometric shape provided by different wall lengths in a rectangular environment (Hermer & Spelke, 1994). Based on Hupbach and

Nadel’s results, as well as their own unpublished data, Spelke, Lee, and Izard (2010) suggest that the “geometric reorientation system […] fails to capture the Euclidean geometrical relationship of *angle*” (p. 869). Newcombe, Ratliff, Shallcross, and Twyman (2010) also comment that “overall, the available data on use of geometry suggest that wall length is a more distinctive feature than size of angle” (p. 216).

A few recent studies suggest that adult humans can sometimes use angular information to reorient. Reichert and Kelly (2011a) presented participants with a rectangular array created by four L-shaped objects. One pair of diagonally-opposite objects had 50° angles and the other pair had 75°angles. Participants were trained to locate geometrically equivalent objects defined by both the rectangular shape of the array and the angles. Males, but not females, used the angular amplitudes of the objects for orientation. In a simple choice discrimination that did not require orientation, Reichert and Kelly (2011b) showed that adults readily discriminated between 50° and 75° angles, although generalization tests suggested that smaller angles are more salient, consistent with the suggestions by Tommasi and Polli (2004) for chicks.

Recently, Bodily, Eastman, and Sturz (2011) trained adults in a virtual environment to locate one corner of a trapezoid-shaped enclosure. For all participants, the correct corner intersected equal wall lengths and had an obtuse angle. For some participants, the correct corner was also defined by the principal axis of the room, whereas for others, the principal axis did not provide a reliable cue. On subsequent parallelogram tests, the angles were either consistent or conflicted with the principal axis. Participants trained with a reliable principal axis chose accurately when angles were consistent with the principal axis, but randomly when they were not. Participants trained with an unreliable principal axis chose the correct angles on both tests. These results show that adults can encode angular information for reorientation, but reliable principal axis cues appear to override use of angles.

Thus, the existing literature suggests that use of angles for reorientation by adult humans is at best secondary to the use of other geometric cues. Children seem less able to use angular information than wall length information, and adults may use angles only when other geometric cues are unavailable or unreliable. The conflicting findings on how humans and animals encode angular and configural geometry, and the theoretical importance of encoding angles for reorientation (Spelke, Lee, & Izard, 2010), suggest the need for further research. Our experiment was designed after the procedure used with chicks and pigeons to test whether angles are encoded and how they are weighted when placed in conflict with both wall lengths and a principal axis. In the current experiment, adult humans were tested in a first-person navigable virtual environment similar to that used in many other studies of orientation strategies (e.g., Kelly & Gibson, 2007; Sturz & Bodily, 2011; Sturz, Gurley, & Bodily, 2011). Participants were trained to locate two geometrically equivalent corners in a parallelogram-shaped room. The task could be solved on the basis of any of three types of geometric cues: angular amplitude, relative wall lengths, or a principal axis. They were then tested in three novel environments: 1) a rhombic-shaped room, which removed the wall length information and drastically reduced the salience of the principal axis; 2) a rectangular-shaped room which removed the angular information; and 3) a reverse parallelogram-shaped room which placed angular information in direct conflict with both the wall length information and the principal axis.

Method

Participants

Participants were 99 University of Alberta undergraduate students who received class credit for participating.

Apparatus

Platform. The 3D virtual environment ran in the Open Simulator online server (an open source version of the virtual world Second Life). The server allowed multiple participants to be tested simultaneously on individual computers by saving the collected data in an online database in real time. Hippo Open Sim, an open source virtual world viewer, was used to set parameters for each participant (e.g., which corners were correct). Communication between the virtual worlds and Hippo Open Sim was via HTTP using the XML-RPC method.

Stimuli. In training, participants experienced a featureless gray parallelogram-shaped room (17.2 *x* 8.6 m; Figure 2-1, top left). Initial orientation direction was randomized across trials. In testing, participants experienced three manipulated environments: 1) Rhombic (12.9 m wall lengths; Figure 2-1, top right); 2) Rectangular (17.2 *x* 8.6 m; Figure 2-1, bottom left); and 3) Reverse parallelogram (17.2 *x* 8.6 m; Figure 2-1, bottom right). In all environments the tops of the walls were not visible to the participants, as they were not able to look up.

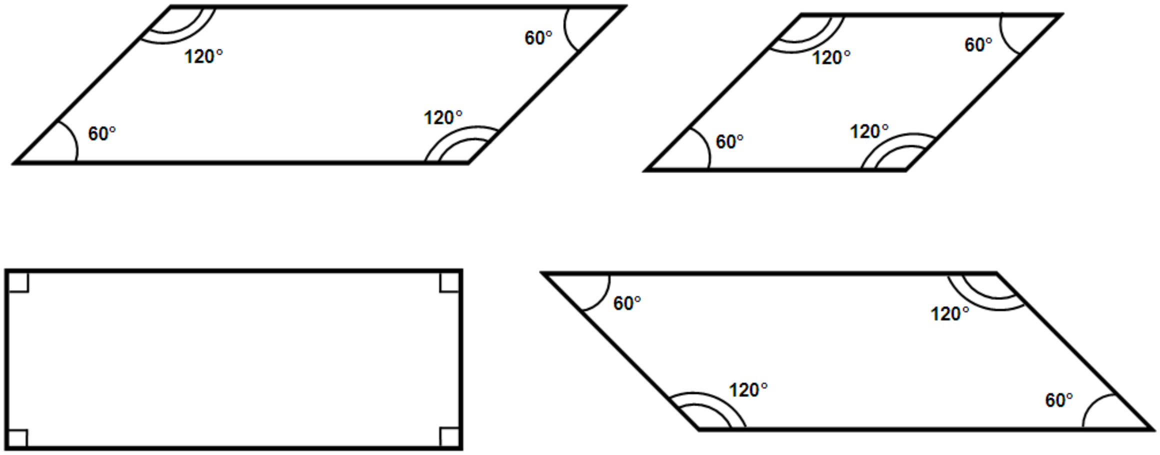

Figure 2-1. Schematic representations of four virtual environments used in the current experiment: *Top left:* parallelogram-shaped training environment; *Top right:* rhombic-shaped testing environment; *Bottom left:* rectangular testing environment; *Bottom right:* reverse parallelogram-shaped (conflict) testing environment.

General Procedures

Participants were instructed on how to navigate using the arrow keys and were told that they could choose only one corner per trial by walking into the corner. Participants could look and walk around so that they could view the entire environment before making a choice. They were informed that they would sometimes receive feedback about the accuracy of their choice, but sometimes the display would say “no feedback” regardless of whether they chose the correct corner. To encourage participants to maintain a consistent strategy based on training, participants were told that they would continue to accumulate points for correct choices, even on no-feedback trials.

Participants were pseudo-randomly assigned to a goal corner group (acute or obtuse), while balancing gender across groups. For the acute group, correct corners were 60° angles intersected by a long wall on the left and a short wall on the right. For the obtuse group, 120° corners intersected by a long wall on the right and a short wall on the left were correct.

Training

Participants were trained in a parallelogram-shaped environment (Figure 2-2, top left). Training was presented in blocks of ten trials and each stage of training continued until participants achieved an accuracy of 80% to one of the two correct corners within a block. In the first stage, each corner choice was followed by feedback indicating correct or incorrect, followed by transport into the next trial. In the second stage, participants received feedback on only half of the trials; the remaining trials said “no feedback”. This was to prepare participants for testing, which never included feedback. If participants did not complete training within 30 minutes they were told that the experiment was over.

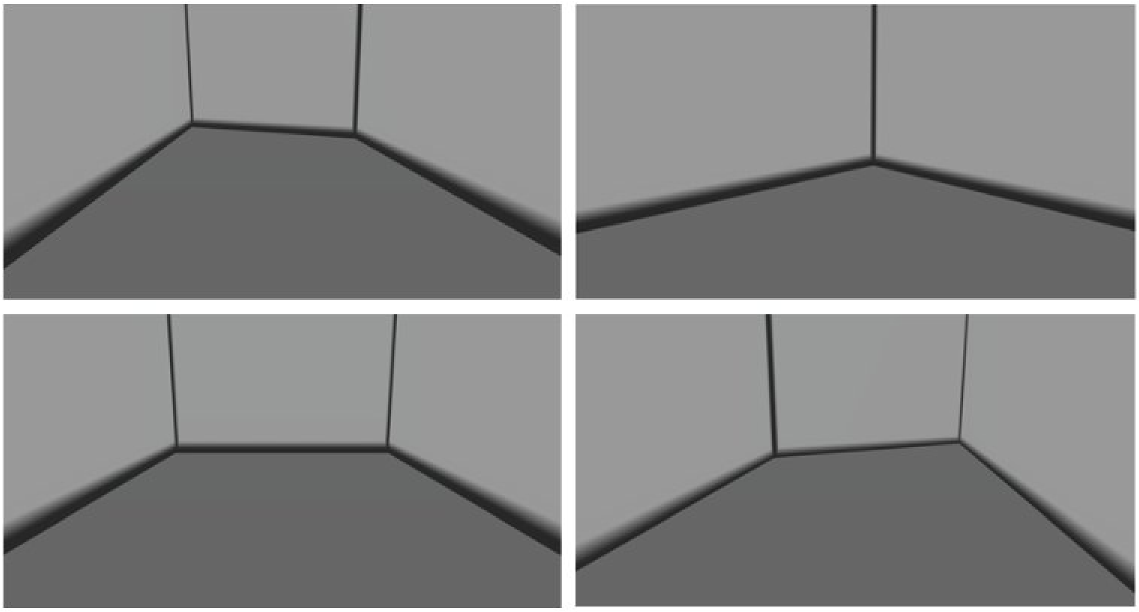

Figure 2-2. Example first person views of training *(top left)* and testing *(top right:* Rhombic; *Bottom left:* Rectangular; *Bottom right:* Reverse parallelogram-shaped) virtual environments. Participants were able to freely navigate throughout environments in both training and testing, and therefore experienced several viewpoints in addition to the ones shown.

Testing

Participants received five test trials in each of the three testing environments: Rhombic (Figure 2-2, top right), rectangular (Figure 2-2, bottom left), and reverse parallelogram (Figure 2-2, bottom right). Test trials were presented in random order. Participants made only one corner choice per trial and they never received informative feedback so that choices would continue to be based on what they learned during training.

Control

Following testing, participants received ten no-feedback trials in the original parallelogram-shaped training environment. Only participants who achieved 70 percent correct or higher were included in analysis to ensure that test results did not reflect forgetting or confusion.

Results

Five men and 7 women from the Acute group and 1 man and 9 women from the Obtuse group were excluded because they did not complete training within 30 minutes or scored lower than 70 percent on the control block. Therefore, final data analysis included 36 Acute participants (9 men and 27 women) and 41 Obtuse participants (15 men and 26 women).

A Shapiro-Wilk test revealed a non-normal distribution and unequal variances in the test data. We therefore used randomization analyses (a sub-type of re-sampling techniques), which imposed no assumptions of normality or equal variances (see Eddington, 1995). Confidence intervals on Cohen's *d* were obtained through bootstrapping techniques (see Efron & Tibshirani, 1994). Although we report only the results of randomization analyses, all reported conclusions were also consistent with results of conventional ANOVA.

Analyses revealed no significant difference between the groups in number of blocks to complete training (Acute $M = 1.38$, SD = .80; Obtuse $M = 1.58$, SD = 1.44, $d = .17$, 95% CIs [-0.5, 0.3], $p = .53$) or choice accuracy by the last block of training (Acute *M* = .96, SD = .08; Obtuse *M* = .94, SD = .09, *d* = 0.15, 95% CIs [-0.3, 0.5], *p* = .47). There was also no significant sex effect in accuracy on the last block of training (Male *M* = .95, SD = .07; Female *M* = .95, SD = .09, *d* = .04, 95% CIs [-0.4, 0.5], *p* = .12) or number of blocks required to complete training (Male *M* = 1.15, SD = 0.47; Female *M* = 1.64, SD =1.37, *d* = .35, 95% CIs [-0.8, 0.06], *p* = .85).

There was no significant effect of group or sex for either the rhombic (Acute *M* = .80, SD = .24; Obtuse *M* = .75, SD = .28, *d* = .17, 95% CIs [-.25, .62], *p* = .57; Male *M* = .78, SD = .25; Female *M* = .77, SD = .27; *d* = .017, 95% CIs [-.43, .50], *p* = .96) or rectangular test environments (Acute *M* = .76, SD = .26; Obtuse *M* = .66, SD = .34, *d* = .30, 95% CIs [-.12, .74], *p* = .82; Male *M* = .70, SD = .29; Female *M* = .71, SD = .31, *d* = .031, 95% CIs [-.52, .46], *p* = .88).

In the reverse-parallelogram test, there were no "correct" responses because participants had to choose *either* the corners that provided the correct angle from training *or* the corners that provided the correct wall length relationships and principal axis from training. Analyses on choice of the angle-consistent corners revealed no effect of group or sex in the conflict test (Acute *M* = .61, SD = .40; Obtuse *M* = .62, SD = .39, *d* = .02, 95% CIs [-.48, .43], *p* = .09; Male M = .70, SD = .34; Female *M* = .58, SD = .41; *d* = .31, 95% CIs [-.13, .81], *p* = .77).

All test data were collapsed across group and sex for the remaining analyses. First, accuracy in choosing the correct corners did not differ between the rhombus and the rectangular tests (Rhombus *M* = .77*,* SD = .26; Rectangle *M* =.71*,* SD = .31, *d* = 0.23, 95% CIs [-0.08, 0.5], *p* = .85). As evident in Figure 2-3, accuracy in choosing the correct angle (60° for the acute group and 120° for the obtuse group) was significantly above chance (50%) in the Rhombus (95% CIs [.71, .83], *p* < .001) and accuracy in choosing the correct wall length relationship (long wall on the left and short wall on the right for the acute group and opposite for the obtuse group) was significantly above chance (50%) in the Rectangle (95% CIs [.64, .77], *p* < .001).

In the reverse parallelogram-shaped environment, both groups primarily chose the correct angles from training (i.e., 60° for acute and 120° for obtuse), despite them being paired with incorrect relative wall lengths and principal axis cues (*M* = .62, SD = .39, *d* = .62, 95% CIs [0.5, 0.7], *p* < .05; Acute: Figure 2-3, bottom left; Obtuse: bottom right).

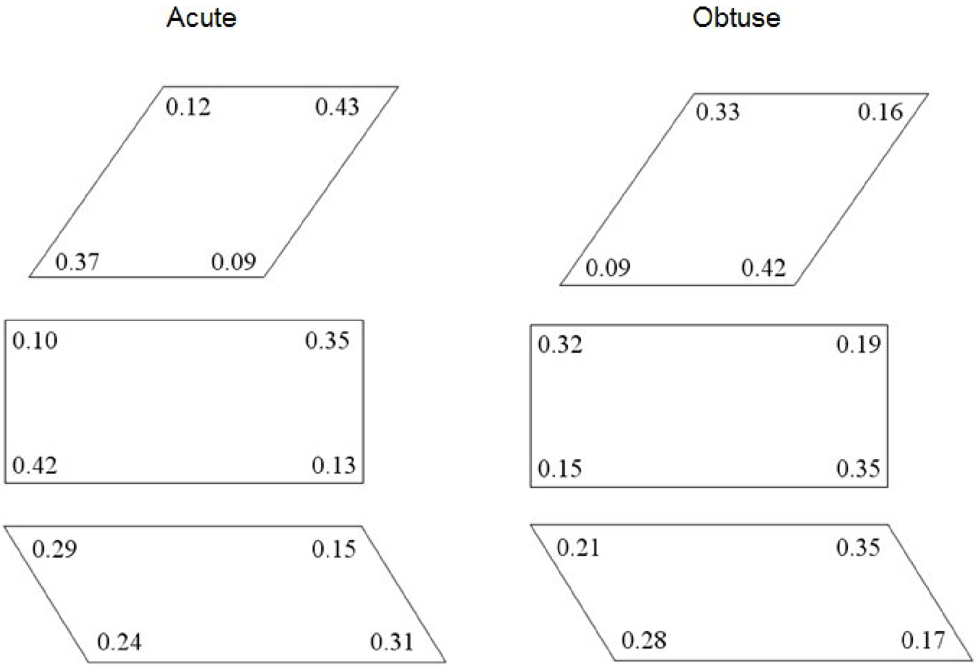

Figure 2-3. Proportion of acute (n = 36; *left*) and obtuse (n = 41; *right*) choices to each of the four corners in the rhombic *(top)*, rectangular *(middle)*, and reverse parallelogram *(bottom)* test enclosures. Figures not exactly to scale. Proportions are rounded to two decimal places.

Discussion

Our results show that adult humans easily learned to locate the two geometrically equivalent goal corners in a parallelogram-shaped virtual environment that provided both angular amplitude (e.g., 60°), relative wall length relationships (e.g., long wall on the left and a short wall on right), and a principal axis as geometric cues for orientation. Most participants learned the task within two 10-trial training blocks, as well as achieved an average accuracy of over 90% correct by the end of training. Moreover, the angle to which they were trained (either 60° or 120°) had no significant effect on either the speed of learning or their final accuracy.

Results in the rhombus and rectangle tests indicated that not only were participants able to locate their goal corners in both test environments at a rate significantly higher than chance, but there was also no difference in participants' mean accuracy between the two tests. This suggests that participants were able to orient equally well in the absence of either local geometric cue. The accurate orientation when angular information is removed is not surprising given the numerous previous demonstrations of orientation in rectangular environments (Cheng, 1986; Kelly & Spetch, 2004a, 2004b; Sturz & Kelly, 2009). However, the equally high accuracy on the rhombus test is interesting for a couple reasons.

First, use of angles for orientation seems to develop at a later age in children than use of relative wall lengths (Hupbach & Nadel, 2005). Second, the results of Bodily et al. (2011) suggest that use of angles might be subject to overshadowing by a principal axis. Although one might argue that participants used the principal axis rather than angles in the rhombus environment, the salience of the principal axis was drastically reduced in the rhombus as compared to the rectangle, and therefore use of a principal axis strategy should lead to a difference in accuracy between these tests. However, the current results that humans performed equally well in the rhombus and rectangle test environments are consistent with those found in similar tests with both pigeons (Lubyk & Spetch, 2011), and domestic chicks (Tommasi & Polli, 2004). This finding is interesting and suggests considerable cross-species generality.

In the reverse-parallelogram test, participants primarily chose the correct angle from training. This result clearly shows that angular amplitude was weighted most heavily. Moreover, preference for the correct angular information was similar whether participants were trained to find an acute corner (60 degrees) or an obtuse corner (120 degrees). These results are also consistent with those reported for pigeons (Lubyk & Spetch, 2011), but not chicks (Tommasi & Polli, 2004); chicks trained to locate acute angles chose the correct angles, whereas chicks trained to locate obtuse angles chose the correct relative wall lengths. The authors suggest that acute angles may be more visually salient than obtuse angles, and therefore in a conflict situation chicks would rate the acute angle higher than relative wall length but would rate the obtuse angle lower than wall length information. Although the suggestion that smaller angles are more salient is consistent with the generalization results of Reichert and Kelly (2011b) with humans, we did not see a difference between acute and obtuse angles in our experiment.

A further interesting finding from the reverse-parallelogram test is that the results are inconsistent with a principal axis strategy (see Cheng, 2005), which several studies have proposed (e.g., Gallistel, 1990; Cheng & Gallistel, 2005; Sturz et al., 2011). In our parallelogram training environment, use of such a strategy would mean that participants follow the principal axis and turn left (acute condition) or right (obtuse condition). In the conflict test, this would bring obtuse-trained participants to choose the acute corner and acute-trained participants to choose the obtuse corner, which is the opposite of our results. Recent results with pigeons (Lubyk & Spetch, 2011; Kelly, Chiandetti, & Vallortigara, 2011) and domestic chicks (Kelly et al., 2011), have also been inconsistent with a principal axis strategy. Newcombe et al. (2010) also found that two-year old children *were* able to orient in an octagon-shaped room which contained only obtuse angles and had no single principal axis of symmetry.

The present results are consistent with those of Bodily et al. (2011) in suggesting that people use more than one type of geometric cue for orientation. However, our results differ from their results in that people in our study not only encoded angular information but also weighted angles more heavily than other geometric cues even though wall lengths and a principal axis provided reliable cues in training. One interesting possible reason for the discrepant results is that distinctive features were present in the positive corners in the Bodily et al. study. These features may have reduced or overshadowed the salience of the angular information. We are currently exploring this possibility in studies with both pigeons and humans. Additionally, the finding that angles were weighted heavier than relative wall lengths is especially interesting in light of recent findings by Sturz, Forloines, and Bodily (2012), which suggest that angles, like features, may be more salient in large enclosures. The training environment size in our study was intermediate in size to those used in the Sturz et al. (2012) study, but was considerably closer in size to their small enclosure than their large enclosure. Thus, although weighting of angles and wall length may change as function of room size, our finding of strong weighting of angular geometry was not a result of using an extremely large environment.

Our study addressed the question of how adult humans represent and weight different types of geometric information to orient and navigate to a goal. We conclude that humans are able to encode and subsequently navigate using angular amplitude, but also encode relative wall length or a principal axis because they continued to orient well when angular information was removed. Results from the conflict test show that participants reliably weight the angular information from training heavier than either the relative wall length information or the principal axis. This strategy of preferentially weighting angles is shared by pigeons, but interestingly, not domestic chicks. The preference for angular information when placed in conflict with both relative wall length and a principal axis suggests that for both pigeons and adult humans, angles are a salient part of the geometric orientation system.

Bibliography

Bodily, K. D., Eastman, C. K., & Sturz, B. R. (2011). Neither by global nor local cues alone: evidence for a unified orientation process. *Animal Cognition, 14*, 665-674. doi:10.1007/s10071-011-0401-x

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23*, 149–178. doi:10.1016/0010-0277(86)90041-7

Cheng, K. (2005). Reflections on geometry and navigation. *Connection Science, 17*, 5-21. doi:10.1080/09540090500138077

Cheng, K. & Gallistel, C. R. (2005). Shape parameters explain data from spatial transformations: comment on Pearce et al. (2004) and Tommasi and Polli (2004*). Journal of Experimental Psychology Animal Behavior Processes, 31*, 254–259. doi:10.1037/0097-7403.31.2.254

Cheng, K. & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? squaring theory and evidence. *Psychonomic Bulletin & Review, 12,* 1–23. doi:10.3758/BF03196346

Eddington, E. S. (1995). *Randomization tests*. New York, NY: Marcel Dekker Inc.

Efron, B. & Tibshirani, R. J. (1994). *Introduction to the bootstrap*. New York, NY: Chapman & Hall.

Gallistel, C. R. (1990). *The Organization of Learning.* Cambridge, MA: MIT Press.

Jones, P. M., Pearce, J. M., Davies, V. J., Good, M. A., & McGregor, A. (2007). Impaired processing of local geometric features during navigation in a water maze following hippocampal lesions in rats. *Behavioral Neuroscience, 121*, 1258-1271. doi: 10.1037/0735-7044.121.6.1258

Hermer, L. & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature, 370,* 57–59. doi:10.1038/370057a0

Hupbach, A. & Nadel, L. (2005). Reorientation in a rhombic environment: no evidence for an encapsulated geometric module. *Cognitive Development, 20*, 279–302. doi:10.1016/j.cogdev.2005.04.003

Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2011). Re-orienting in space: do animals use global or local geometry strategies? *Biology Letters, 7*, 372-375. doi:10.1098/rsbl.2010.1024

Kelly, D. M. & Gibson, B. M. (2007). Spatial navigation: orienting in real and virtual environments. *Comparative Cognition & Behavior Reviews, 2*, 111-124. Retrieved from http://psyc.queensu.ca/ccbr/

Kelly, D. M. & Spetch, M. L. (2004a). Reorientation in a two-dimensional environment: I. Do humans encode the featural and geometric properties of a two-dimensional schematic of a room? *Journal of Comparative Psychology, 118*, 82-94. doi:10.1037/0735-7036.118.1.82

Kelly, D. M. & Spetch, M. L. (2004b). Reorientation in a two-dimensional environment: II. Do pigeons encode the featural and geometric properties of a two-dimensional schematic of a room? *Journal of Comparative Psychology, 118,* 384-395. doi:10.1037/0735-7036.118.4.384

Learmonth, A. E., Nadel, L., & Newcombe, N. S. (2002). Children's use of landmarks: implications for modularity theory. *Psychological Science*, *13*, 337-341. doi:10.1111/1467-9280.00461

Learmonth, A. E., Newcombe, N. S., Sheridan, N., & Jones, M. (2008). Why size counts: children's spatial reorientation in large and small enclosures. *Developmental Science*, *11,* 414-426. doi:10.1111/j.1467-7687.2008.00686.x

Lubyk, D. M. & Spetch, M. L. (2012). Finding the best angle: pigeons *(Columba livia)* weight angular information more heavily than relative wall length in an open-field geometry task. *Animal Cognition, 15, 305-312.* doi: 10.1007/s10071-011-0454-x

Newcombe, N. S., Ratliff, K. R., Shallcross, W. L., & Twyman, A. D. (2010). Young children's use of features to reorient is more than just associative: further evidence against a modular view of spatial processing. *Developmental Science*, *13*, 213-20. doi:10.1111/j.1467-7687.2009.00877.x

Reichert, J.F. & Kelly, D.M. (2011a). Use of local and global geometry from object arrays by adult humans. *Behavioral Processes, 86,* 196-205. doi:10.1016/j.beproc.2010.11.008

Reichert, J. F. & Kelly, D. M. (2011b). Discrimination of geometric angles by adult humans. *Animal Cognition*. Advance online publication. doi: 10.1007/s10071-011-0452-z

Spelke, E. S., Lee, S. A., & Izard, V. (2010). Beyond core knowledge: natural geometry. *Cognitive Science. 34*, 863-884. doi:10.1111/j.1551-6709.2010.01110.x

Sturz, B. R. & Bodily, K. D. (2011). Is surface-based orientation influenced by a proportional relationship of shape parameters? *Psychonomic Bulletin & Review, 18,* 848-854. doi: 10.3758/s13423-011-0111-z

Sturz, B. R., Forloines, M. R., & Bodily, K. D. (in press). Enclosure size and the use of local and global geometric cues for reorientation. *Psychonomic Bulletin & Review.* Advance online publication. doi: 10.3758/s13423-011-0195-5

Sturz, B. R., Gurley, T., & Bodily, K. D. (2011). Orientation in trapezoid-shaped enclosures: implications for theoretical accounts of geometry learning. *Journal of Experimental Psychology Animal Behavior Processes*. doi:10.1037/a0021215

Sturz, B. R. & Kelly, D. M. (2009). Encoding of relative enclosure size in a dynamic three-dimensional virtual environment by humans. *Behavioural Processes, 82,* 223-227. doi: 10.1016/j.beproc.2009.06.007

Tommasi, L. & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick *(Gallus gallus). Animal Cognition, 7*, 53-59. doi:10.1007/s10071-003-0182-y

Twyman, A., Friedman, A., & Spetch, M. L. (2007). Penetrating the geometric module: catalyzing children's use of landmarks. *Developmental Psychology, 43*, 1523-1530. doi: 10.1037/0012-1649.43.6.1523

Chapter 3:

A Comparison of Angle and Feature Use in a 3D Fully-Immersive Virtual Environment by Adult Humans[3]

Introduction

All species tested to date, including humans, are able to use the geometric information in their environment for orientation and navigation (for a review see Cheng & Newcombe, 2005). A geometric property is defined as any property relating to the overall shape of the environment. The study of geometry for the purpose of orientation began with Cheng (1986), when he showed that disoriented rats sometimes ignored the informative featural cues present in a rectangular enclosure and instead relied on the geometry of the environment to search for a food reward. Since then, use of geometry for orientation has been studied in a long list of species. The vast majority of these studies have used enclosed environments and most have been conducted in rectangular environments in which wall length differences provide a salient geometric cue.

Recently, researchers have expanded the investigation of geometric reorientation to include both non-rectangular enclosures in which the angular amplitudes of corners provide potentially informative cues, and 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

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[3] *A version of this chapter has been submitted for publication. Lubyk, Zhou, Spetch, & Mou. Reorientation in a diamond-shaped environment: encoding of features and angles in enclosures versus arrays in adult humans. Animal Cognition.*

Nadel (2005) tested children in a locomotor hide-and-seek task using a rhombic-shaped (i.e., diamond-shaped) enclosure which provided angular information 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. Lee, Sovrano, and Spelke (2012) tested two year old children in a variety of rectangular- and diamond-shaped environments created by connected surfaces or by an array of freestanding angles or walls. The children successfully oriented in the enclosed rectangle and diamond as well as in rectangular- and diamond-shaped environments created by freestanding walls. However, they failed to reorient in environments created by arrays of free-standing angles. Thus, their study suggested that two year old children could use the distance and direction properties of surfaces to reorient, but were unable to use local angular information. These results, combined with evidence suggesting that children sometimes ignore informative featural cues in favour of less informative geometric cues (Hermer & Spelke, 1994, but see Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, Sheridan, & Jones, 2008), has led some researchers to suggest that reorientation via geometry does not include the seemingly geometric attribute of angle (Spelke, Lee, & Izard, 2010) or at least that “wall length is a more distinctive feature than size of angle” (Newcombe, Ratliff, Shallcross, & Twyman, 2010, p. 216).

In contrast to the results with young children, both birds (Tomassi & Polli, 2004; Lubyk & Spetch, 2012) and adult humans (Bodily, Eastman, & Sturz, 2011; Lubyk, Dupuis, Gutiérrez, & Spetch, 2012), seem to readily use the angular amplitudes of the corners of an enclosure to orient. However, there have been some discrepancies: Bodily et al. (2011) found that in adult humans, angular information was overridden by principal axis information (i.e., the axis of symmetry which runs through the centroid of the search space; see Cheng, 2005; Sturz & Bodily, 2011), whereas angular information was weighted more heavily than both relative wall length and the principal axis by adults in a study by Lubyk et al. (2012). One procedural variable that may have contributed to the different weighting of angular information is the presence of featural information. The Lubyk et al. study was conducted in a featureless space, whereas in the Bodily et al. study, distinctly coloured orbs were present in the corners of the various training environments, which potentially could have overshadowed the angular information. In a study with chicks (Tommasi & Polli, 2004), the relative weighting of angular and wall length information appeared to depend on which angle contained the goal; birds trained to find the goal in the acute corners weighted the angles more heavily in a conflict situation, whereas birds trained to find the goal in the obtuse corners weighted wall length information more heavily. Lubyk and Spetch, however, found that pigeons weighted angles more heavily than wall length regardless of which angle contained the goal.

In contrast to the wealth of literature on human and non-human orientation in enclosed environments, only a few studies have been conducted in arrays, where the environment is composed of individual landmarks which create a global shape as opposed to continuous boundaries, as previously discussed. Indeed, there is some evidence suggesting that separate cognitive and neural processes may be at work in these two types of environment (e.g., Doeller, King, & Burgess, 2008), and that surfaces or boundaries may be processed differently than free-standing landmarks (Lever, Wills, Cacucci, Burgess, & O'Keefe, 2002; Lee & Spelke, 2010). As mentioned previously, surface information appeared to be particularly important for young children in the Lee, Sovrano, and Spelke (2012) study: children were able to orient in diamond-shaped arrays which contained extended surfaces but no corner information, but *not* in arrays which contained corner information but no extended surfaces connecting them. 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 results suggest that young children need walls to extract global shape and are not able to use angular information alone to orient. In addition, several behavioral studies have shown that both human (Lee & Spelke, 2011; Reichert & Kelly, 2011) and non-human animals (Vallortigara, Zanforlin, & Pasti, 1990; Spetch, Cheng, MacDonald, Linkenhoker, Kelly, & Doerkson, 1997; Pecchia & Vallortigara, 2010), tend to favour local cues present over the global shape formed by an array (for a review see Lew, 2011). Nevertheless, this dichotomy has been questioned by some researchers (see Gibson, Wilks, & Kelly, 2007; Pecchia & Vallortigara, 2012; Sutton, 2009).

The current study was designed to further explore the use of geometric information for orientation in adult humans within enclosed environments and environments created by arrays of free standing angles. Because adults can readily orient using angular information (e.g. Lubyk & Spetch, 2012) and because even older children can orient using free-standing arrays (e.g., Gouteaux & Spelke, 2001), we used an overshadowing procedure to compare the use of angular information in enclosed and array environments. Specifically, adult humans were trained in fully immersive three-dimensional virtual environments to find a goal in either the acute or obtuse corners of a diamond-shaped environment. For some participants the environment was constructed from a set of connected walls (enclosure) and for others it was constructed from an array of free-standing angles (array). Importantly, the geometrically correct corners were also marked with distinctively colored feature panels so that either geometric or featural cues could be used to orient. Tests with the geometric or featural cues in isolation or placed in conflict were used to directly compare the relative salience of angular and featural information within both enclosed and array environments. Additionally, we examined sex differences in encoding of the features and angles to explore the possibility that angular information may be encoded as featural, rather than geometric, information.

Method

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 condition and the other half the Enclosed condition. Within each condition, goal corners were counterbalanced to be either acute (60 degrees) or obtuse (120 degrees).

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). Participants' visual orientation was tracked by an InterSense (Massachusetts) IS-900 motion tracking system. For training, both the enclosed diamond and diamond-shaped array were 6.45 *x* 6.45 m with a wall height of 4.30 m. The blue feature panels located in the correct corners were 1.5 m wide and extended from the floor to the top of the walls. In the diamond-shaped array, each arm of the free-standing angles was 1.5 m wide (see Figure 3-1). Dimensions of the test environments were identical to training (see Figure 3-2).

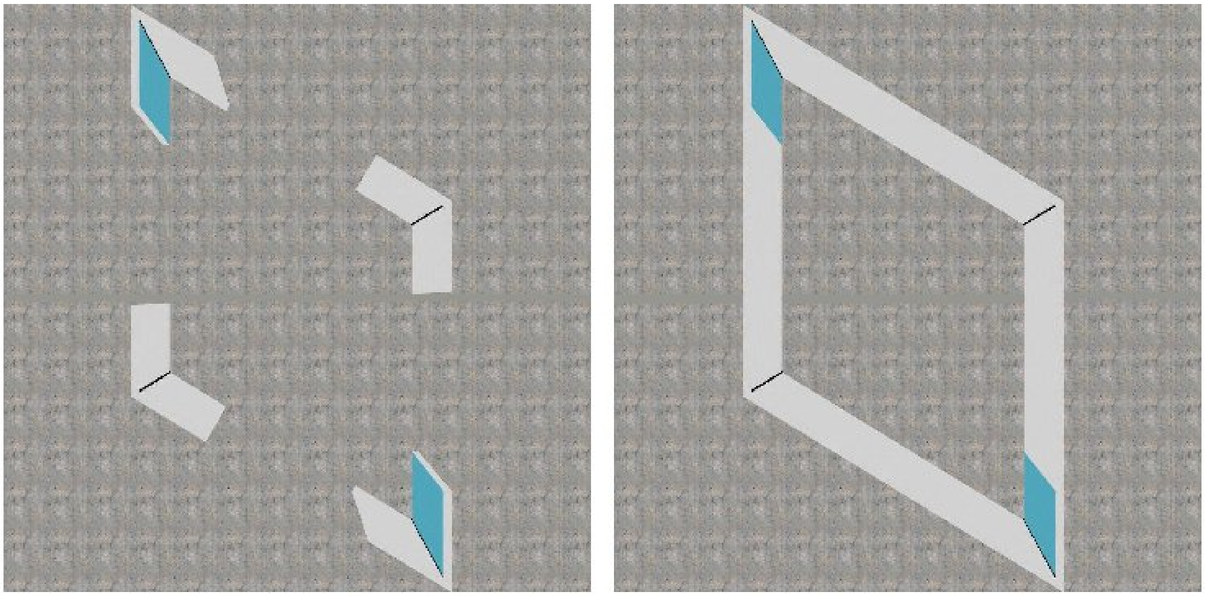


Figure 3-1. Top-down views of the Array *(left)* and Enclosed *(right)* training environments. Both are examples of groups where the acute (60 degree) corners contain the feature panels and are correct.

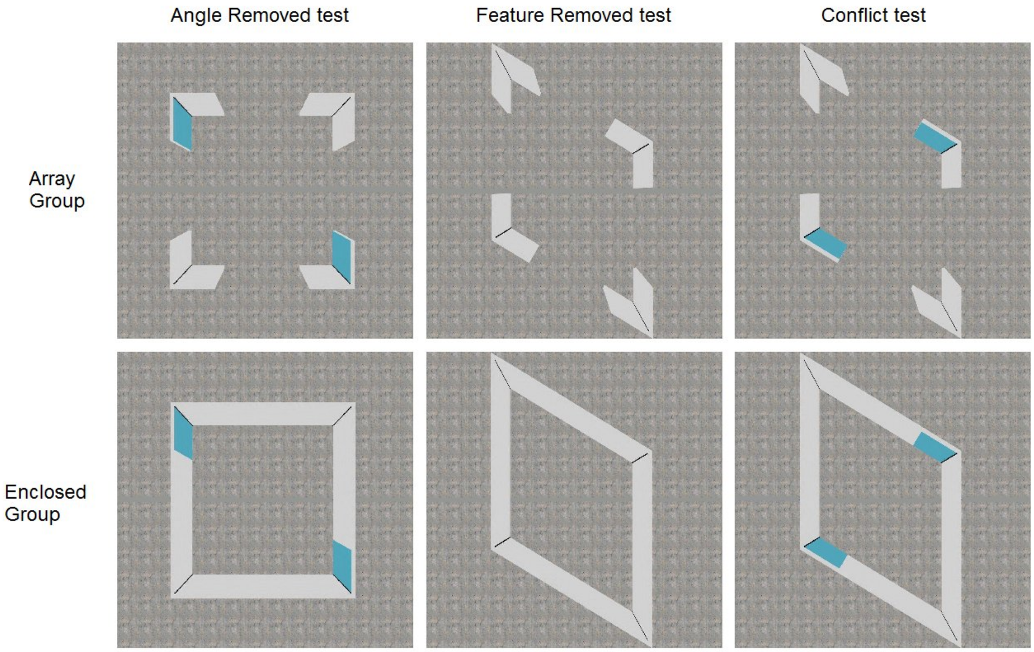


Figure 3-2. Top-down views of the three manipulated test environments for both the Array *(top row)* and Enclosed *(bottom row)* conditions. All are examples of groups where the acute (60 degree) corners contain the feature panels and are correct.

General Procedures

Participants were run individually using the virtual reality headset, which allowed them to physically turn to face any angle 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 positive, negative, or uninformative, depending on the correctness of their choice and the stage of the experiment. Following feedback, the environment faded and after a two-second 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 features and “incorrect” feedback from the other two). Goal corners were counterbalanced across both enclosed and array groups so that half of the participants were trained to locate the acute corners and the other half were trained to locate the obtuse corners. The blue feature panels always were located in the correct corners. Following the practice trial, training was organized into blocks of five trials. In the first phase, participants were always given informative feedback regarding their choice. In order to move to the second phase of training, participants had to choose one of their correct corners on four out of the five trials. The second phase was identical to the first, except that three of the five trials were non-reinforced; on these trials, the participant’s choice, regardless of its accuracy, was followed by uninformative feedback in the form of a neutral noise (a click) and a neutral visual cue (an “OK”) to indicate that a choice had been logged. The criterion to pass phase two was the same as phase one.

Testing. In testing participants saw three manipulated environments, which matched the training environment in that 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; 2) a diamond-shaped environment identical to training but with the blue feature panels removed; and 3) a diamond-shaped environment with the blue panels shifted so that they were located in the non-reinforced angular locations from training. All test trials resulted in non-informative feedback. Control trials identical to the participant’s training environment were dispersed between the test trials, but were followed by non-informative feedback. These were later used to assess whether a participant remembered their initial correct corners, and only participants who scored a minimum of 80 percent correct were included in analysis. Testing was presented in five blocks of four trials each. 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 conditions was counterbalanced so that all four combinations of environment (enclosed or array) and correct angle (acute or obtuse) had 10 male and 10 female participants. Participants in all conditions 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 environments across the factors of sex (male or female), condition (array or enclosed), and goal corners (acute or obtuse). All alpha levels were set at .05.

Results from the square Angle Removed test showed a significant interaction between condition and goal corners [$F(1, 80) = 4.20$, $p < .05$, $\eta_p^2 = .05$; see Figure 3-3]. This interaction was driven by higher accuracy for participants trained to locate the acute corners in Array condition and higher accuracy for participants trained to locate obtuse corners in the Enclosed condition. 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, $p < .001$].

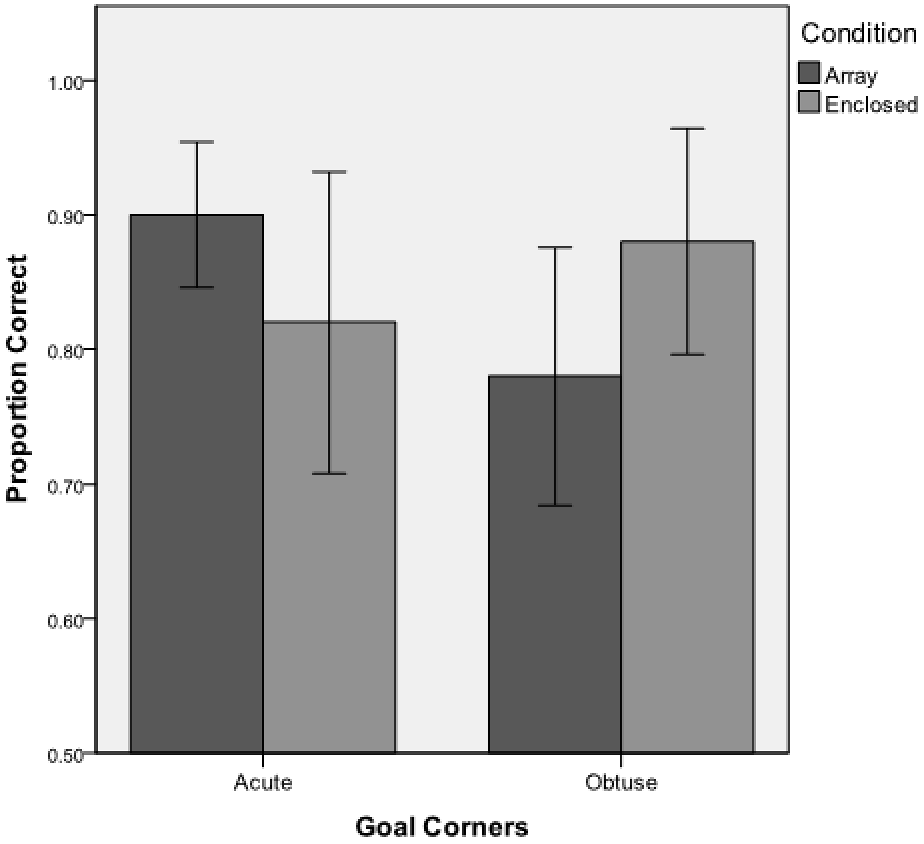
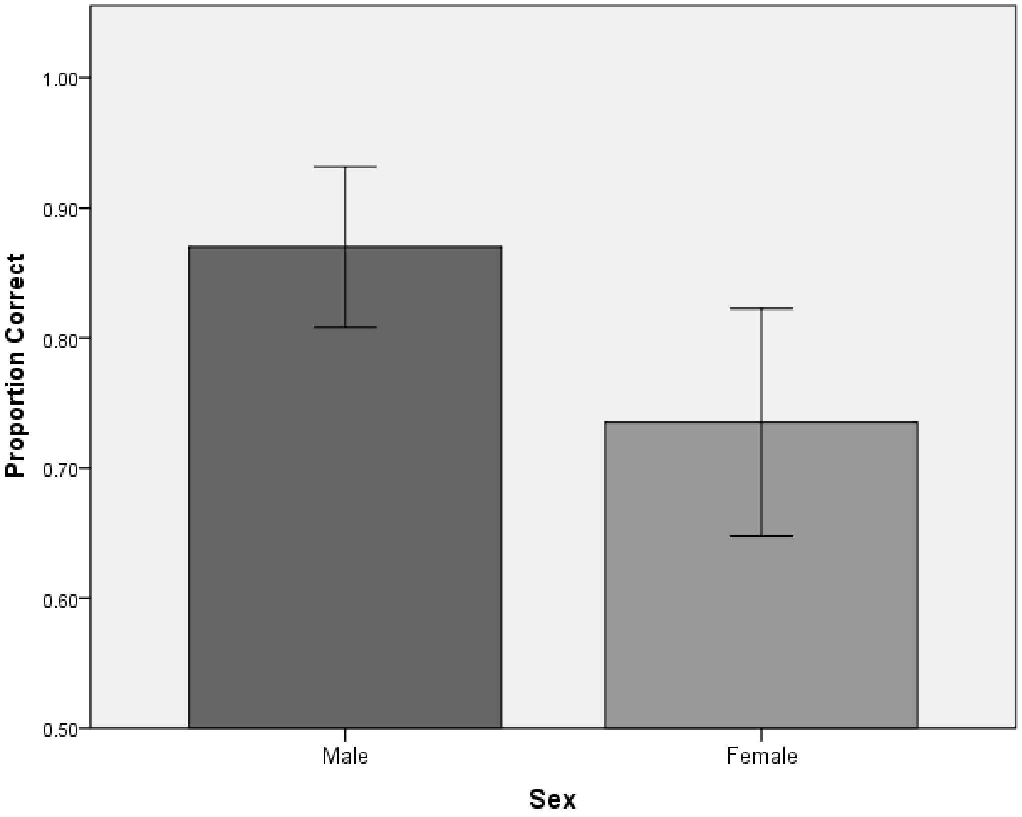


Figure 3-3. Bar graph representing Condition - Goal Corner interaction on Angle Removed test. Participants in the Array condition *(dark)* were significantly more accurate to their goal corners when located in the Acute (60 degree) corners, while participants in the Enclosed condition *(light)* were significantly more accurate when located in the Obtuse (120 degree) corners.

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 Figure 3-4, top], and condition [F(1, 80) =

6.86, $p = .01$, $\eta_p^2 = .09$; see Figure 3-4, 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 conditions performed significantly better than females. In addition, participants in the Array condition were significantly more accurate at locating their goal corners than those in the Enclosed condition, although participants in both conditions performed better than chance (50%) [Array: $M = .87$, $SD = .19$, $t(39) = 12.33$, $p < .001$; Enclosed: $M = .74$, $SD = .28$, $t(39) = 5.30$, $p < .001$].


Proportion Correct
1.00
0.90
0.80
0.70
0.60
0.50
Male
Female
Sex

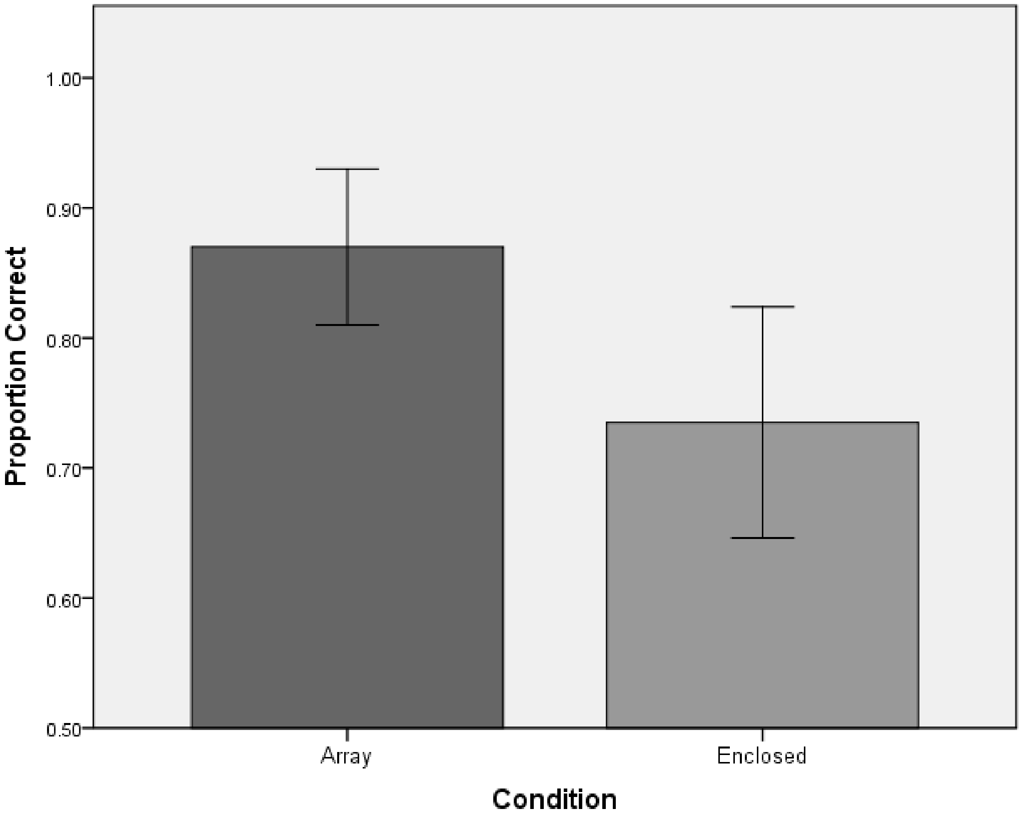

Proportion Correct
1.00
0.90
0.80
0.70
0.60
0.50
Array
Enclosed
Condition

Figure 3-4. Bar graphs indicating proportion of choices correct on the Feature Removed test by sex *(top)* and condition *(bottom)*. Error bars represent standard error of the mean.

In the Conflict test, where participants had to choose *either* the correct angular amplitude from training *or* the blue feature that was previously associated with the correct corner, there was a main effect of sex [$F(1, 80) = 10.30$, $p < .005$, $\eta_p^2 = .13$; see Figure 3-5]: Females weighted the blue feature panel 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 feature or correct angle at a rate that significantly differed from chance [Feature: $M = .45$, $SD = .40$; Angle: $M = .55$, $SD = .40$; $t(39) = .70$, $p = .49$]. However, an examination of individual male participants showed that 80 percent showed consistent preferences in the conflict environment (i.e., choice of either the features or angles for at least four out of five trials).

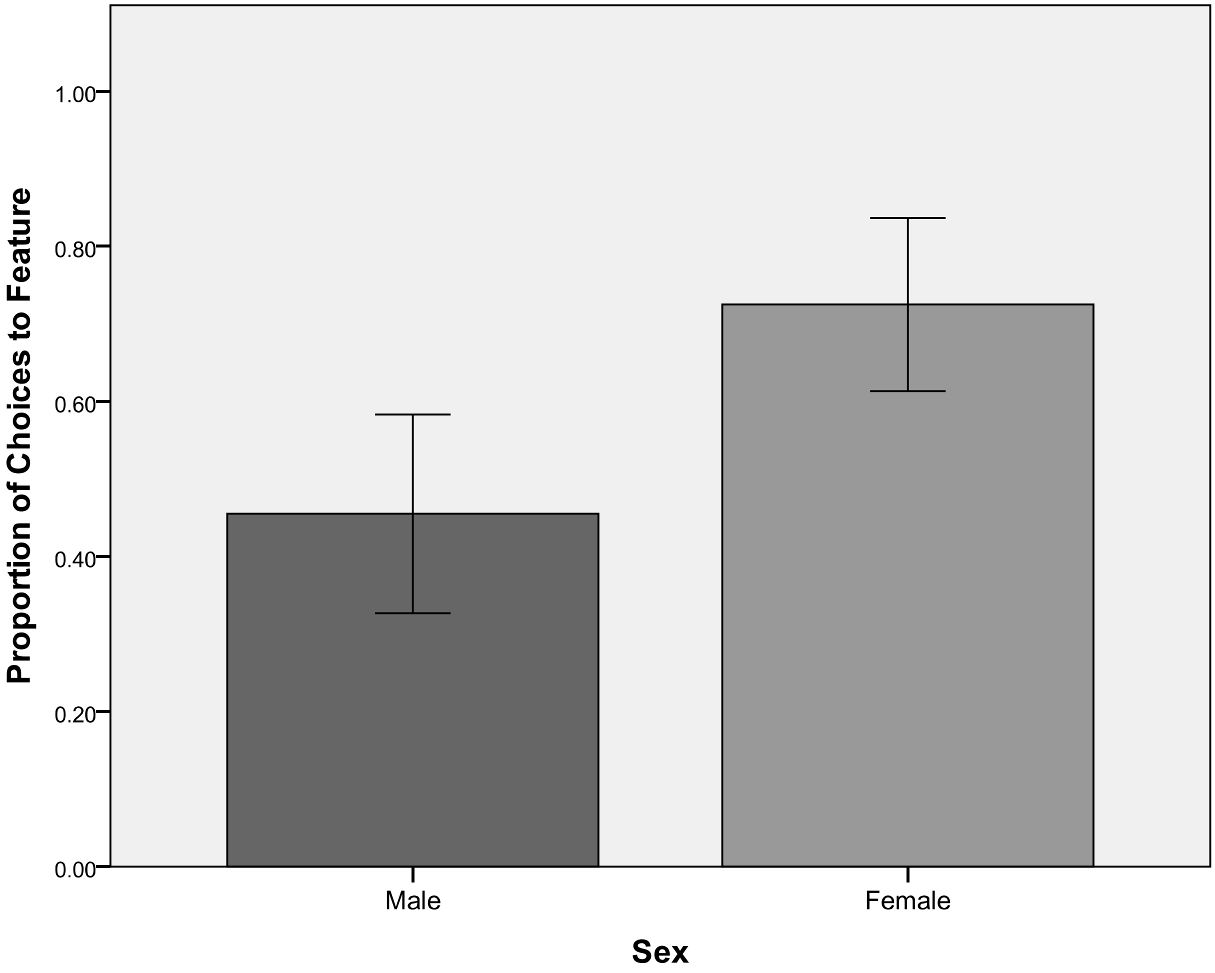


Figure 3-5. Bar graph indicating proportion of choices made by males and females to one of the correct corners as indicated by the blue feature panels in the Conflict test. Data are collapsed across both Array and Enclosed conditions. Error bars represent standard error of the mean.

Discussion

In contrast to most previous studies examining the role of geometry in reorientation, which commonly have paired informative relative wall length information with uninformative angular information in enclosed environments, in the current study we removed the wall lengths and added informative angular information and features in both enclosures and arrays. In the square Angle Removed test, there was a significant interaction between condition and goal corner. Specifically, for participants in the *array* condition, those who were trained to locate the acute corners which contained the blue feature panels performed better than those who were trained to locate the obtuse corners and feature panels. Interestingly, the opposite was true for participants in the enclosed condition; participants trained to locate the obtuse corners of the diamond-shaped *enclosure* outperformed those who were trained to find the acute corners when they were tested in the square Angle Removed environment. These findings suggest that the blue feature panels in the array training environment were more salient when located in acute corners, but in the enclosed environment were more salient when located in the obtuse corners. This is the first demonstration, to the best of our knowledge, of feature salience changing as a function of whether the environment is enclosed or formed by an array of angles.

In the diamond-shaped Feature Removed test, irrespective of condition and goal corners, males were more accurate than females at locating their goal corners when the featural information was removed, suggesting 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 environment to an extent which was sufficient to use it to locate their goal corners. In addition, participants in the array condition were significantly better at locating their goal corners on the Feature Removed test than those in the enclosed condition. This strong encoding of angular information from free-standing arrays is interesting in light of recent research by Reichert and Kelly (2011) in which only males showed evidence of encoding the distinct angular amplitudes of four free-standing angles which created a rectangular array. However, in a subsequent study, Reichert and Kelly (2012) found that both males and females readily discriminated between the two angular amplitudes when placed side-by-side, suggesting that the reorientation process played a key factor in females' inability to distinguish the two amplitudes from one another in the 2011 study. Our finding that participants in the array condition outperformed those in the enclosed condition in the Feature Removed test is also interesting in light the previously discussed findings of Lee, Sovrano, and Spelke (2012), in which young children could successfully orient in a diamond-shaped enclosure, but *not* a diamond-shaped array created by free-standing angles, such as in the current study. Additionally, when the angular information of the corners was removed, and only truncated walls joining the goal corners were present, the children were able to orient. These results suggest that the children were using the walls to assess distance and direction information, rather than using the local information of the angles. In the current study, the better performance on the Feature Removed test by participants in the array condition than by participants in the enclosed condition suggests that by adulthood, humans not only become able to extract geometric information from angles without the contribution of extended surfaces, but the encoding of geometric information from angles may even be more impervious to overshadowing by a feature.

In the Conflict test, females relied on the feature more than the angle when it was shifted to an incorrect angular location. Although males as a group responded at chance level, 80 percent of males consistently chose either the correct feature or correct angle. Therefore, most individuals of both sexes showed selective preferences for either features or angles. However, females consistently preferred the features whereas males showed more individual differences. Furthermore, it is interesting that there was no significant effect of group (enclosed or array) in participants' choices in the conflict test, suggesting that preference for angles over features is not influenced by the *type* of environment. Some recent studies have proposed that angles, due to the high degree of visual salience between differing amplitudes, may be encoded as featural rather than geometric information (Spelke, Lee, & Izard, 2010; Sturz, Forloines, & Bodily, 2012). However, the sex difference found in our study mirrors a common sex effect found in studies examining spatial reorientation in enclosed environments which contain both geometric and featural information, where men tend to rely more heavily on geometric information, whereas women primarily rely on featural information (Astur, Ortiz, & Sutherland, 1998; MacFadden, Elias, & Saucier, 2003; Saucier, Bowman, & Elias, 2003; Kelly & Bischof, 2005; Anderson, Dahmani, Konishi, & Bohbot, 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 & Bischof, 2008); it simply appears to be the case that features serve as a primary source of information for reorientation in females. The fact that a similar preference for the wall panel feature 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.

It should be noted that the current study did not specifically separate the properties of angle and principal axis information, and consequently there are two ways in which participants could have used the angles to orient. One possibility is that they used the angular amplitude to discriminate between the correct and incorrect corners. A second possibility is that they used the principal axis to orient (e.g., by following the axis then turning left). Use of this strategy would bring the participants to the correct angular locations in the conflict test. However, we think use of angular amplitude was more likely the controlling cue because in our previous research conducted in similar environments, participants chose angular information over the principal axis in a conflict situation (Lubyk, Dupuis, Gutiérrez, & Spetch, 2012). Nevertheless, the results are interesting regardless of exactly how the angles were used to extract geometric information, because in either case they show that adults, unlike children, have no problem extracting geometric information without extended surfaces.

Bibliography

Andersen, N. E., Dahmani, L., Konishi, K., & Bohbot, V. D. (2012). Eye tracking, strategies, and sex differences in virtual navigation. *Neurobiology of Learning and Memory*, *97*, 81-89. doi:10.1016/j.nlm.2011.09.007

Astur, R. S., Ortiz, M. L., & Sutherland, R. J. (1998). A characterization of performance by men and women in a virtual Morris water task: A large and reliable sex difference. *Behavioural Brain Research, 93,* 185–190. doi:10.1016/S0166-4328(98)00019-9

Bodily, K. D., Eastman, C. K., & Sturz, B. R. (2011). Neither by global nor local cues alone: evidence for a unified orientation process. *Animal Cognition, 14*, 665-674. doi:10.1007/s10071-011-0401-x

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23*, 149–178. doi:10.1016/0010-0277(86)90041-7

Cheng, K. (2005). Reflections on geometry and navigation. *Connection Science*, *17,* 5-21. doi:10.1080/09540090500138077

Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? squaring theory and evidence. *Psychonomic Bulletin & Review*, *12*, 1-23. doi:10.3758/BF03196346

Doeller, C. F., King, J. A. & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences, 105,* 5915-5920. doi:10.1073/pnas.0801489105

Gibson, B. M., Wilks, T. J., & Kelly, D. M. (2007). Rats *(Rattus norvegicus)* encode the shape of an array of discrete objects. *Journal of Comparative Psychology, 121*, 130-44. doi:10.1037/0735-7036.121.2.130

Gouteux, S. & Spelke, E. S. (2001). Children's use of geometry and landmarks to reorient in an open space. *Cognition, 81*, 119–148. doi:10.1016/S0010-0277(01) 00128-7

Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature, 370,* 57–59. doi:10.1038/370057a0

Hupbach, A. & Nadel, L. (2005). Reorientation in a rhombic environment: no evidence for an encapsulated geometric module. *Cognitive Development, 20*, 279–302. doi:10.1016/j.cogdev.2005.04.003

Kelly, D., & Bischof, W. F. (2005). Reorienting in images of a three-dimensional environment. *Journal of Experimental Psychology Human Perception and Performance*, *31*, 1391-403. doi:10.1037/0096-1523.31.6.1391

Kelly, D., & Bischof, W. F. (2008). Orienting in virtual environments: How are surface features and environmental geometry weighted in an orientation task? *Cognition*, *109*, 89-104. doi:10.1016/j.cognition.2008.07.012

Learmonth, A. E., Nadel, L., & Newcombe, N. S. (2002). Children's use of landmarks: implications for modularity theory. *Psychological Science*, *13*, 337-341. doi:10.1111/1467 9280.00461

Learmonth, A. E., Newcombe, N. S., Sheridan, N., & Jones, M. (2008). Why size counts: children's spatial reorientation in large and small enclosures.

Developmental Science, 11, 414-426. doi:10.1111/j.1467-7687.2008.00686.x

Lee, S. A., Sovrano, V. A, & Spelke, E. S. (2012). Navigation as a source of geometric knowledge: young children’s use of length, angle, distance, and direction in a reorientation task. *Cognition*, *123*, 144-61. doi:10.1016/j.cognition.2011.12.015

Lee, S. A. & Spelke, E. S. (2010). Two systems of spatial representation underlying navigation. *Experimental Brain Research, 206*, 179-88. doi:10.1007/s00221-010-2349-5

Lee, S. A. & Spelke, E. S. (2011). Young children reorient by computing layout geometry, not by matching images of the environment. *Psychonomic Bulletin & Review, 18,* 192–198. doi:10.3758/s13423-010-0035-z

Lever, C., Wills, T., Cacucci, F., Burgess, N., & O’Keefe, J. (2002). Long-term plasticity in hippocampal place-cell representation of environmental geometry. *Nature, 416,* 90-94. doi:10.1038/416090a

Lew, A. R. (2011). Looking beyond the boundaries: time to put landmarks back on the cognitive map? *Psychological Bulletin*, *137*, 484-507. doi:10.1037/a0022315

Lubyk, D. M. & Spetch, M. L. (2012). Finding the best angle: pigeons *(Columba livia)* weight angular information more heavily than relative wall length in an open-field geometry task. *Animal Cognition, 15,* 305-312. doi:10.1007/s10071-011-0454-x

Lubyk, D., Dupuis, B., Gutiérrez, L., & Spetch, M. L. (2012). Geometric orientation by humans: angles weigh in. *Psychonomic Bulletin & Review, 19,* 436-442. doi:10.3758/s13423-012-0232-z

MacFadden, A., Elias, L., & Saucier, D. (2003). Males and females scan maps similarly, but give directions differently. *Brain and Cognition, 53,* 297–300. doi:10.1016/S0278-2626(03)00130-1

Newcombe, N. S., Ratliff, K. R., Shallcross, W. L., & Twyman, A. D. (2010). Young children's use of features to reorient is more than just associative: further evidence against a modular view of spatial processing. *Developmental Science, 13*, 213-20.doi:10.1111/j.14677687.2009.00877.x

Pecchia, T. & Vallortigara, G. (2010). Reorienting strategies in a rectangular array of landmarks by domestic chicks *(Gallus gallus). Journal of Comparative Psychology, 124*, 147–158. doi:10. 1037/a0019145

Pecchia, T. & Vallortigara, G. (2012). Spatial reorientation by geometry with freestanding objects and extended surfaces: a unifying view. *Proceedings of the Royal Society Biological Sciences, 279,* 2228-2236. doi:10.1098/rspb.2011.2522

Reichert, J. F. & Kelly, D. M. (2011). Use of local and global geometry from object arrays by adult humans. *Behavioural Processes, 86*, 196-205. doi:10.1016/j.beproc.2010.11.008

Reichert, J. F. & Kelly, D. M. (2012). Discrimination of geometric angles by adult humans. *Animal Cognition, 15,* 271-284. doi: 10.1007/s10071-011-0452-z

Saucier, D., Bowman, M., & Elias, L. (2003). Sex differences in the effect of articulatory or spatial dual-task interference during navigation. *Brain and Cognition, 53,* 346–350. doi:10.1016/S0278-2626(03)00140-4

Spelke, E. S., Lee, S. A., & Izard, V. (2010). Beyond core knowledge: natural geometry. *Cognitive Science, 34*, 863-884. doi:10.1111/j.1551-6709.2010.01110.x

Spetch, M. L., Cheng, K., MacDonald, S. E., Linkenhoker, B. A., Kelly, D. M., & Doerkson, S. R. (1997). Use of landmark configuration in pigeons and humans: II. Generality across search tasks. *Journal of Comparative Psychology, 111,* 14–24. doi:10.1037/0735-7036.111.1.14

Sturz, B. R., & Bodily, K. D. (2011). Is surface-based orientation influenced by a proportional relationship of shape parameters? *Psychonomic Bulletin & Review*, *18*, 848-54. doi:10.3758/s13423-011-0111-z

Sturz, B. R., Forloines, M. R., & Bodily, K. D. (in press). Enclosure size and the use of local and global geometric cues for reorientation. *Psychonomic Bulletin & Review*. Advanced online publication 5 January 2012. doi: 10.3758/s13423-011-0195-5

Sutton, J. E. (2009). What is geometric information and how do animals use it? *Behavioural Processes*, *80*, 339-343. doi:10.1016/j.beproc.2008.11.007

Tommasi, L., & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick *(Gallus gallus). Animal Cognition*, *7,* 53-9. doi:10.1007/s10071-003-0182-y

Vallortigara, G., Zanforlin, M., & Pasti, G. (1990). Geometric modules in animals’ spatial representation: a test with chicks. *Journal of Comparative Psychology, 104*, 248–254. doi:10. 1037/0735-7036.104.3.248

Chapter 4:

A Comparison of Angle and Feature Use in an Open-Field Environment by Pigeons *(Columba livia)*[4]

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 to aid in the process of orientation. One such example is the *geometry* of an environment, defined as any property related to the overall shape. Any other cues present which do not fall under this category are referred to as nongeometric, or *featural* cues. These are cues such as colours, textures, smells, etc. In a pioneer study, Cheng (1986) discovered that rats, when trained to locate food in one corner of a rectangular enclosure which contained a distinctly coloured wall, consistently made rotational errors and chose the two geometrically equivalent corners (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 & Spelke, 1994). However, it has been shown that rats are able to use featural information when geometry is uninformative or unreliable (Gibson, Wilks, & Kelly, 2007), and similarly, children can also use features in larger environments (Learmonth, Nadel, & Newcombe, 2002; Learmonth,

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[4] *A version of this chapter has been submitted for publication. Lubyk & Spetch. Reorientation in a diamond-shaped environment: Use of featural and angle information in pigeons (Columba livia). Animal Cognition.*

Newcombe, Sheridan, & Jones, 2008) or when the features are incorporated into the geometric properties of the room (Wang, Hermer, & Spelke, 1999; Lee & Spelke, 2010a). Other studies have shown that featural information in some contexts can even facilitate the learning of geometric information (e.g., Graham, Good, McGregor, & Pearce, 2006; Kelly, 2010; Horne & Pearce, 2011). However, in many species salient featural information will override geometric information in a conflict situation (e.g., humans: Kelly & Bischof, 2005; Kelly & Bischof, 2008). Though preference for geometric or featural information varies by species and context, all species studied to date have been able to encode the geometric properties of their environment (for a review see Cheng & Newcombe, 2005).

This dynamic relationship between geometric and featural information is further complicated by a recent debate in the literature surrounding the encoding of *angular amplitudes*. Though long assumed to belong to the umbrella category of geometry, recent findings suggesting that smaller angles may be more salient that larger angles (Tommasi & Polli, 2004; Reichert & Kelly, 2011, 2012), combined with the tendency of angular information to sometimes override global geometric information (e.g., wall length information or a principal axis of symmetry; Lubyk & Spetch, 2012; Lubyk, Dupuis, Gutiérrez, & Spetch, 2012) has cast doubt on this assumption. Several researchers have suggested that angles may not be included in the category of geometric information, and rather, may be encoded as a type of *feature* (Spelke, Lee, & Izard, 2010; Sturz, Forloines, & Bodily, 2012). Additionally, recent findings which show that young children are unable to use the angular amplitudes of corners to orient (Hupbach & Nadel, 2005; Lee, Sovrano, & Spelke, 2012), much like the way they are often unable to use environment features, furthers the argument that angles may be encoded as featural information.

This debate regarding the encoding of angular information is further complicated by the fact that most studies to date examining geometric encoding in both human and non-human animals have trained the subjects in environment shapes which contain informative relative wall length information and non-informative angular information (e.g., rectangular environments). However, some investigations in training environments which do not contain relative wall length information have been conducted in young children; Lee, Sovrano, and Spelke (2012) tested two year old children in rhombic-shaped environments and found that they were unable to use the angular information of the corners to orient, and instead used the directional information provided by the global shape. Similarly, Hupbach and Nadel (2005) found that children could not use the angular amplitudes of the corners of a rhombic-shaped room to reorient until the age of four. Recently, training environment shapes which contain informative angular information have become more common in studies of non-human animal reorientation (e.g., parallelogram: Tommasi & Polli, 2004; Lubyk & Spetch, 2012; Lubyk et al., 2012; trapezoidal: Sturz, et al., in press; Sturz, Gurley, & Bodily, 2011; non-traditional: Sturz & Bodily, 2011), however, this failure to remove the relative wall length information in training limits the examination of how other cues are encoded in environments where wall length is not an option for reorientation.

In addition to a general lack of diversity in training environments, most studies to date have used enclosed environments to examine reorientation and small-scale navigation. A few studies have used arrays, where discrete landmarks rather than continuous surfaces, create the global shape of the environment. Several of these studies have demonstrated that both human and non-human animals have difficulty orienting within arrays of identical objects, especially when the array is placed proximally (i.e., centrally) in a larger environment (Gouteux & Spelke, 2001; Lee & Spelke, 2008; Pecchia & Vallortigara, 2010a) or when the array is asymmetrical (Lew, Gibbons, Murphy, & Bremner, 2010; for a reviews see Lew, 2011; Pecchia & Vallortigara, 2012). However, one question that has largely remained unanswered is how orientation in arrays is affected if the landmarks that form the global shape are angles which provide distinct corner information. Lee, Sovrano, and Spelke (2012) recently tested young children in rhombic- and rectangular-shaped environments created by freestanding corner segments and found that participants were unable to use the angular information of the corners for either directional orientation or as individual local landmarks. Though, interestingly, orientation could be accomplished if truncated walls placed between the objects were present, suggesting that, at least in children, there may be something unique regarding the presence of continuous surfaces in the encoding of a global shape. Similarly, Reichert and Kelly (2011) found that adult humans were unable to orient based on the global shape of a rectangular array created by four freestanding angles, and females even failed to encode the local angular information. These results prove interesting in light of subsequent tests in which reorientation was not necessary, where participants of both sexes could easily discriminate between the two angular amplitudes when placed next to one another, as opposed to in an array (Reichert & Kelly, 2012).

The discrepant results among studies of angular information encoding in both enclosed environments and arrays demonstrate the need for further research examining this encoding process. Additionally, the possibility that angles may be encoded as featural rather than geometric information has strong implications for studies examining corner usage in arrays. The goals of the current experiment were: 1) to examine pigeons' use of features and angular amplitudes in enclosures and arrays in a small scale orientation task; 2) to compare the relative weighing of featural and angular cues in both environments; and 3) explore the possibility that angular information may be encoded as features. In Experiment 1, we used an overshadowing procedure to compare the use of angular information in enclosures and arrays. Specifically, we trained adult pigeons to locate two geometrically equivalent corners in either a diamond-shaped enclosure, or a diamond-shaped array created by four independent angles. Importantly, blue feature panels were always located in the two trained corners so that either the features or the angular amplitudes could be used for orientation and navigation to the goal. Relative wall length was not an informative cue in training as all walls had the same dimensions. Following training, pigeons were tested in three manipulated environments (Angle Removed, Feature Removed, and Conflict) which matched the environment type from training (i.e., either enclosed or array). In Experiment 2, the birds were switched to the other environment type and re-trained to locate the same goal corners. The blue feature panels remained in the trained corners, as in Experiment 1 training, so that the only difference between Experiment 1 and 2 was that they took place in different environment types. This design allowed us not only to examine any differences in initial cue encoding between the array and enclosed environments, but also to determine whether the order of environment presentation either facilitated or hindered the re-learning in the second phase of training. Also, by limiting the available cues in training to angular and featural information, we were able examine pigeons' cue preference in order to determine if the cue competition resembled that which is typical in studies looking at geometry and features, or if the cue competition could potentially be between two types of features.

General Method

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 hour light:dark cycle with light onset at 6 AM. Birds were housed individually in metal cages and kept at 85 percent 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 condition, all apparatus had the same wall dimensions (85 cm *x* 85 cm; 60 cm height) and corner angular amplitudes (60 degrees and 120 degrees; see Figure 4-1, right; Figure 4-2, bottom). For the array condition, each arm of the free-standing angles was 20 cm wide and 60 cm high and when placed together created a global shape with dimensions similar to those of the enclosed group (82 cm *x* 82 cm) and the same angular amplitudes as the enclosed group (60 degrees and 120 degrees; see Figure 4-1, left; Figure 4-2, top). The array was placed within a large circular enclosure approximately 130 cm in diameter. For both groups, the blue feature panels (20 cm wide *x* 60 cm height) 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 *x* 4 cm height) covered with a thin sheet of paper towel and secured with an elastic band were attached to the floor with Velcro in 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 long white translucent curtain hung from the ceiling around the apparatus to block out external visual cues. Four 40-watt fluorescent bulbs illuminated the apparatus from outside of the curtains. Four noise machines were located around the apparatus which played white noise and blocked out external auditory cues.

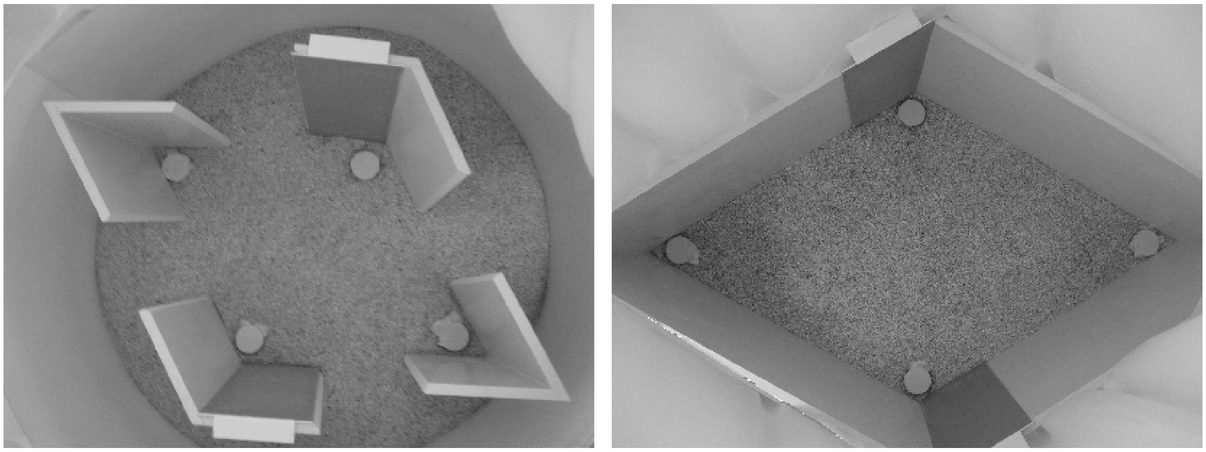

Figure 4-1. Top-down views of training enclosures for both the Array *(left)* and Enclosed *(right)* groups. Both are examples in which the obtuse (120 degree) corners were correct in training. For birds trained to locate the acute (60 degree) corners, the blue feature panels were located in the two opposite acute corners.

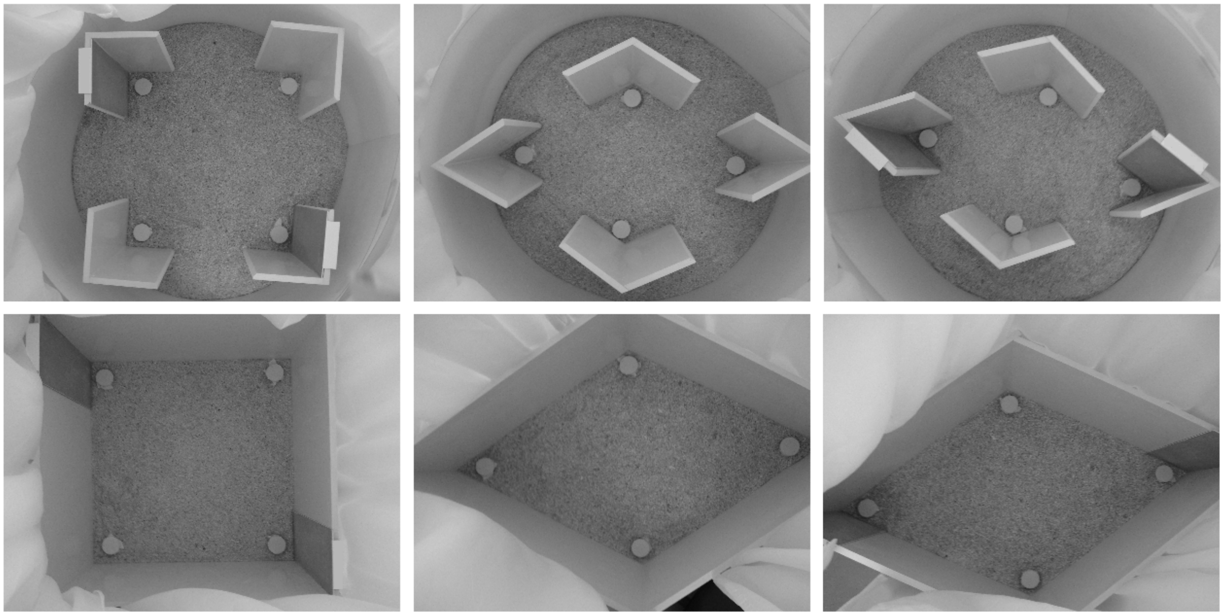

Figure 4-2. Top-down views of test enclosures for both the Array *(top row)* and Enclosed *(bottom row)* groups: Angle Removed *(left),* Feature Removed *(middle),* and Conflict *(right).* All are examples in which the obtuse (120 degree) corners were correct in training.

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 seconds. 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 area. In the array environment, subjects were placed in the space between the freestanding angles facing in. Light onset signalled the start of the trial and, in all phases except Habituation, the subject had a maximum of five minutes 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 while preparations for the next trial were made. 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.

Experiment 1

Method

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 therefore initially trained in the diamond array (see Figure 4-1, left), while the other half were assigned to the Enclosed group and were first trained in the diamond enclosure (see Figure 4-1, right). Birds were also counterbalanced within each group so that half were trained to locate the smaller acute corners and half the larger obtuse corners. The first phase of training was Habituation, which was designed to allow the pigeon to become comfortable in the arena and also to give it a chance to learn which two corners the food rewards were located in. One container was secured in each of the four corners and was full of grit, but no paper towel was present, and only the two correct corners for the particular pigeon were reinforced with 15 food pellets each 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 minutes to locate and consume all 30 pellets. If this was accomplished in under twenty minutes, subsequent identical trials were administered until a total of twenty minutes elapsed or until four trials had been carried out. Habituation was considered successfully passed when the pigeon consumed all 30 pellets in the arena in less than one minute for four consecutive trials in one session. Following completion of Habituation, the pigeon progressed to the second phase of training, in which 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 each of the containers and was secured with an elastic band. The amount of grit present in the containers was also slowly decreased so that by the time the paper towel covered the tops of the containers there was only a small amount of grit in them. In the second phase of training, as well as for the remaining phases, only four food pellets served as reinforcement in each of the correct corners. In addition, for the remainder of training, daily experimental sessions consisted of a fixed ten trials. In order to progress, the pigeon needed to direct their first choice on eight of the ten trials to one of the two correct corners. Phase three was identical to the end of the second, in that all ten trials were conducted with the paper towel fully covering the containers, except 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 score of eight out of ten correct.

Testing. Testing took place in three manipulated arenas designed to examine whether pigeons had encoded and could individually use both cues (i.e., blue features and angles), as well as whether they preferred one over the other. All test arenas matched the environment type that the pigeon was trained in; i.e., birds trained in the array were tested in arrays. All test trials were non-reinforced. The first test was the Angle Removed test (see Figure 4-2, left column), in which the informative angular information from training was replaced with uninformative uniform right angles. The second test was the Feature Removed test (see Figure 4-2, center column), in which the global shape of the arena was identical to training, but the blue feature panels were removed, leaving only the angular amplitudes for orientation. The third test was the Conflict test (see Figure 4-2, right column), where the blue feature panels were shifted to the incorrect angular amplitude locations from training, placing the features and angles in conflict with one another; this meant that a choice to the corner marked by the blue feature panel, for example, would be inconsistent with the correct angle from training, and vice versa. Each daily test session consisted of six baseline trials, which were reinforced training trials in the training arena; three non-reinforced test trials, one of each type; and one control trial, which was a non-reinforced training trial. Order of trials was randomized from day to day, but was controlled so that there were never two non-reinforced trials (i.e., test or control) in a row. In the test and control trials, corner choices were operationally defined as pecking through the paper towel (as confirmed from the overhead camera and confirmed by a break in the paper towel). Testing was complete when the pigeon completed (i.e., made a choice) eight trials in each of the test and control trials. This could be accomplished in eight sessions, but took longer if pigeons failed to make a choice on some trials.

Results

All birds completed both initial training with perfect or near perfect accuracy to their correct corners as defined by both the angular amplitudes and blue feature panels. Univariate analyses of variance were carried out examining performance on each of the three tests (i.e., Angle Removed, Feature Removed, and Conflict) for the subjects’ first round of testing, which for half of the birds was in the array environment, and for the other half the enclosed environment.

Fixed variables for all comparisons were Goal Corners (Acute or Obtuse) and Condition (Array or Enclosed).

All pigeons achieved perfect accuracy in the Control trials during testing (i.e., selected one of the two trained corners on every trial), indicating that all birds recalled the correct corners from the training environment throughout testing. In addition, all birds also had perfect accuracy in the array Angle Removed test, in which the blue feature panels were paired with uninformative right angles, 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 encoded the angular amplitudes from training in addition to the blue features, despite the fact that the blue features were sufficient to locate the goal corners.

On 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, there was a main effect of *goal corners* [$F(1,7) = 31.22$, $p < .01$, $\eta^2_p = .89$]: birds that were trained to go to the obtuse (120 degree) corners which contained the blue feature panels did not differ from chance (50%) in their choices to the blue feature panel [$M = .54$, $SD = .28$, $t(3) = .25$, $p = .82$], meaning they chose to go to the corner which contained the correct angular amplitude and correct feature equally often. However, birds that were trained to go to the acute (60 degree) corners which contained the blue feature chose the blue feature panel significantly less than would be expected by chance, indicating that they were choosing the correct angular amplitudes instead [*M* = .07, *SD* = .08, *t*(3) = -11.60, *p* < .001].

There was no effect of Condition (i.e., Array or Enclosed) in any of the three tests, indicating similar performance across both environment types throughout the experiment.

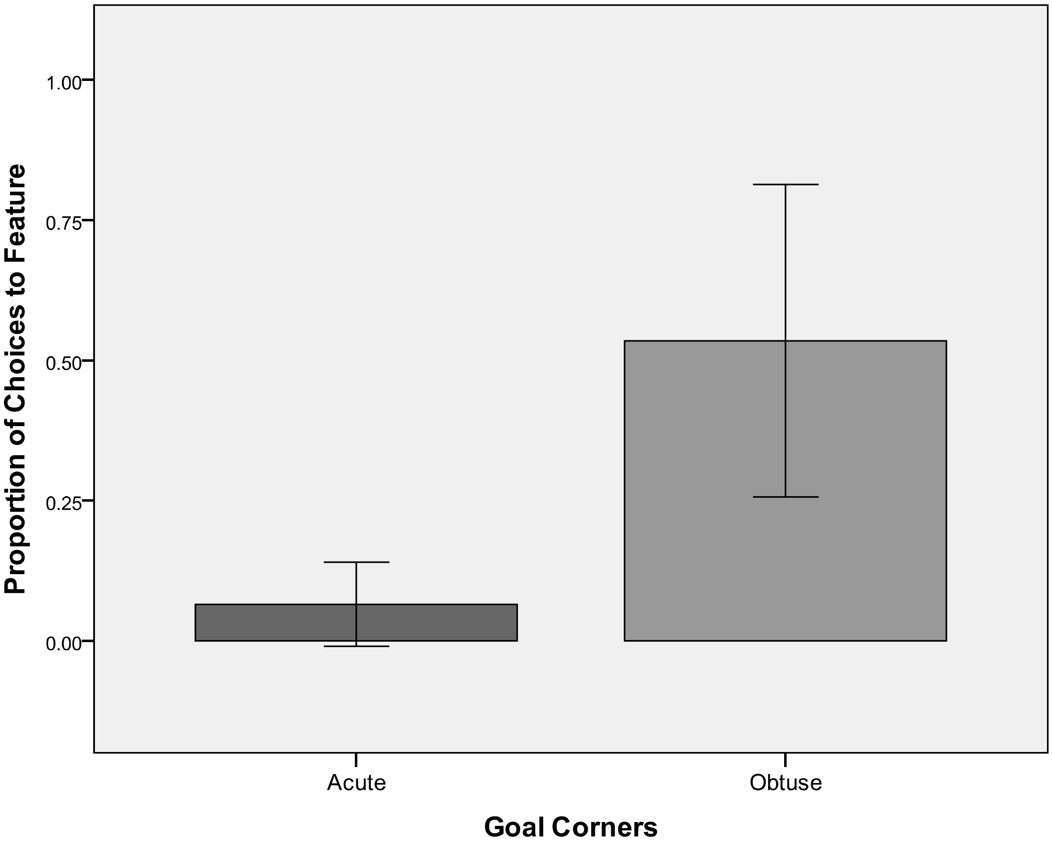

Figure 4-3. Bar graph showing main effect of goal corner in the Conflict test. The *y*-axis represents the proportion of choices made to the corner containing the blue feature panel. Pigeons trained to locate the acute corners in training chose the blue feature significantly less than would be expected by chance, indicating a heavier reliance on the inverse choice, which was the correct angular location. Birds trained to locate the obtuse corners did not differ from chance (50 percent),

meaning they chose both the blue feature panel and the correct angular location equally often. Error bars reflect the standard error of the mean.

Experiment 2

Method

Re-training. Following successful completion of Experiment 1, pigeons were re-trained in the other environment type (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 of the ten trials in the old training environment and the other five in the new training environment. All trials were reinforced in the correct corners and were randomized for order of presentation. Birds had to direct a minimum of four out of five of their first choices in each of the old and new environment trials to one of the correct corners to proceed. The second phase of re-training was similar to the first, except that all ten trials were in the new environment type. Pigeons again had to get a minimum of eight of the trials correct before proceeding on to the last phase of re-training, which was the same as the second except 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 Experiment 1. Birds again had to successfully complete eight trials in each of the Angle Removed, Feature Removed, and Conflict test (see

Figure 4-2, left, center, and right columns, respectively) in addition to eight Control trials, in order to successfully complete the experiment.

Results

The tests conducted in Experiment 2 were identical to those in Experiment 1 except they were conducted in the environment type (i.e., array or enclosed) that the subjects were not tested in during Experiment 1. All birds maintained perfect accuracy to their trained goal corners in the Control tests, demonstrating that throughout testing the birds remembered their correct corners from training. As in the square Angle Removed test of Experiment 1, in which the informative acute and obtuse angles were replaced with uninformative right angles, birds had near perfect accuracy to the blue feature panels, indicating that reorientation was not affected by the absence of the angular information from training. In the Feature Removed test, birds' accuracy to their trained goal corners was significantly higher than what would be expected by chance [50%; $M = .76$, $SD = .32$, $t(7) = 2.33$, $p = .05$]. In the Conflict test, birds in both the Array and Enclosed conditions chose the corner associated with the blue feature panel significantly more than chance despite its association with the incorrect angular location [50%; $M = .78$, $SD = .26$, $t(7) = 3.03$, $p < .05$]. There was no effect of Goal Corners (i.e., Acute or Obtuse) in any of the three test environments, indicating that angular amplitude did not effect the use of either the featural or angular cues in Experiment 2.

General Discussion

In both Experiment 1 training and Experiment 2 re-training, both cues of feature and angle were present, and learning either one in isolation would have been sufficient to complete the task. In Experiment 1 testing, pigeons performed significantly above chance in the proportion of correct corner choices 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 birds whose initial training and testing took place in the diamond-shaped enclosure, given the existing research which shows that both human and non-human animals, including pigeons, are able to encode angular information in enclosed environments; this encoding takes place despite the presence of other informative cues such as relative wall length (Tommasi & Polli, 2004; Lubyk & Spetch, 2012; Lubyk, Dupuis, Gutiérrez, & Spetch, 2012; but see Sturz & Bodily, 2011). However, the fact that the environment type did *not* have an effect on the extent to which the local angular information was encoded is interesting, especially in light of recent literature with young children in similar diamond-shaped environments (Lee, Sovrano, & Spelke, 2012), which suggests that children use the boundary information of arrays to orient rather than the local angular information. Similarly, Reichert and Kelly (2011) demonstrated that adult humans had difficulty using the distinct angular amplitudes of the corners of a rectangular array to orient, yet could easily discriminate between the two amplitudes in a subsequent task which did not require orientation (Reichert & Kelly, 2012). However, in the current experiment, pigeons in both the array and enclosed conditions performed similarly (and above chance) in the Feature Removed test, suggesting that they were in fact using the angular amplitudes of the corners to orient, rather than directional cues derived from the wall boundaries (as children did). This result is consistent with the aforementioned findings with pigeons in parallelogram-shaped enclosures, in which the angular information was encoded despite the presence of both relative wall length and principal axis information (Lubyk & Spetch). Clearly, despite the presence of the blue feature panels in training, the angular information provided by the corners in both the array and enclosure was also a salient part of the environment.

In addition, the Experiment 1 Conflict test showed an interesting effect of goal corners: pigeons that were trained to locate the obtuse (120 degree) corners of the diamond-shaped enclosure or array did not exhibit a preference to either the correct angular location or the blue feature panel when forced to choose between the two. On the other hand, birds that were trained to locate the acute (60 degree) corners showed a preference to the correct angular location over the blue feature panel. This is interesting because it is in line with recent suggestions, based on research conducted with other species in both enclosures and arrays, that acute angles may be more salient than obtuse angles (chicks: Tommasi & Polli, 2004; adult humans: Reichert & Kelly, 2011, 2012). However, up until now, this effect of amplitude on angle salience has not been found in pigeons; Lubyk and Spetch (2012) trained pigeons to locate two geometrically equivalent corners of a parallelogram-shaped enclosure which provided the cues of relative wall length, angular amplitude, and a principal axis of symmetry. In subsequent conflict tests, pigeons weighted the correct angular location heavier than both relative wall length and principal axis information, irrespective of goal corner amplitude. It is interesting to note that the amplitudes of the corners in the Lubyk and Spetch study were identical to those used in the current study: 60 and 120 degrees. However, the Lubyk and Spetch training environment also contained informative relative wall length information, whereas the current study provided salient featural information instead. One possibility is that the featural information present in the current experiment facilitated the encoding of the angular amplitudes (see Graham, Good, McGregor, & Pearce, 2006; Kelly, 2010; Horne & Pearce, 2011). However, that would not explain why only the acute-trained birds weighted the angles heavier, as the blue feature panels were also associated with the correct angular locations for the birds trained to go to the obtuse corners.

In all three Experiment 1 test environments (Angle Removed, Feature Removed, and Conflict), there was no effect of Condition (i.e., Array or Enclosed). This finding shows that when pigeons did not have previous experience in the other environment type, there was no difference in accuracy to the goal corners when the individual cues from training were isolated (i.e., in the Angle Removed and Feature Removed tests), or in weighting preference (i.e., in the Conflict test) between the diamond-shaped enclosure and array. Overall, the results of Experiment 1 show that pigeons trained in both arrays and enclosures are able to encode and use both the angular and featural information present in a similar fashion. The preference to the correct angular location in the Conflict test by pigeons trained to locate the acute corners could be because they were encoding the corner angles via the distance between the intersecting walls; this would suggest that the angular information, in both the array and enclosed environments, was being treated as featural information. However, this finding is not definitive, as previous research with pigeons in similar environments has demonstrated that angle information can override other environmental cues such as relative wall length (Lubyk & Spetch, 2012). Future studies will have to examine this further.

The purpose of Experiment 2 was to examine pigeons' performance in the same test conditions as were conducted in Experiment 1, but in the other environment type, to determine if the accuracy to, or weighting of, the featural and angle information changed as a result of prior experience. Performance in the Angle Removed and Feature Removed tests of Experiment 2 were similar to those of Experiment 1 for both the Array and Enclosed birds; in other words, the prior training and testing in the other environment type did *not* affect pigeons' ability to orient and locate their goal corners in environments which did not contain the angular (i.e., Angle Removed test) and featural (i.e., Feature Removed test) information from training. This makes sense, as in Experiment 2 the birds were re-trained to locate their same goal corners with the blue feature panels still present, so if anything, the re-training in the new environment type only reinforced what they had already learned in Experiment 1.

However, when the blue feature panels were shifted to the incorrect angular locations in the Experiment 2 Conflict test, birds in both the Array and Enclosed conditions weighted the blue features significantly heavier than the correct angular locations. This result differs from that of the Conflict test of Experiment 1, in which birds in both environments (i.e., Array and Enclosed) showed an effect of goal corners; birds that had been trained to locate the acute corners weighted the correct angular location from training heavier, while those trained to locate the obtuse corners weighted the locations which contained the blue feature panels heavier. This discrepant result of the Experiment 2 Conflict test, that pigeons weighted the correct featural location heavier, irrespective of goal corner or environment type in Experiment 2, could potentially be the result of the extended exposure to the blue feature panel.

To conclude, in contrast to previous studies which have examined angle use in pigeons, the current experiment removed the informative cue of relative wall length from training, and explored the use of featural and angular information in both enclosures and arrays. Results indicated that neither environment type, nor prior experience in the other environment, had an effect on the pigeons’ ability to use the blue feature panels or angular amplitudes in isolation. This suggests that featural information is used similarly in enclosures and arrays, and likewise for angular information. This finding differs from that of other behavioral studies examining angle use in arrays by children (Hupbach & Nadel, 2005; Lee, Sovrano, & Spelke, 2012) and adults (Reichert & Kelly, 2011), which have shown a distinct differences in use of angles in enclosures and arrays. The current study also reports a novel finding in pigeons that smaller angles may be more salient than larger angles in both enclosures and arrays. This is consistent with findings in both chicks (Tommasi & Polli, 2004) and adult humans (Reichert

& Kelly, 2011, 2012), but is inconsistent with the existing literature on angle use in pigeons in an enclosed environment (Lubyk & Spetch, 2012). This novel finding with pigeons supports recent suggestions that angular information may be encoded as featural, rather than geometric, information (see Spelke, Lee, & Izard, 2010; Sturz, Forloines, & Bodily, 2012). However, more studies examining angle salience as a function of amplitude are needed in order to fully understand which environmental factors contribute to the relative salience of angular information.

Bibliography

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23*, 149–178. doi:10.1016/0010-0277(86)90041-7

Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review*, *12*, 1-23. doi:10.3758/BF03196346

Gibson, B. M., Wilks, T. J., & Kelly, D. M. (2007). Rats *(Rattus norvegicus)* encode the shape of an array of discrete objects. *Journal of Comparative Psychology, 121*, 130-44. doi:10.1037/0735-7036.121.2.130

Gouteux, S. & Spelke, E. S. (2001). Children's use of geometry and landmarks to reorient in an open space. *Cognition, 81*, 119–148. doi:10.1016/S0010-0277(01) 00128-7

Graham, M., Good, M. A, McGregor, A., & Pearce, J. M. (2006). Spatial learning based on the shape of the environment is influenced by properties of the objects forming the shape. *Journal of Experimental Psychology Animal Behavior Processes*, *32*, 44-59. doi:10.1037/0097-7403.32.1.44

Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature, 370,* 57–59. doi:10.1038/370057a0

Horne, M. R., & Pearce, J. M. (2011). Potentiation and overshadowing between landmarks and environmental geometric cues. *Learning & Behavior, 39*, 371-82. doi:10.3758/s13420-011-0032-8

Hupbach, A. & Nadel, L. (2005). Reorientation in a rhombic environment: no evidence for an encapsulated geometric module. *Cognitive Development, 20*, 279–302. doi:10.1016/j.cogdev.2005.04.003

Kelly, D. (2010). Features enhance the encoding of geometry. *Animal cognition*, *13*, 453-62. doi:10.1007/s10071-009-0296-y

Kelly, D., & Bischof, W. F. (2005). Reorienting in images of a three-dimensional environment. *Journal of Experimental Psychology Human Perception and Performance*, *31*, 1391-1403. doi:10.1037/0096-1523.31.6.1391

Kelly, D., & Bischof, W. F. (2008). Orienting in virtual environments: How are surface features and environmental geometry weighted in an orientation task? *Cognition*, *109*, 89-104. doi:10.1016/j.cognition.2008.07.012

Learmonth, A. E., Nadel, L., & Newcombe, N. S. (2002). Children's use of landmarks: implications for modularity theory. *Psychological Science*, *13*, 337-341. doi:10.1111/1467 9280.00461

Learmonth, A. E., Newcombe, N. S., Sheridan, N., & Jones, M. (2008). Why size counts: children's spatial reorientation in large and small enclosures. *Developmental Science, 11*, 414-426. doi:10.1111/j.1467-7687.2008.00686.x

Lee, S. A., Sovrano, V. A, & Spelke, E. S. (2012). Navigation as a source of geometric knowledge: young children's use of length, angle, distance, and direction in a reorientation task. *Cognition*, *123*, 144-61. doi:10.1016/j.cognition.2011.12.015

Lee, S. A., & Spelke, E. S. (2008). Children's use of geometry for reorientation. *Developmental Science, 11,* 743–749. doi:10.1111/j.1467-7687.2008.00724.x

Lee, S. A., & Spelke, E. S. (2010a). A modular geometric mechanism for reorientation in children. *Cognitive Psychology, 61*, 152–176. doi: 10.1016/j.cogpsych.2010.04.002

Lew, A. R. (2011). Looking beyond the boundaries: time to put landmarks back on the cognitive map? *Psychological Bulletin*, *137*, 484-507. doi:10.1037/a0022315

Lew, A. R., Gibbons, B., Murphy, C., & Bremner, J. G. (2010). Use of geometry for spatial reorientation in children applies only to symmetric spaces. *Developmental Science, 13,* 490–498. doi:10.1111/j.1467-7687.2009.00904.x

Lubyk, D. M. & Spetch, M. L. (2012). Finding the best angle: pigeons *(Columba livia)* weight angular information more heavily than relative wall length in an open-field geometry task. *Animal Cognition, 15,* 305-312. doi:10.1007/s10071-011-0454-x

Lubyk, D., Dupuis, B., Gutiérrez, L., & Spetch, M. L. (2012). Geometric orientation by humans: angles weigh in. *Psychonomic Bulletin & Review, 19,* 436-442. doi:10.3758/s13423-012-0232-z

Pecchia, T. & Vallortigara, G. (2010a). Reorienting strategies in a rectangular array of landmarks by domestic chicks *(Gallus gallus). Journal of Comparative Psychology, 124*, 147–158. doi:10. 1037/a0019145

Pecchia, T. & Vallortigara, G. (2012). Spatial reorientation by geometry with freestanding objects and extended surfaces: a unifying view. *Proceedings of the Royal Society Biological Sciences, 279,* 2228-2236. doi:10.1098/rspb.2011.2522

Reichert, J. F. & Kelly, D. M. (2011). Use of local and global geometry from object arrays by adult humans. *Behavioural Processes*, *86*, 196-205. doi: 10.1016/j.beproc.2010.11.008

Reichert, J. F. & Kelly, D. M. (2012). Discrimination of geometric angles by adult humans. *Animal Cognition, 15,* 271-284. doi: 10.1007/s10071-011-0452-z

Spelke, E. S., Lee, S. A., & Izard, V. (2010). Beyond core knowledge: natural geometry. *Cognitive Science, 34*, 863-884. doi:10.1111/j.1551-6709.2010.01110.x

Sturz, B. R. & Bodily, K. D. (2011). Is surface-based orientation influenced by a proportional relationship of shape parameters? *Psychonomic Bulletin & Review*, *18*, 848-54. doi:10.3758/s13423-011-0111-z

Sturz, B. R., Forloines, M. R., & Bodily, K. D. (in press). Enclosure size and the use of local and global geometric cues for reorientation. *Psychonomic Bulletin & Review*. Advanced online publication 5 January 2012. doi: 10.3758/s13423-011-0195-5

Sturz, B. R., Gurley, T., & Bodily, K. D. (2011). Orientation in trapezoid-shaped enclosures: implications for theoretical accounts of geometry learning. *Journal of Experimental Psychology Animal Behavior Processes*, *37*, 246-53. doi:10.1037/a0021215

Tommasi, L., & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick (*Gallus gallus*). *Animal Cognition, 7*, 53–59. doi: 10.1007/s10071-003-0182-y

Wang, R. F., Hermer, L., & Spelke, E. S. (1999). Mechanisms of reorientation and object localization by children: a comparison with rats. *Behavioral Neuroscience, 113*, 475–485. doi: 10.1037/0735-7044.113.3.475

General Discussion and Conclusions

Multiple Cue Encoding in Diverse Environments

The preceding chapters examined how pigeons and adult humans encode and represent the salient properties of their environment such as relative wall length, angles, principal axes, and features. In all experiments, pigeons and humans were presented with multiple cues in training, and encoding of any one of the cues would have resulted in successful completion of the task. However, subsequent transformational tests indicated that in all cases, pigeons and humans were able to orient and locate their goals with any of the initial cues from training presented in isolation, meaning that while there may be a preference to a particular cue type as shown in the Conflict test (e.g., angular information in Chapter 1), both human and nonhuman animals are able to encode multiple cues and use them independently. This has been shown in several other species (for a review see Cheng & Newcombe, 2005), and makes sense from an evolutionary perspective, as our surroundings are constantly growing, changing, and updating with the weather and seasons, for example; encoding a single source of information would prove to be extremely unbeneficial as soon as the environment changed. Instead, having multiple sources of information to fall back on is adaptive when one source is no longer informative.

Angular Salience

Chapter 1 was based off of a previously conducted study with domestic chicks (*Gallus gallus*; Tommasi & Polli, 2004), which showed that chicks are able to use both relative wall length and angular amplitude to orient. However, one difference between Tommasi and Polli's findings and the current findings reported in Chapter 1 is that in chicks, the size of the angle had an effect on how it was weighted in the Conflict test; chicks that had been trained to locate the smaller acute angles weighted the angles heavier in the Conflict test, whereas chicks that had been trained to locate the larger obtuse angles weighed the relative wall length locations heavier. This finding in chicks suggested that angle salience varied as a function of amplitude, and that smaller angles may have been more visually salient than the larger ones. In pigeons, the corner defined by the correct angular amplitude from training was weighted heavier irrespective of goal angle, which suggested that this relative salience based on angle size was not a factor in pigeons. A similar effect of angle amplitude on salience has since been found in adult humans in environments created by an array of freestanding acute angles (Reichert & Kelly, 2011); participants were trained to locate two geometrically equivalent corners of a rectangular array which contained two sets of freestanding angles of 50 and 75 degrees. After a set amount of training trials, participants progressed to testing, where either the angular information of the corners was removed to test if the participants had encoded the global shape of the array, or where the global rectangular shape was replaced with a square in which the local angles were maintained to test for angle encoding. Results indicated that none of the participants were able to use the global information of the array alone to orient, and only male participants had encoded the local angular information of the corners. Interestingly, of the participants who successfully encoded the local angles, those whose corner corners were the smaller 50 degree angle were significantly more accurate to the correct corners in testing than those who had been trained to locate the 75 degree angles. This suggests that the smaller angles were more salient to the participants and therefore aided in their encoding. It also shows that angle salience is not a simple acute-obtuse dichotomy, as both angular amplitudes in the Reichert and Kelly study were acute. Rather, angle salience is likely situated on an absolute continuum, where angles range from the very salient at the smaller end to not salient at all as the amplitude increases. However more research would be needed to confirm this.

This salience based on angular amplitude had been demonstrated in domestic chicks and adult humans, but had not yet been shown in pigeons, which suggested a functional species difference in the way chicks and pigeons encoded and represented the cues in their environment. However, the Chapter 4 study trained pigeons in a diamond-shaped environment which contained angular information and features, but no relative wall length information. Results showed that in the Conflict test, in which the features that had previously been associated with the correct angular amplitudes from training were shifted to the incorrect corners, that pigeons behaved differently in their choices depending on the angular amplitude that they had been trained on; as in the domestic chick study (Tommasi & Polli, 2004), pigeons' preference for the features over the angles (or vice versa) was dependent on their training angle. Pigeons that were trained to locate the acute corners of the diamond chose the correct corner as defined by the angular amplitude over the corner which contained the feature, while obtuse-trained pigeons did the opposite and weighted the feature that had acted as a beacon in training as more reliable. This result was very similar to the one found with the domestic chick, suggesting that smaller angles may be more salient in some environment types but not others.

Use of Principal Axes

The current studies, as they were not exclusively designed to examine principal axis use, do not conclusively support or refute the existing literature on the subject. The findings of Chapters 1 and 2, in which pigeons and humans were trained in the parallelogram-shaped environments, suggest that while principal axis information could have played a role, it was not the main cue at work. In both studies, the relative wall length information was confounded with the principal axis in training, and using either one as a strategy would have led the subjects to the same corners. However, in the Conflict test, in which the subjects were placed in a mirror-image environment in which the correct relative wall length/principal axis location was no longer the correct corner as defined by the angular amplitudes from training, both pigeons (Chapter 1) and adult humans (Chapter 2) relied more heavily on the angular amplitudes from training at the cost of both the relative wall length information and the principal axis of symmetry.

The goals of Chapters 3 and 4 were to examine the use of feature and angle information in enclosed environments and arrays, and as such did not contain a specific test to examine principal axis use. Similar to Chapters 1 and 2, in training in the diamond-shaped environment, using the principal axis of symmetry would have brought the subjects to the same corners as using the angular amplitudes, and the two strategies would have been indistinguishable in the diamond Feature Removed test. However, based on our findings in both pigeons (Chapter 1) and adult humans (Chapter 2), in which the angular information was weighted heavier than the principal axis of symmetry, we are confident that the local angular amplitudes of the corners were driving the orientation process. Additionally, the angular amplitudes of the corners in Chapters 3 and 4 were identical to the ones in Chapters 1 and 2, making it easier to generalize between the two. Also, because the principal axis of any environment exists only down the length of the space, the principal axis in the diamond-shaped environment would have been much less salient compared to the parallelogram-shaped environment, as all walls were the same length in the diamond. However, it is crucial that future studies should examine how a principal axis may interact with angular information, especially in light of recent studies in diamond-shaped environments (Lee, Sovrano, & Spelke, 2012), which show that young children do not use the local angular amplitudes of the corners to orient, but instead use the distance and direction properties from the wall boundaries.

Other recent investigations into whether pigeons use principal axes as a main source of orientation information have also failed to support this hypothesis (Kelly, Chiandetti, & Vallortigara, 2010). However, the findings in humans have been more varied, with several recent studies supporting the use of principal axes for orientation and navigation in small-scale virtual environments (e.g., Bodily, Eastman, & Sturz, 2011; Sturz & Bodily, 2011; Sturz, Gurley, & Bodily, 2011). It seems that the use and hierarchical weighting of such information is both species- and context-dependent. More research is needed in order to more closely examine use of principal axis information and how it may vary by species and environment.

Angles as a Subset of Featural Information?

Based on a wealth of recent studies which have suggested that angular information may in fact be encoded as a type of feature, rather than geometry, Chapters 3 and 4 compared the use of angles and features in both humans and pigeons. Both studies showed interesting results which cast light on these questions. In the human study in Chapter 3, the Conflict test shifted the blue feature panels to the incorrect angular amplitudes, forcing participants to choose which cue represented a more reliable source of information. Results showed an interesting effect of sex: male participants as a group did not weight either cue heavier than the other, and chose each approximately 50 percent of the time. Females, however, showed a significant preference for the blue feature panel from training, showing a heavier reliance on the features over the angles. This finding is interesting because it is similar to the typical sex effect found in the spatial literature when features and *geometry* are placed in conflict with one another: while males tend to the prefer the geometric information present, females will reliably weight the featural information more heavily (Astur, Ortiz, & Sutherland, 1998; MacFadden, Elias, & Saucier, 2003; Saucier, Bowman, & Elias, 2003; Kelly & Bischof, 2005; Anderson, Dahmani, Konishi, & Bohbot, 2012). This observed sex effect does not provide conclusive evidence that adult humans encode angular information as geometry rather than features, as recently suggested. However, as the first empirical investigation of this hypothesis, it provides a crucial first step to examining the possibility that angular information is, at the very least, encoded and used in a slightly different way than other types of geometric information. The findings in humans are extremely interesting, as they show that the cue competition between the features and the angles reflects that of the competition between geometry and features, rather than between two features, as would take place if angular information was not geometric.

Chapter 4 provided the same comparison of angles and features as Chapter 3 but with pigeons. Similarly, the Conflict test yielded some surprising results. As previously discussed, recent investigations of angle salience in other species have found that smaller angles tend to be relied upon more than larger angles when placed in conflict with other environmental cues (chicks: Tommasi & Polli, 2005; adult humans: Reichert & Kelly, 2011, 2012). This finding had not yet been shown in pigeons, despite comparable investigations having taken place (e.g., Chapter 1 study). However, in the Conflict test of Chapter 4, we see an effect of trained angular amplitude on cue preference: pigeons that had been trained in the diamond-shaped environment to locate the acute corners weighted the angular information heavier than the features, whereas pigeons that were trained to locate the obtuse corners weighted the blue features heavier. This result not only shows that the angles were more salient when they were of smaller amplitude, but also that the difference in salience was substantial enough to cause the overshadowing of the blue feature for the pigeons in the acute condition. This is the first experimental demonstration in pigeons of local angular information varying by salience, as well as being weighted heavier than a distinct feature in the orientation process. While not conclusive, these data showing that for pigeons, visual angular amplitude affects the overall salience of the angle, support recent suggestions that angular information may be encoded and represented as featural, rather than geometric information. More research is needed in order to determine if the same effect would appear in angles of varying amplitude and relative size. However, based on similar findings in the Reichert and Kelly (2011) study, in which the angles were both acute and very similar in amplitude, we are confident that the current results would be replicated in subsequent studies.

Conclusion

Overall, the preceding studies have contributed significantly to the body of literature on both human and pigeon spatial orientation and navigation. From these studies we have concluded that both pigeons and humans are able to encode and use the local cues of relative wall length and angular amplitude to orient (Chapters 1 and 2), comparisons which had not yet been conducted. Both species weighted the angular amplitudes of their environments heavier than the relative wall length relationships and the principal axis of symmetry, which added informative data to the growing literature on angular information. Chapters 3 and 4 further explored the use of angles in enclosures and arrays in pigeons and humans with respect to how the information was encoded and represented. Results showed for the first time in the literature that angle salience changes as a function of amplitude for pigeons, suggesting that angular information may in fact be encoded visually as a feature, rather than as integrated with other geometric information. Findings in humans, which showed that females weighted the features as significantly more reliable than the angular information in the Conflict test, suggest that, contrary to recent suggestions, angular information is encoded as geometric information for humans.

Future investigations of angle use in pigeons and humans should more closely examine the relationship between angular amplitude and salience by systematically increasing the absolute amplitude of the angles as well as the relative difference in amplitudes compared to one another. By doing this, one could determine if angle salience is on an absolute continuum, or if the relative difference in amplitude between the angles present is what is driving the discrimination. Additionally, more tests should be carried out in order to directly control for principal axis cues as well as distance and direction cues in both enclosures and arrays.

Bibliography

Andersen, N. E., Dahmani, L., Konishi, K., & Bohbot, V. D. (2012). Eye tracking, strategies, and sex differences in virtual navigation. *Neurobiology of Learning and Memory*, *97*, 81-89. doi:10.1016/j.nlm.2011.09.007

Astur, R. S., Ortiz, M. L., & Sutherland, R. J. (1998). A characterization of performance by men and women in a virtual Morris water task: A large and reliable sex difference. *Behavioural Brain Research, 93,* 185–190. doi:10.1016/S0166-4328(98)00019-9

Bodily, K. D., Eastman, C. K., & Sturz, B. R. (2011). Neither by global nor local cues alone: evidence for a unified orientation process. *Animal Cognition, 14*, 665-674. doi:10.1007/s10071-011-0401-x

Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? squaring theory and evidence. *Psychonomic Bulletin & Review*, *12*, 1-23. doi:10.3758/BF03196346

Kelly, D., & Bischof, W. F. (2005). Reorienting in images of a three-dimensional environment. *Journal of Experimental Psychology Human Perception and Performance*, *31*, 1391-403. doi:10.1037/0096-1523.31.6.1391

Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2010). Re-orienting in space: Do animals use global or local geometry strategies? Biology Letters, 7, 372-375. doi:10.1098/rsbl.2010.1024

Lee, S. A., Sovrano, V. A, & Spelke, E. S. (2012). Navigation as a source of geometric knowledge: young children’s use of length, angle, distance, and direction in a reorientation task. *Cognition*, *123*, 144-61. doi:10.1016/j.cognition.2011.12.015

MacFadden, A., Elias, L., & Saucier, D. (2003). Males and females scan maps similarly, but give directions differently. *Brain and Cognition, 53,* 297–300. doi:10.1016/S0278-2626(03)00130-1

Saucier, D., Bowman, M., & Elias, L. (2003). Sex differences in the effect of articulatory or spatial dual-task interference during navigation. *Brain and Cognition, 53,* 346–350. doi:10.1016/S0278-2626(03)00140-4

Sturz, B. R., & Bodily, K. D. (2011). Is surface-based orientation influenced by a proportional relationship of shape parameters? *Psychonomic Bulletin & Review*, *18*, 848-54. doi:10.3758/s13423-011-0111-z

Sturz, B. R., Gurley, T., & Bodily, K. D. (2011). Orientation in trapezoid-shaped enclosures: implications for theoretical accounts of geometry learning. *Journal of Experimental Psychology Animal Behavior Processes, 37*, 246-53. doi:10.1037/a0021215

Reichert, J. F. & Kelly, D. M. (2011). Use of local and global geometry from object arrays by adult humans. *Behavioural Processes, 86*, 196-205. doi:10.1016/j.beproc.2010.11.008

Reichert, J. F. & Kelly, D. M. (2012). Discrimination of geometric angles by adult humans. *Animal Cognition, 15,* 271-284. doi: 10.1007/s10071-011-0452-z

Tommasi, L. & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick *(Gallus gallus). Animal Cognition, 7,* 53-59. doi:10.1007/s10071-003-0182-y