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A Comparative Examination of the Use of Metric Information in Spatial Orientation and Navigation

by

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Abstract

In daily life, both animals and humans are often faced with the task of returning to previously visited locations. In many cases, an organism must be able to (1) establish a directional frame of reference and (2) determine location based on surrounding cues in order to solve this problem. Moreover, successful navigation is generally thought to rely on how an organism learns and uses the metric relationships between various locations in its environment. This thesis examines various factors that affect the way animals encode and use metric information in their environment, both to orient and to navigate. A transformation approach is used to determine what aspects of metric information are learned and/or preferred. Additionally, this thesis follows a comparative approach in order to examine similarities and differences among species.

In chapter 2, I show that two closely related species of chickadees differently use geometric and featural information when establishing a directional frame of reference. I suggest that ecological factors, but not rearing condition, affect the way that chickadees preferentially use metric or featural information to orient. In chapter 3, I used a similar paradigm to show that a pre-existing directional frame of reference can interact with rats' use of metric cues to navigate. More specifically, chapter 3 shows that experience gained through training procedures affects the way that rats use metric information in a navigation task. Chapter 4 expands upon this idea, and shows that pigeons encode directional metric differently based on their past experience. Finally, in chapter 5, I

examined the flexibility of use of metrics by comparing how search strategies of human adults and children can change based on a goal's proximity to an edge.

To summarize, this thesis shows that use of metric information is malleable and situation-specific and can be affected by a variety of factors including ecology, past experience and boundary information.

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Chapter 1

General Introduction

A fundamental problem faced by most organisms is that of returning to previously visited locations. Animals must be able to learn and remember the location of their homes, food and water sources and/or mating sites. Humans, as well, must be able to remember places such as their houses, offices, grocery stores or favourite restaurants. This ability to learn and remember places requires the ability to accurately determine direction and pinpoint specific locations based on external cues. In other words, successful navigation requires that an organism be able to (1) determine heading, or develop a stable directional frame of reference, and (2) determine location based on surrounding cues, also called piloting (Gallistel, 1990).

Research has revealed a variety of ways that animals are able to determine either heading or location. For example, an organism may use cues such as celestial cues (such as the sun or stars), large scale landmarks, and the geometric properties of an environment. The ability to encode the global geometric shape of an enclosed environment seems to be a ubiquitous and predominant means of orienting in humans and other animals and, as such, has received a great deal of empirical attention over the past two decades (see Cheng & Newcombe, 2005 for a review).

However, once an animal has determined it's heading, it often still faces the problem of actually locating a particular goal. A common, and often studied, mechanism for determining location is the use of landmarks and surfaces (see Spetch & Kelly, 2006 for a review). An organism may use a landmark as a beacon if it is located right at or very near to the goal location. In this case, a single landmark could be used both to orient and to guide the animal to the goal. Alternatively, if the goal is not located right at or near a landmark, organisms may specifically pinpoint a goal location through a process called piloting (Cheng & Spetch, 1998). Piloting requires that an animal learn about the distance and direction from one or more landmarks to the location of the goal.

Although research has identified a number of mechanisms by which animals are able to orient and navigate, how organisms form a spatial representation and, more specifically, what type of information is included in that spatial representation is controversial. The idea that animals form complex representations of their environments was first proposed by Tolman (1948). He suggested that animals and people form a *cognitive map* – a mental representation of space which allows organisms to flexibly and efficiently navigate their environment. Although there is a considerable amount of evidence supporting the theory of cognitive maps (e.g., O'Keefe & Nadel, 1978; Gallistel, 1990), theories regarding the structure of cognitive maps differ considerably (e.g., Jacobs & Schenk, 2003; Poucet, 1993; Wang & Spelke, 2002).

Cognitive Maps

Tolman's (1948) theory of the cognitive map was based upon experiments with rats, and centered on the finding that rats were able to develop novel shortcuts between two points. The theory was further developed and extended by O'Keefe and Nadel (1978) who suggested that animals can form two types of spatial representations: routes or maps. Route learning was considered to be a simple stimulus-response relationship where an animal could navigate by remembering a specific sequence of movements or landmarks. A route, then, requires only simple knowledge of the environment and can result in quick spatial processing. However, routes are also inflexible; the sequence of landmarks must be encountered in order for effective navigation. Removal or movement of the landmark can disrupt navigation. Map learning, in contrast, allows for the representation of relationships between places and objects. Maps are flexible and allow for creation of novel short cuts, but require higher informational content and more time for mental calculations or processing.

O'Keefe and Nadel (1978) further suggested that cognitive maps are allocentric representations of space formed in the hippocampus. Allocentric representation, or what they termed absolute space, refers to a representation of a spatial layout independent of the organism's location within that space. In their words, allocentric representations are considered to be:

> "a framework or container within which material objects can be located but which is conceived as existing independently of particular objects or objects in general. Objects are located relative to the places of the framework and only indirectly, via this framework, to other objects. Movement of a body (including the observer) changes its position within the framework but does not alter the framework or the relationship of other objects to the framework." (p. 7)

That is, places or objects are encoded as a set of coordinates on the overall framework. An organism's movement will change their own location, but the coordinates of the other locations are constant with reference to the framework. In contrast, an egocentric representation (or relative space, as termed by O’Keefe and Nadel) involves learning the location of an object in relation to the organism’s own position. Thus, moving through an environment will change an objects' location within an egocentric representation.

However, the structure and development of cognitive maps remains controversial. Bennett (1996), for example, suggests that no experiments have effectively shown the existence of cognitive maps as defined by Tolman (1948) and O’Keefe and Nadel (1978). Specifically, he suggests that instances of novel shortcutting can be explained by simpler mechanisms, such as path integration or recognition of familiar landmarks. Similarly, Wang and Spelke (2002) have argued that the postulation of enduring allocentric maps is unnecessary to explain navigation in humans and animals. They suggest that animals form a frame of reference based on the shape of the environment, but that navigation occurs by constantly updating egocentric representations. Specifically, they suggest that both animals and humans “navigate by forming, maintaining and dynamically updating a representation of their momentary relationship to significant environmental locations” (p. 380).

Supporting the view that cognitive maps do involve an allocentric representation of space, Poucet (1993) proposed a theoretical framework of how a cognitive map is developed. He suggested that two types of information can be acquired about spatial layouts: topologic information and metric information. Topological information refers to the spatial relationships between objects, such as ‘in front’ or ‘between’. This type of information can be gained from egocentric representations. In contrast to Wang and Spelke’s (2002) strict ‘updating’ system, Poucet suggests that movement and exploration of the environment allows the animal to integrate multiple view points and create *place representations* that are independent of specific view-points. Furthermore, as the animal gains experience in the environment, they acquire metric information, that is, specific distance and angular information. A collection of these place representations is referred to as a local chart, which integrates both the loose topological relationships between objects in the environment and the specific metric information. Thus, the local chart represents an allocentric representation of a specific area.

Naturally, as an animal moves through its environment, some areas will be better explored than others. For example, a consistently viable food source will be visited more frequently than inconsistent source. Similarly, an animal may avoid areas that are prone to predation. Thus, Poucet (1993) suggests that animals only form well developed maps through repeated experience with a particular environment. Specifically, he proposed that animals may initially form *location-dependent representations* that serve as reference points for determining the distance and direction to other locations, similar to O’Keefe and Nadel’s (1978) idea of route learning. With experience, animals acquire more vectorial information (i.e., distance and direction to a greater number of locations) that can be applied to the “map” (Poucet, 1993). In order to form a more global, allocentric representation, animals must be develop a directional frame of reference that allows them to link the locations together within a single reference system. As discussed earlier, a directional frame of reference can be based on a variety of cues, such as celestial cues or large-scale landmarks.

More recently, Jacobs and Schenk (2003) proposed that cognitive maps are actually an integration of two distinct maps containing directional and place information. In particular, rather than having a directional frame of reference as the ‘last step’ in map formation, they suggest that two maps, a *bearing map* and a *sketch map*, operate in parallel. A cognitive map is developed when the two maps are integrated. The first map, the *bearing map*, is a coordinate system that is developed from self-movement and directional cues. In particular, directional cues can be used to establish a 1-D vector or gradient. The intersection of two of these directional vectors, then, establishes a coordinate system. Self-motion along these gradients allows an animal to establish a frame of reference based on the intensity of the given cues. Second, the *sketch map* is a topographical map of local landmarks, encoded relative to each other. This map represents an allocentric representation of the positional cues within an environment, including distance and directional information between landmarks.

A notable aspect of Jacobs and Schenk’s (2003) parallel map theory is that it provides specific behavioural predictions about the impairment of either or both map types. Specifically, animals should be able to navigate with a single map, but should make systematic errors when a map is impaired. For example, if the sketch map is intact but the bearing map is impaired, an animal should show significant initial impairment since they will be unable to direct themselves to the correct location. With continued training, however, the animal should be able to recognize the correct landmarks when they are near to the goal location, and then make small “local loops” as they use the intact sketch map to locate the particular goal. On the other hand, if the bearing map is intact and sketch map impaired, an animal would be able to determine the direction to the goal, but not be able to use landmarks to pinpoint its specific location. In this case, an animal would travel along transects moving in the direction of the goal. Impairment of both maps, however, would result in a total loss of spatial ability.

Transformational Approach

Although these theories propose different frameworks for the structure and development of a cognitive map, one aspect that is common to all theories is the use of metric information to encode distances and directions from landmarks. A fundamental question, then, is how is this metric information learned and remembered? In other words, what aspects of distance and directional information are entered into the map? In order to better understand what animals learn about distance and direction, many studies have employed a transformational approach pioneered by Tinbergen (1972). To study digger wasps’ use of landmarks, Tinbergen placed a circle of pinecones around wasps’ nests. After the wasps left their nest, he transformed the spatial arrangement by moving the circle of pinecones to a nearby location. The returning wasps searched for their nest in the center of the pinecones, indicating that the pinecones served as important landmarks to guide the wasps’ search.

Subsequent research using this transformational approach has uncovered a great deal of information regarding organisms’ use of metric information to orient and navigate (Cheng & Spetch, 1998). In a typical paradigm, animals are trained to some criterion to search for a goal that is hidden at a constant distance and direction from a set of cues, such as a landmark array or environmental geometry. During pivotal test trials, the cue set is transformed to assess what the animals have learned. For example, to assess what is learned about distance to the goal, the set of cues can be shifted or expanded. Similarly, to study what the animals have learned about the directional information, part of the cue set might be rotated.

Use of Metric Information to Orient

The study of animals' use of metric information to orient began with Cheng (1986), who studied rats' ability to use the geometry of a rectangular environment to orient and find a hidden goal. In this case, geometry alone provides an ambiguous situation; specifically, the corner diagonally opposite to the correct corner is geometrically identical to the correct corner. Thus, non-metric featural information, such as a differently coloured wall, is needed to disambiguate the situation. However, Cheng (1986) found that rats were reluctant to use the feature to reorient, and frequently made rotational errors. That is, when searching for hidden food, rats oriented according to the environmental geometry, making rotational error even though featural information made the environment unambiguous. Cheng concluded that rats orient according to the geometric shape of the environment and that featural information is later "pasted" onto a metric frame of reference. Since Cheng's initial finding that rats predominantly orient based on metric information, use of geometry for orientation has also been found with a variety of other species, including human children and adults (Hermer & Spelke, 1994, 1996), rhesus monkeys (Gouteux, Thinus-Blanc & Vauclair, 2001), fishes (Sovrano, Bisazza & Vallortigara, 2002, 2003; Vargas, López, Salas & Thinus-Blanc, 2004) and ants (Wystrach & Beugnon, 2009).

The transformational approach has helped to reveal the predominance of geometry use. In particular, the use of transformation tests has shown that geometry use is remarkably resistant to cue competition. Cue competition, such as overshadowing and blocking, is often found in the spatial domain (e.g., Biegler & Morris, 1999; Diez-Chamizo, Sterio & Mackintosh, 1985; Roberts & Pearce 1999; Rodrigo, Chamizo, McLaren & Mackintosh, 1997; Spetch, 1995). For example, landmarks that are nearer to the goal can block learning of other, more distal landmarks (Spetch, 1995). In contrast, in most cases, featural information neither blocks nor overshadows learning of geometric shape. For example, placing a beacon at the goal location does not prevent animals from learning about the shape of the environment (Pearce, Ward-Robinson, Good, Fussel & Aydin, 2001; Hayward, McGregor, Good & Pearce, 2003). Similarly, several studies have shown that featural information does not overshadow geometric information. In most cases, animals trained with redundant featural and geometric cues do not learn less about geometry than animals trained with geometric cues alone; when tested in the absence of featural cues, most animals are still able to use the remaining geometric cues to orient (e.g., Kelly, Spetch & Heth, 1998; Sovrano et al., 2003). Only a few cases of cue competition between geometric and featural information have been reported (e.g., Gray, Bloomfield, Ferry, Spetch & Sturdy, 2005; Pearce, Graham, Good, Jones & McGregor, 2006) and this does not seem to be the typical outcome.

Although use of metric information seems to be a robust strategy for orientation, the transformational approach has also revealed some limitations of geometry use, such as the size of the environment or previous experience. Studies have shown that humans and animals are more reliant on geometric information if they are trained in a small environment (see Chiandetti & Vallortigara, 2008 for a review). For example, human adults were trained in either a small or large rectangular environment with a featural cue along one wall (Ratliff & Newcombe, 2008). During transformational tests, the feature was displaced to indicate a geometrically incorrect location. In the small environment, adults were more likely to rely upon the geometric properties of the room whereas adults in the large environment relied more on the featural cue to direct their search. Additionally, when these participants were displaced from the large to the small environment, they still preferred to rely on the featural cue.

Similarly, Sovrano, Bisazza and Vallortigara (2005) found that fish that were trained in a small environment and tested in a large environment made more errors based on geometric information. That is, fish in this group made the majority of their errors at a geometrically correct, but featurally incorrect, corner of the rectangular environment. Conversely, fish trained in a large environment and tested in a small environment made more errors based on featural information, making the majority of their errors at a featurally correct, but geometrically incorrect, corner.

Using a slightly different paradigm, Chiandetti, Regolin, Sovrano and Vallortigara (2007) found a similar pattern of results with domestic chicks. Again, chicks were trained to find a goal corner of either a small or large rectangular environment with featural cues placed in each corner. Following training, two separate transformational tests were performed: a geometry test in which all the featural cues were removed, and a feature test where the chicks were tested in a square environment. In the square enclosure, metric information is completely ambiguous, so the chicks would need to rely on the featural cues to search correctly. Chiandetti et al. found that chicks trained in the small environment showed better retention of the geometric information and chicks trained in the large environment showed better retention of the featural cues. That is, on the geometry tests, chicks in the small environment searched more at the geometrically correct corners than the chicks in the large environment. On the featural tests, chicks in the large environment searched more at the featually correct corner than chicks in the small environment. Thus, converging evidence seems to suggest that environmental size is a factor that can limit the use of metric information to orient, and that metric information is used more predominantly in small environments.

A second factor which has been shown to limit the use of metric information to orient is past experience (Kelly et al., 1998). Two groups of pigeons were trained to orient in a rectangular environment; however, one group was trained with both geometric and featural information available throughout the study and one group received initial training with geometric cues only before featural information was introduced. On test trials, the featural cues were moved and placed in confict with geometric cues. Pigeons that had received the initial experience with geometry only made more searches at geometrically correct corners than the pigeons that had been trained with both geometric and featural information available throughout.

In addition to revealing both the high level of control by geometry and the limitations of the use of metric information to orient, the transformational approach has also been used to provide evidence regarding how animals represent geometric information. For example, Kelly and Spetch (2001) used the transformational approach to determine whether pigeons use absolute or relative metrics of a rectangular environment to orient. Encoding of absolute metrics would involve learning the specific lengths of the walls, such as the goal is to the left of the 200cm wall. In contrast, learning relative metrics involves a more abstract representation, such as the goal has a short wall to the right and longer wall to the left. Importantly, both absolute and relative representations would result in the animal concentrating their searches to geometrically correct corners. Kelly and Spetch trained pigeons to search for food in one corner of a rectangular environment; during test trials, the length of each wall was reduced to two thirds of the training size. In this test, use of absolute metrics would lead to an unsolvable situation. Specifically, none of the walls would match the learned metrics, so use of absolute metrics would result in chance responding. However, the pigeons continued to search in the geometrically correct corners, indicating use of relative metrics. That is, the pigeons responded most to the corners that preserved the relative metrics of the training enclosure.

Tommasi and Polli (2004) also examined how geometric information is represented by studying how domestic chicks orient in a parallelogram shaped enclosure. After being trained to search for food in one corner of a parallelogram, chicks were tested in three novel enclosures: a rectangular enclosure, rhombus-shaped enclosure or a mirror parallelogram-shaped enclosure. The rectangular enclosure preserved the wall lengths of the training enclosure, and thus tested whether the chicks had encoded the relative lengths of the walls. The rhombus-shaped enclosure preserved the angular information from the corners, but not the relative wall lengths. In both of these tests, chicks searched in the appropriate corners, indicating that they had learned both the relative lengths of the walls and the angular information from the corners. In the final test, wall length ratios and the corner angles were placed in conflict. In this case, chicks that were trained with the goal in an acute-angled corner were more likely to rely on the angular information whereas chicks trained with the goal in an obtuse-angled corner relied on the relative wall lengths. This pattern of results indicates that geometric information may be hierarchically organized and that corner saliency played an important role in determining the nature of the hierarchy.

In summary, the use of metric information is a predominant means of orientation and is an ability found in a wide variety of species (Cheng & Newcombe, 2005). Moreover, studies employing the transformational approach have revealed it is a particularly robust ability and often resistant to cue competition (Kelly et al., 1998; Sovrano et al., 2003). However, geometric representations are affected by a variety of factors, including the size of the environment and past experience, and may be hierarchically organized based on the saliency of the geometric cue.

Use of Metric Information to Navigate

In addition to elucidating the factors of metric information used for orientation, the transformational approach has also been instrumental in determining what aspects of metric information animals use to navigate. In particular, piloting on the basis of nearby landmarks requires that an animal learn both the distance and direction from landmarks to a goal location. When searching according to a single landmark or beacon, only a single distance and direction are needed to locate the target. However, what animals learn about distance and direction when multiple landmarks are available is less clear. Cheng (1988, 1989) proposed the vector-sum model, suggesting that animals (specifically pigeons) learn specific vectors from each landmark to the goal, although the vectors may be weighted according to various factors such as landmark saliency, preference or distance to the goal. The model predicts that when a landmark is shifted, the pigeon will average the weighted vectors and adjust their search pattern according to the averaged vectors.

Although it was initially thought that the vectors were averaged as whole vectors (i.e., including both distance and directional information), Cheng (1994) subsequently discovered that distance and direction seem to be processed independently. Cheng trained pigeons to search for food at a specific distance and direction from a landmark with a distinctive stripe on one side. During training, both the stripe and room cues redundantly indicated the direction of the goal from the landmark. On test trials, the landmark was rotated, placing the directional cues from the room and the landmark stripe in conflict. Pigeons averaged the direction of the competing cues, but maintain a constant distance from the landmark. If the pigeons had been averaging whole vectors to guide their search, the distance from the landmark would have varied according to the specific vectors used and the weighting given to each vector. That the distance remained constant indicates that the pigeons were only averaging the directional cues, not distance.

One approach to studying how animals use metric information to navigate has been to examine whether animals encode the absolute or relational metrics from environmental cues to a goal. In a typical paradigm, subjects are trained to find the center of an array of landmarks and tested in transformed arrays, such as expanded or rotated arrays. In this type of landmark paradigm, however, only adult humans have been found to consistently use relational distance (Spetch, Cheng & MacDonald,1996; Spetch et al., 1997). Other species, such as pigeons (Spetch et al. 1996, 1997, but see Sturz & Katz, 2009 for an exception), squirrel monkeys (Sutton, Olthof & Roberts, 2000), marmoset monkeys and human children (MacDonald, Spetch, Kelly & Cheng, 2004) tend to rely predominantly on absolute distances. However, the use of absolute distances with landmark arrays appears to reflect a preferred strategy rather than an inability to encode relational distances. Specifically, when trained with landmark arrays that maintain shape but vary in absolute metrics, Clark's nutcrackers (Kamil & Jones, 1997, 2000) and pigeons (Jones, Antoniadis, Shettleworth, & Kamil, 2002; Spetch, Rust, Kamil, & Jones, 2003) showed learning of relational distance.

This preference for absolute distance seems to be in contrast with Kelly and Spetch's (2001) finding that pigeons used relative metrics to orient in a rectangular environment; however, evidence suggests that animals may be more likely to prefer to search according to relational metrics when disoriented. In a paradigm similar to that of Kelly and Spetch (2001), chicks (Tommasi, Vallortigara, & Zanforlin, 1997; Tommasi & Vallortigara, 2000) and pigeons (Gray, Spetch, Kelly & Nguyen, 2004) were trained to find a food reward in the center of a square arena then tested in different sized enclosures. When tested in expanded enclosures, both species showed some evidence of dividing their searches between areas corresponding to the absolute learned distance from the walls and an area in the center. Thus, both pigeons and chicks seemed to encode both the absolute and relational metrics of the enclosure. That is, they seemed to learn both an absolute strategy that entails searching for the goal at a fixed learned distance and/or direction from a wall and a relational strategy in which the goal location is defined in terms of the relationship between the walls and the goal (in this case, that the goal is in the center). Similarly, Sturz and Katz (2009) found that pigeons trained and tested in the presence of conspicuous orientation cues searched according to an absolute distance. Conversely, when disoriented, the pigeons searched in the center of the landmarks, that is, according to relational metrics.

Although oriented animals seem to prefer to use absolute distance, research on use of directional metrics is somewhat less clear. The use of rotational tests is a common way to determine the way in which directional metrics are encoded. Specifically, animals are trained to find a goal within an array of landmarks. On the rotational tests, the array is transformed by rotating the landmark array. If an animal encoded direction according to absolute metrics, or absolute bearings, their search pattern would be based on global directional cues, such as cues provided by the test room rather than the landmark array. Relational metrics, on the other hand, involves learning the location of the goal relative to an array of environmental cues, such as the goal is ‘in the middle’ of the array.

Various studies, however, have found different uses of directional metrics which may depend on factors such as past experience or species (e.g., Sturz & Katz, 2009; Kamil & Jones, 2000). For example, through the use of rotational tests, Kamil and Jones (2000) found that Clark’s nutcrackers used absolute bearings when trained to search in the center of a two landmark array. In contrast, pigeons used relational metrics (both distance and direction) when trained with a similar two landmark array (Sturz & Katz, 2009). However, in addition to the species difference between the studies, the pigeons in Sturz and Katz’s study had additional experience with other landmark arrays before being tested for use of relational metrics. Additionally, the number of landmarks in an array may also affect how animals encode and use directional metrics. In a three landmark array, for example, gerbils appeared to encode direction according to both absolute and relational metrics (Collett, Cartwright & Smith, 1986). In contrast, pigeons relied only upon relational metrics when trained and tested in a four landmark array (Gray & Spetch, 2006).

In summary, while navigating, distance and direction provide separate sources of metric information. While most oriented animals tend to prefer to use absolute metric distances, adult humans provide a clear exception and usually show exclusive use of relational metrics. Disoriented animals, in contrast, seem more likely to use relational metrics, or a combination of both absolute and relational metric distances. Directional metrics have yielded mixed results, and preferences may depend on factors such as species, past experience or the type of array used.

Summary

Overall, the use of metric information to navigate provides a unique platform for comparative studies. Specifically, although theories of cognitive mapping are controversial and can differ considerably from each other, all theories require that organisms learn and use metric information from the environment to navigate. Moreover, it would be difficult to explain the patterns of data reviewed here without assuming that animals are able to encode metric information (Cheng & Spetch, 1998).

The use of metric information, specifically geometric shape, has been revealed to be a dominant means of orientation in a widespread variety of species, include humans (Cheng & Newcombe, 2005). Additionally, factors that limit use of geometry to orient affect different species in very similar ways. As reviewed earlier, chicks, fish and humans all seem to rely more heavily on geometric information when they are in a small environment. These overriding commonalities seem to suggest that use of metric information is a basic and fundamental process, and that metric information may be encoded in a similar way across species. However, despite these commonalities, use of metric information during navigation has revealed a number of differences. Most notably, although many animals are able to use relational metrics, only human adults have shown a marked preference for such a strategy.

A comparative approach to the study of spatial cognition, and specifically the use of metric information, is essential to understanding the development of navigation in animals and humans. Studying the commonalities and differences in how animals learn and remember spatial information can lead to a better understanding of how spatial abilities have evolved and adapted. The use of metric information in particular seems to be a fundamental building block which provides a basis for more complex spatial abilities, such as the formation of cognitive maps.

Within this framework, this thesis examines a number of issues regarding how animals encode and use metric information to orient and navigate. Chapter 2 examines how two closely related species of chickadees differently use geometric and featural information to orient, and focuses on how ecological factors may have influenced their navigational preferences. Chapter 3 examines how a pre-existing directional frame of reference interacts with the use of metric cues to navigate. In particular, although past research has shown that geometric information is a prominent means of orientation in rats, how do rats use the geometric properties of an environment to navigate when it is not necessary to establish heading? Chapter 3 also investigates how training procedures can affect use of metric information. Chapter 4 further investigates how past experience affects the learning and use of metric information, and focuses on how pigeons learn directional metrics. Chapter 5 examines how proximity to a boundary affects use of metric information, and in particular, whether human adults and children are more likely to use absolute metrics if a goal is near an edge. In all, this thesis contributes greatly to my understanding of how different species encode and use metric information to pinpoint target locations, and reveals a variety of factors that can affect navigational strategies.

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Chapter 2

Comparing black-capped (*Poecile atricapillus*) and mountain chickadees' (*Poecile gambeli*): Use of geometric and featural information in a spatial orientation task

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Introduction

In most situations, successful navigation first requires that an organism be able to determine its heading, or develop a directional frame of reference (Gallistel, 1990). Because this ability to get oriented is such an integral part of spatial ability and navigation, it has been the focus of a significant amount of research in recent years. Although there are several ways to determine heading (for example, the use of large scale landmarks, beacons, path integration and celestial compass cues), animals' ability to use the *geometry* of an environment to orient has garnered much attention over the last 20 years. Specifically, researchers have investigated the ability of many animals to determine heading by using the geometric shape formed by the walls of an enclosure, or by landmarks in an arena (see Cheng and Newcombe, 2005 for a review).

The study of animals' use of geometric properties to orient began with Cheng (1986), who found that rats predominantly relied on the rectangular shape of an enclosure to find food, even at the expense of featural information. Use of geometry for orientation has since been found with a variety of species including human children and adults (Hermer and Spelke, 1994, 1996), rhesus monkeys (Gouteux et al., 2001), fishes (Sovrano et al., 2002, 2003; Vargas et al., 2004) and ants (Wystrach and Beugnon, 2009). However, a variety of factors have been shown to affect the degree to which an organism will rely on geometric shape to orient. These factors include broad level variables such as species and more specific variables such as the size of the environment (see Chiandetti and Vallortigara, 2008b for a review) and training procedures (Lourenco and

Huttenlocher, 2006, 2007). For example, although avian species have also been found to use geometric information to orient, they seem to rely more heavily upon featural information (pigeons: Kelly et al., 1998, chicks: Vallortigara et al., 1990) which stands in contrast to many mammalian species such as rats and humans.

Although avian species tend to be more influenced by features, past experience has also been shown to affect the degree of preference (Kelly et al., 1998). Kelly et al. trained two groups of pigeons in a rectangular environment: one group initially received training with only geometric information available before featural information was introduced, and one group was trained with both geometric and featural information available throughout. During tests where geometric and featural information was placed in conflict, Kelly et al. (1998) found that pigeons that were initially trained with geometry only were more likely to be influenced by geometric information than pigeons that always had both geometric and featural information available during training.

Another factor that has been suggested to affect the use of geometry to reorient is the type of disorientation procedure that is used immediately prior to training or testing trials (Lourenco and Huttenlocher, 2006, 2007). Two different types of disorientation procedures are typically used in studies of geometry: one in which the viewer (i.e.,, participant) is rotated, and one in which the environment itself is rotated (out of view of the participant). Although both procedures prevent tracking the target location, Lourenco and Huttenlocher (2006) provide evidence that the two procedures are not equivalent. In their study, children were asked to find a toy hidden in one corner of a testing environment in the shape of an isosceles triangle. After watching the experimenter hide the toy, the child was disoriented through either a viewer-movement procedure or a space-movement procedure. The results indicated that when the toy was hidden in a non-unique corner, only children in the viewer-movement disorientation condition were able to use geometric shape to locate the toy. Children in the space-movement disorientation procedure responded at chance levels to the non-unique corners.

The size of the environment can also affect the use of geometric and featural information (Learmonth et al., 2002). Learmonth et al. tested children in both large and small rectangular rooms and found that, in larger spaces, children were more likely to make use of featural information than when tested in smaller spaces. Similar results where size of testing environment influence search strategies have been found with chicks (Vallortigara et al., 2005, Chiandetti et al., 2007) and fish (Sovrano et al., 2005, 2007).

However, regardless of preferences and training procedures, the majority of studies (with a few exceptions) have shown that subjects spontaneously encode the geometric information available (Cheng and Newcombe, 2005). That is, when trained with redundant featural and geometric information, subjects are still able to orient when only geometric information is available. One exception to this trend was a study by Gray et al. (2005) using wild-caught mountain chickadees (*Poecile gambeli*) as subjects. Gray et al. trained three groups of mountain chickadees to find a mealworm in one corner of a rectangular environment, using a space-movement disorientation procedure. One group was trained with geometric information only (geometry-only condition), one group was trained with the correct corner opposite to a differently coloured wall (far-feature condition) and one group was trained with the correct corner adjacent to a differently coloured wall (near-feature condition). Birds in the geometry-only and far-feature conditions were able to use geometric information to orient in the absence of featural information. The birds in the near-feature condition, however, responded at chance levels when tested without featural information, indicating that the feature had overshadowed encoding of geometric information. Gray et al. suggested that a lack of extensive early experience with right-angled environments could have affected the chickadees' ability or willingness to use geometric information.

Brown et al. (2007) found that rearing conditions *did* affect the degree to which fish (convict cichlids, *Archocentrus nigrofasciatus*) preferred featural information. In their study, one group of fish was raised in a circular environment and another group was raised in a rectangular environment. During tests in which geometric and featural information were placed in conflict, fish reared in the circular environment were less likely to use geometric information than fish reared in a rectangular environment. However, fish in both rearing conditions were able to use geometric information in the absence of featural information. Similarly, Chiandetti and Vallortigara (2008a) found that there were no differences in use of geometry between chicks raised in circular, rectangular or c-shaped environments.

The current study was conducted to extend and elaborate on Gray et al's (2005) findings. I trained and tested both hand-reared and wild-caught black-capped chickadees (*Poecile atricapillus*), a closely related sister species of mountain chickadees, in order to determine if early experience with salient geometric environments affects use of geometry in chickadees. Hand-reared and wild-caught black-capped chickadees were trained in similar conditions to that of Gray et al. (geometry-only, far-feature and near-feature). Additionally, because there were some procedural changes in the current study, a group of wild-caught mountain chickadees was also trained in the near-feature condition to provide a direct species comparison.

One major procedural difference between the current study and that of Gray et al. is the way in which birds in the pivotal near-feature condition were tested with only geometric information. For birds in the near-feature condition, the correct corner always contains both one white wall and one featural wall (in this case, a blue wall). For example, a bird may be trained to locate the corner with a white wall to the left and blue wall to the right. The incorrect corners in this example would be the corner with a blue wall to the left and white wall to the right, and the two corners that contain both white walls. When tested with geometric information only, if the feature wall is simply removed, all four corners would thus look featurally incorrect (i.e., all would consist of both white walls). This contrasts with the far-feature condition where the correct corner always consists of two white walls, so removal of the feature makes all corners look featurally correct. In the current study, we accounted for this difference by placing short blue walls on one side of each corner for the near-feature condition, making each corner appear featurally correct.

Methods

Subjects

Subjects were 22 black-capped chickadees (17 male, 5 female) and 4 mountain chickadees (3 male, 1 female). None of the birds had any previous experience with experimental spatial tasks or with the apparatus. Chickadees were captured between June 2003 and March 2006 from Edmonton, Alberta, Canada and areas around Kananaskis, Alberta, Canada. Eleven of the black-capped chickadees and all four of the mountain chickadees were mature at time of capture (wild-caught) whereas 11 black-capped chickadees were captured as hatchlings (5-14 days, hand-reared). Although not directly trained to cache, all birds (hatchlings included) frequently cached sunflower seeds and mealworms within their homecages. All birds were mature (minimum 10 months) at the beginning of training. The average age of the hand-reared birds at beginning of training was 16 months (STD = 5). Sex identification was conducted by DNA analysis (Griffiths and Double, 1998). Birds were housed at the University of Alberta (Edmonton, Alberta) in individual Jupiter Parakeet cages (0.3m wide × 0.4m high × 0.4m deep; Rolf C. Hagen, Inc., Montreal Canada) which allowed visual and auditory communication but not physical contact between birds.

When housed in the colony room birds had food (Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, Missouri), water (vitamin supplemented on alternate days; Hagen, Rolf C. Hagen, Inc, Montreal, Canada), grit, and cuttlebone ad libitum. Birds also received 3-5 sunflower seeds daily, plus one mealworm three times a week and a mixture of eggs and greens twice a week. Birds were maintained on a light-dark cycle that mimicked the natural cycle for Edmonton, Alberta. Temperature was maintained at about 20°C.

Apparatus

The experimental apparatus was a uniformly white Plexiglas rectangular chamber, 50 × 100 × 60 cm high. Centered at the bottom of each wall was a 13 × 13 cm guillotine style door through which the birds entered and exited the chamber. The top of the chamber was covered with a wire mesh screen and the floor of the arena was covered with approximately 1 cm depth of aspen chips. Small 15W lights were affixed to the top of each corner of the chamber. White curtains surrounded the apparatus to block the use of visual room cues for directionality. On each wall, four white Velcro pieces were attached in the corners so that a blue plastic wall could be attached to any of the walls. The apparatus was placed on a wheeled wooden platform so that the entire apparatus could be easily rotated between trials. The birds were observed and behaviour was recorded by a video camera mounted above the apparatus.

Identical white perches were placed 2–3 cm from each corner. The perches were 15 cm tall cylinders (diameter: 5 cm) with a second smaller cylinder (diameter: 1.3 cm) affixed horizontally 7.5 cm from the bottom. Above the small cylinder was a hole (diameter: 1.3 cm), which could be covered with a Velcro piece to hide a reward.

The birds were transported to and from the experimental room in a either a black semi-translucent case covered with a black cloth or an opaque black case. Both cases were 13 cm wide, 19 cm long and 13 cm tall with a guillotine style door at the front.

Procedure

All birds were initially trained in their home cages to pull at a piece of Velcro to retrieve a worm from the perch. Once a bird consistently obtained the worm within 5 minutes, it was habituated to handling and to being placed in the carrying case; the bird was removed from its home cage and placed in the carrying container while the perch was baited. The bird was then released back into its home cage and allowed to retrieve the worm. Once the bird quickly and consistently obtained the worm, it moved onto training in the experimental chamber.

The chickadees were trained in one of three conditions: geometry, near-feature or far-feature. Birds in the geometry group (3 wild-caught black-capped chickadees and 3 hand-reared black-capped chickadees) were trained to use the geometry of the chamber to find a correct corner (i.e.,, trained without the blue wall). In the far-feature condition (4 wild-caught black-capped chickadees and 4 hand-reared black-capped chickadees), birds were trained with one blue wall that was not adjacent to the correct corner. Finally, in the near-feature condition (4 wild-caught black-capped chickadees, 4 hand-reared black-capped chickadees and 4 mountain chickadees), birds were trained with one blue wall adjacent to the correct corner. The assignment of correct corners and location of the blue wall was counterbalanced across birds. For each bird, the correct corner varied randomly on a trial by trial basis between two geometrically equivalent corners, however the apparatus was always set up such that the relationship between the correct corner and the feature (blue wall) remained the same. All birds received five trials per day for five days per week.

At the beginning of each training session, the bird was removed from its home cage, placed in the carrying case and taken to the experimental room. The lights inside the chamber were illuminated and the room lights were extinguished. The carrying case was placed flush against a randomly selected door to the chamber and both the guillotine doors to the chamber and carrying case were opened, allowing the bird to enter the apparatus. Once the bird was inside the chamber, the door was closed. The bird was allowed up to 7 min during initial training sessions and 3 min during regular training to obtain and eat the worm. The chamber lights were then extinguished and the entry door was re-opened. A flashlight was placed above the carrying case to illuminate it; if the bird did not enter the case, the experimenter gently moved the bird towards the door. Between trials, the apparatus was rotated by 90° at random so compass information obtained during the first trial would not have helped to solve the task. As well, the aspen chip on the floor was swept, and the perches were swapped between corners. The perch in the correct corner was baited and the blue wall was moved as necessary. The carrying case was moved to another randomly selected door, and the above procedure was repeated. The birds were observed on a video monitor attached to an overhead video camera.

In the initial phase of training, only the correct corner contained a perch. The hole in the perch was half covered so that the bird could easily see and retrieve the worm. Once the bird habituated to the apparatus and retrieved the worm within the allotted time on the first two trials of the sessions, the hole of the perch was gradually covered more until it was completely occluded. When the bird reached a criterion of obtaining the worm within 5 minutes on the first two trials for three days in a row, identical perches were places in the remaining three corners of the chamber.

Four-perch training continued for a minimum of 30 trials and until an accuracy criterion was met. For this criterion, only the first four trials of each session were used so that effects of satiation near the end of a daily session were minimized. For the geometry birds, the accuracy criterion was a first choice to either the correct corner or a geometrically correct corner on three of the first four trials for two consecutive days. For the feature birds, the accuracy criterion was a first choice to the correct corner on three of the first four trials for two consecutive days. In all cases, a choice was counted when the bird's beak touched the Velcro covering the hole of a perch, as determined by video analysis.

During testing sessions, birds received five trials per day, three training trials and two test trials. All test trials were unreinforced to prevent any olfactory cues. The test trials were run on either the first and third trials, or second and fourth trials of the day, randomly selected. All choices during test trials were recorded for three minutes; if the bird did not make a choice during this time, it was given up to two additional minutes to make a choice. The types of tests administered depended on the training condition of the bird.

Birds trained in the geometry condition received four days (eight test trials total) of *Geometry-Only* tests. The apparatus set up for these tests was identical to training trials (i.e., no feature was available) except that reinforcement was not available. Birds trained in the far-feature and near-feature conditions received three test types over 12 days: *Control* tests, *Conflict* tests and *Geometry-Only* tests. Test types were run in blocks of four days (eight trials of each test type) and the order of tests was counter-balanced across birds. During *Control* tests, the apparatus set up was identical to training trials except that no reinforcement was available. During *Conflict* tests, the blue wall was moved over by one wall (i.e.,, if the bird had been trained with the blue wall on one of the long walls, then the wall was now placed on a short wall and vice versa for birds trained with a short blue wall), thereby placing featural information in conflict with geometric information. Finally, during *Geometry-Only* tests, the features were manipulated so that all four corners provided the same featural information as the correct corner. For far-feature birds, since the correct corner during training was always adjacent to two white walls, the blue wall was completely removed for *Geometry-Only* tests. For near-feature birds, however, the correct corner during training was always adjacent to one blue wall and one white wall. Thus, for these birds, plastic blue stripes (18.5 cm wide) were placed on one side of each corner. Specifically, if a bird had been trained such that the correct corner had a blue wall to the left and white wall to the right, blue stripes were placed to the left of each corner, thus all four corners would contain the ‘correct’ featural information.

Data Analysis

I recorded the total number of choices at each corner during test trials. In order to analyze the data, I used replicated G-tests for Goodness of Fit (Sokal and Rohlf, 1995), which is distributed as a chi-square but allows one to pool data from several subjects (pooled G: G_P) as well as examine the performance of individual subjects (individual G values). The Goodness of Fit tests allowed me to compare the number of choices at particular corners to an expected ratio of responding (chance levels in this case). In order to compare across groups of birds, I carried out analyses of variance (ANOVAs).

Results

Geometry Condition

The mean percentages of total choices at each corner for the two groups of black-capped chickadees (wild-caught and hand-reared) in the geometry condition are shown in Figure 2-1. As a group, the wild-caught black-capped chickadees significantly preferred the geometrically correct corners to the incorrect ones ($G_P(1)=97.30$, $p<0.001$). All three birds showed a significant preference for the geometrically correct corners (G-values for each bird: 27.08, 34.32, 39.57). The hand-reared black-capped chickadees also significantly preferred the geometrically correct corners to the incorrect ones ($G_P(1)=154.12$, $p<0.001$). Again, all birds significantly preferred the geometrically correct corners (G-values for each bird: 26.13, 54.24, 92.04).

Far-feature Condition

The mean percentages of total choices at each corner for each group of black-capped chickadees (wild-caught and hand-reared) and each type of test in the far-feature condition are shown in Figure 2-2. On the *Control* tests, both wild-caught black-capped chickadees and hand-reared black-capped chickadees chose the correct corner significantly more than the other three corners ($G_P(1)=277.46$, $p<0.001$; $G_P(1)=168.56$, $p<0.001$ respectively). All birds chose the correct corner significantly more than any other corner. The individual G-values for the wild-caught black-capped chickadees were 96.13, 41.59, 33.27, 110.58, and the G-values for the hand-reared birds were 41.87, 59.33, 15.47, 69.31

During *Geometry-Only* tests, a comparison of choices to the geometrically correct corners and geometrically incorrect corners revealed both groups of birds significantly preferred the geometrically correct corners to the incorrect ones (wild-caught: $G_P(1)=35.64$, $p<0.001$, hand-reared: $G_P(1)=100.09$, $p<0.001$). All of the wild-caught black-capped chickadees chose the geometrically correct corners significantly more than the other corners (G-values for each bird: 22.08, 3.99, 8.32, 16.64). Three of the four birds chose the geometrically correct corners significantly more often than the incorrect corners (G-values: 38.29, 42.10, 27.11) and one bird showed no preference (G-value: 1.36).

Finally, on *Conflict* tests, I compared choices to the geometrically correct corners with choices to the featurally correct corner (expected ratio of 2:1). Overall, the wild-caught black-capped chickadees did not show a significant preference for either the geometrically correct or featurally correct corner ($G_P(1)=0.62$, $p=0.430$). One of the wild-caught birds showed a significant preference for the geometrically correct corners (G-value: 4.37), one bird chose the featurally correct corner significantly more often (G-value: 8.46) and two birds did not show a preference (G values: 0.27, 3.60). Similarly, the hand-reared black-capped chickadees did not show a significant preference for either the geometrically correct or featurally correct corner ($G_P(1)=1.27$, $p=0.259$. Two of the birds showed a significant preference for the geometrically correct corners (G-values: 7.67, 11.44), one bird chose the featurally correct corner significantly more often (G-value: 23.56) and one bird did not show a preference (G-value: 0.22).

Near-feature Condition

The mean percentages of choices at each corner for the three groups of birds (wild-caught black-capped chickadees, hand-reared black-capped chickadees and wild-caught mountain chickadees) and each type of test in the near-feature condition are shown in Figure 2-3. On the *Control* tests, all three groups of chickadees chose the correct corner significantly more than the other three corners (wild-caught black-capped, $G_P(1)=192.33$, $p<0.001$; hand-reared black-capped, $G_P(1)=257.52$, $p<0.001$; wild-caught mountain, $G_P(1)=279.90$, $p<0.001$). All birds in the wild-caught black-capped chickadee group showed a significant preference for the correct corner (G-values for each bird: 54.52, 69.31, 30.50, 44.36). All birds in the hand-reared black-capped chickadee group also chose the correct corner significantly more than any other corner (G-values for each bird: 122.11, 41.59, 41.59, 63.77). Lastly, all of the wild-caught mountain chickadees chose the correct corner significantly more often than any other corner (G-values for each bird: 50.00, 45.31, 159.47, 33.27).

During *Geometry-Only* tests, wild-caught black-capped chickadees chose the geometrically correct corners significantly more often than the incorrect corners ($G_P(1)=45.36$, $p<0.001$). All birds in this group significantly preferred the geometrically correct corners (G-values for each bird: 17.23, 6.20, 15.25, 8.55). The hand-reared black-capped chickadees also chose the geometrically correct corners significantly more than the incorrect corners ($G_P(1)=76.75$, $p<0.001$). Only three of the four birds showed a significant preference for the geometrically correct corners (G-values for each bird: 43.33, 13.86, 25.95, 1.16). The wild-caught mountain chickadees showed a significant overall preference for the geometrically correct corners compared to the incorrect corners ($G_P(1)=10.90$, $p=0.001$). However, the individual G-values indicate that only two of the four birds showed a significant preference for the geometrically correct corners (G-values for each bird: 7.92, 2.09, 5.62, 0.00).

Finally, on *Conflict* tests, all three groups of chickadees chose the featurally correct corner significantly more than the geometrically correct corners (expected ratio 2:1): wild-caught black-capped chickadees $G_P(1)=20.88$, $p<0.001$; hand-reared black-capped chickadees $G_P(1)=54.80$, $p<0.001$; wild-caught mountain chickadees $G_P(1)=54.30$, $p<0.001$. Three of the wild-caught black-capped chickadees chose the featurally correct corner significantly more often than the geometrically correct corners (G-values: 4.23, 14.63, 15.38), and one bird did not show a preference (G-value: 0.72). Three of the hand-reared black-capped chickadees also chose the featurally correct corner significantly more often than the geometrically correct corners (G-values: 28.31, 26.37, 8.79), and again, one bird did not show a preference (G-value: 0.71). Similarly, three of the wild-caught mountain chickadees showed a significant preference for the featurally correct corner (G-values: 25.83, 12.50, 30.76) and one bird did not show a preference (G-value: 0.55).

Between group comparisons

Two separate ANOVAs were conducted in order to compare the pattern of results across the different groups and conditions. First, I compared the choices on *Geometry-Only* tests to the two geometrically correct corners for each group (i.e.,, species and rearing) and condition (i.e.,, training condition). The ANOVA showed a significant main effect for group ($F_{2,19}$=5.07, p=0.017), whereas both the main effect of condition and the interaction between group and condition were non-significant. A Scheffé's post hoc analysis indicated that the mountain chickadees chose the geometrically correct corners significantly less often than both the wild-caught black-capped chickadees and the hand-reared black-capped chickadees. The wild-caught and hand-reared chickadees did not differ significantly from each other.

A second ANOVA on the results for the black-capped chickadees examined choices to the featurally correct corner on *Conflict* tests for each group (wild-reared and hand-reared) and feature condition (far-feature and near-feature only). The results of this ANOVA indicated a significant main effect of condition

($F_{1,12}$=9.31, p=0.010), where birds in the near-feature group chose the featurally correct corner more often than the birds in the far-feature group. Group effects and the interaction effect were not significant.

Discussion

Both hand-reared and wild-caught black-capped chickadees in all conditions, including the near-feature condition, were able to use geometric information to reorient. This supports the previous findings (Brown et al., 2007, Chiandetti and Vallortigara, 2008a) that rearing condition does not interfere with an animals' ability to encode geometric information. However, unlike Brown et al. (2007), I did not find any evidence that rearing condition affected preference of featural information over geometric information. That is, wild-caught black-capped chickadees were as likely as hand-reared black-capped chickadees to use geometric information when geometric and featural information were placed in conflict (regardless of condition). This could be due to the fact that all the chickadees were kept in the lab for at least 10 months before testing, thus all birds had considerable experience with right-angled environments before the experiment began.

Similar to Gray et al. (2005), I found that chickadees that were trained with the correct corner adjacent to the feature wall (i.e.,, near-feature group) predominantly used featural information when geometric and featural information were placed in conflict. In contrast, chickadees trained with the correct corner opposite to the feature wall (i.e.,, far-feature group) were more likely to split their choices between geometrically correct and featurally correct corners. During the conflict tests, however, the chickadees in this condition almost never chose the geometrically correct corner that was adjacent to the feature wall, suggesting that they did not completely disregard featural information.

A direct comparison of the current results and those of Gray et al. (2005) seems to suggest a difference in sensitivity to the featural information on conflict tests. In particular, the current study shows that birds in the far-feature condition avoided the geometrically correct corner that was adjacent to the blue wall, whereas in the previous study the birds appeared to split their choices between the two geometrically correct corners. I believe this to be mainly due to a procedural difference in the manner in which the data were scored. Since the two geometrically correct corners were alternately baited in the current study, when scoring the test trials, one of the corners could arbitrary be labeled as correct. In the case of far-feature conflict tests, the geometrically correct corner not adjacent to the feature wall was labeled as correct and the opposite was labeled as rotation. In Gray et al., this was not the case since only one corner was ever baited. Although the location of the feature wall varied, the same corner was always labeled as correct regardless of whether it was adjacent or not-adjacent to the blue wall.

The use of geometric information seems to be a less preferred strategy for mountain chickadees than for black-capped chickadees. As shown in the ANOVA, wild-caught black-capped chickadees chose geometrically correct corners significantly more than mountain chickadees when tested in the absence of discriminative featural information. Additionally, the pooled-G values and average individual G-values for both wild-caught and hand-reared black-capped chickadees are substantially greater than those for the mountain chickadees. Moreover, only two of the four mountain chickadees tested in the near-feature condition used geometric information to reorient when tested in the absence of discriminative featural information, thus only partially replicating the results of Gray et al. (2005). Why the mountain chickadees are less likely to use geometric information than black-capped chickadees is, as yet, unclear.

Although many procedural variables have been shown to affect use of geometry, it seems unlikely that they could cause the difference between species in this case since the procedure was identical for both black-capped and mountain chickadees. For example, the size of the environment has been shown to affect the extent to which animals prefer featural information to geometric information (Learmonth et al., 2002, Sovrano et al., 2005, 2007, Vallortigara et al., 2005). However, since mountain and black-capped chickadees are very similar in size, it is unlikely that the size of the environment caused the differences observed between the two species. Moreover, although past studies have shown that featural information is often preferred in large environments, it has not been shown to overshadow geometric information in these cases. Additionally, the specific disorientation procedure used can also affect an animal’s ability to reorient according to geometric information. Lourenco and Huttenlocher (2006) demonstrated that when the apparatus is rotated, rather than the viewer, children were unable to discriminate between equally angled but opposite corners of a triangle. Although the two different disorientation procedures seem to not be equivalent, the space-movement disorientation procedures alone cannot account for the current results since black-capped chickadees were able to use the geometric information more effectively than mountain chickadees.

While procedural variables seem unlikely to account for these results, there are some ecological differences between the species that may play a role in spatial strategies and preferences. Mountain and black-capped chickadees are closely related species, and live in sympatry in some areas. However, even in areas of sympatry, the species seem to be at least somewhat ecologically segregated (Hill and Lein, 1988). For instance, black-capped chickadees tend to nest in smaller trees while mountain chickadees build their nests in larger trees and locate their nest holes higher above the ground. In addition, black-capped chickadees in Hill and Lein's study population were never observed to reuse nest holes. In contrast, mountain chickadees in the same population were frequently observed reusing nest holes. Besides differences in nesting behaviour, there are species differences in foraging behaviour; black-capped chickadees tend to remain on branches (on the periphery of trees) whereas mountain chickadees are more likely to forage on trunks of trees (near the center).

It is my contention that these differences in nesting and foraging behaviour could be contributing to species differences observed in geometrical and featural processing. Specifically, differences in nest hole reuse, with mountain chickadees often reusing their nest holes and black-capped chickadees never reusing nest holes, could explain the reliance on featural information in the former and the use of geometry in the latter. Mountain chickadees must encode the location of particular nest locations, and featural information is likely to play an important role in solving this problem.

Although results here and those of Brown et al. (2007) suggest that rearing environment over one generation does not interfere with the ability to use geometric information to orient, such strategies may be gradually given less weight with many generations of disuse. Moreover, my results suggest that mountain chickadees are able to use geometric information (two of the four subjects were able to use geometric information in the absence of featural information), although it seems to be a less preferred or more difficult strategy.

Indeed, different environmental demands have been shown to affect spatial abilities or strategies even within a species (Pravosudov and Clayton, 2002). Pravosudov and Clayton compared two groups of black-capped chickadees (one group from Alaska and one from Colorado) on their spatial strategies, memory and hippocampal size. They found that the hippocampal volumes of the Alaskan black-capped chickadees, who must endure harsher and more unpredictable environmental conditions, were significantly larger and contained more neurons than the Colorado chickadees. Moreover, the Alaskan black-capped chickadees cached more food and had better spatial memory than the black-capped chickadees from Colorado. Future comparative studies could compare hippocampal sizes in black-capped and mountain chickadees from my study population to determine whether my observed differences in spatial processing have a definable neurobiological basis.

In addition, future research could examine the individual differences in strategy choice and preference. Specifically, why did only some birds predominantly use the geometry of the environment to orient? One possibility is that individual differences in spatial strategies are due to differences in lateralization of function. In particular, previous research has shown that geometric spatial information is strongly lateralized within the avian brain, where the right hemisphere processes global information (including geometric information) and the left hemisphere seems to process more local spatial information (beacons or colour) (e.g., Tommasi et al., 2000; Tommasi and Vallortigara, 2004). Perhaps, then, strong side biases could then affect preference of spatial strategies in individuals. Additionally, it would be worthwhile to study other wild-caught animals of species that may be more likely to use featural information in their natural environment.

As far as I am aware, this is the first direct comparison of different species' use of geometric information to orient. Despite the close relation between black-capped and mountain chickadees, I suggest here that their different use of habitat, and particularly nest use, could result in different spatial strategies. My results clearly demonstrate the value of considering species' ecological environments in comparative cognition research.

Figure 2-1. The mean percentages of choices to each corner for wild-caught black-capped chickadees and hand-reared black-capped chickadees trained in the *Geometry* condition. The correct corner is shown as the top left, however the actual correct corner was counterbalanced across birds.

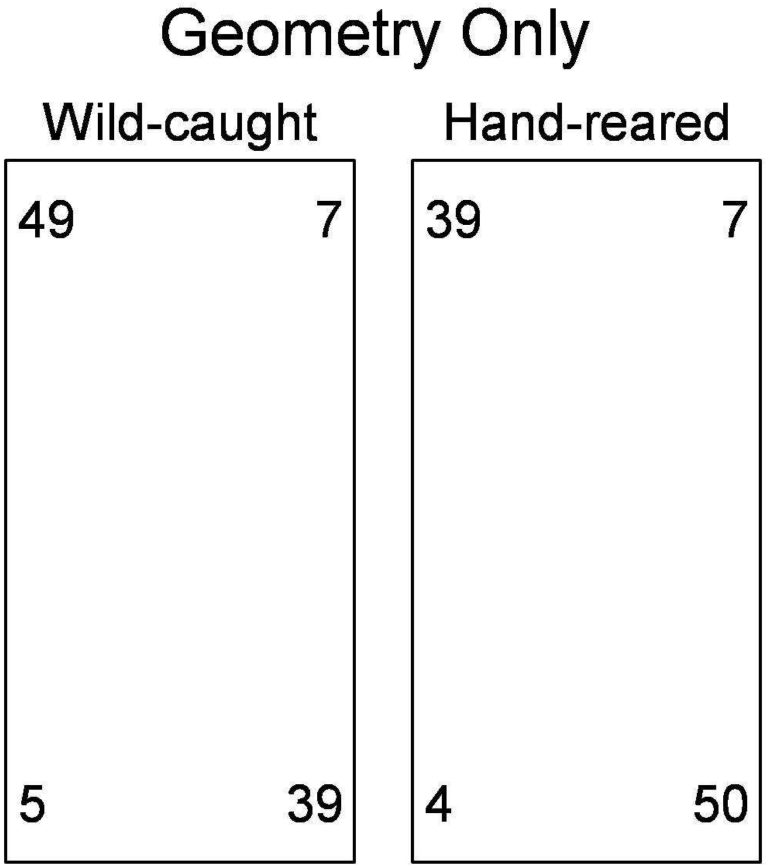


Figure 2-2. The mean percentages of choices to each corner on each type of test for (a) wild-caught black-capped chickadees and (b) hand-reared black-capped chickadees trained in the *Far-Feature* condition. The correct corner is shown as the top left, however the actual correct corner was counterbalanced across birds.

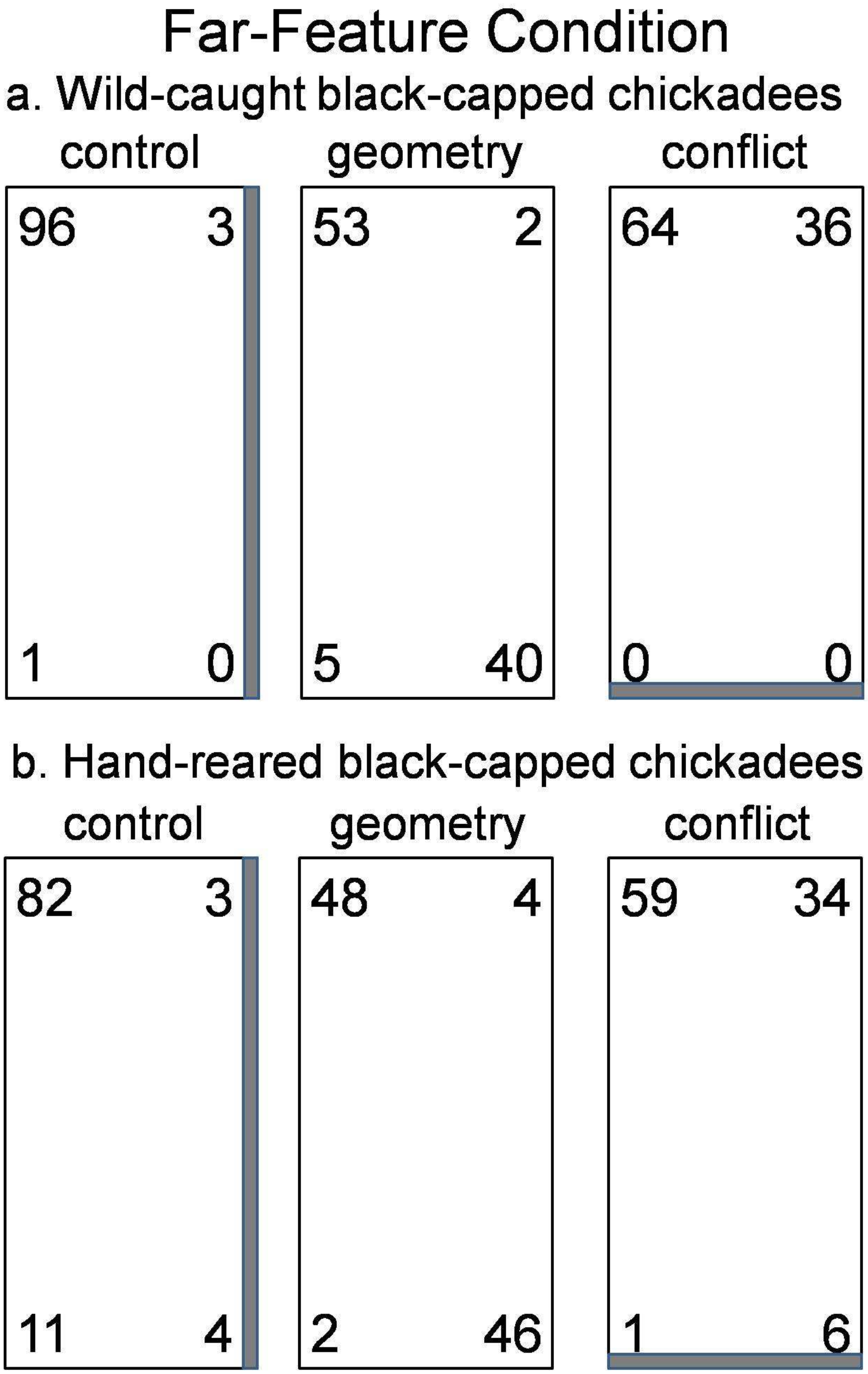
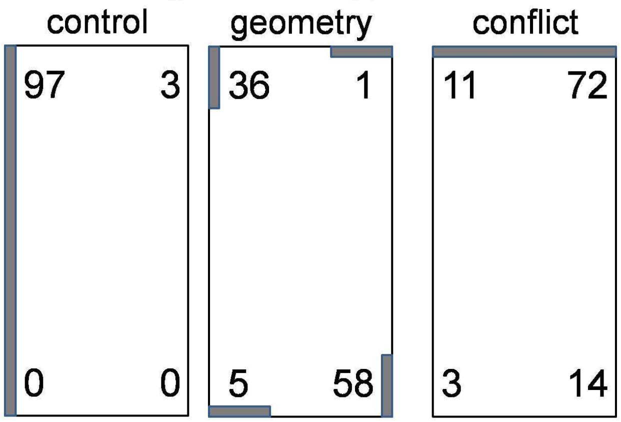


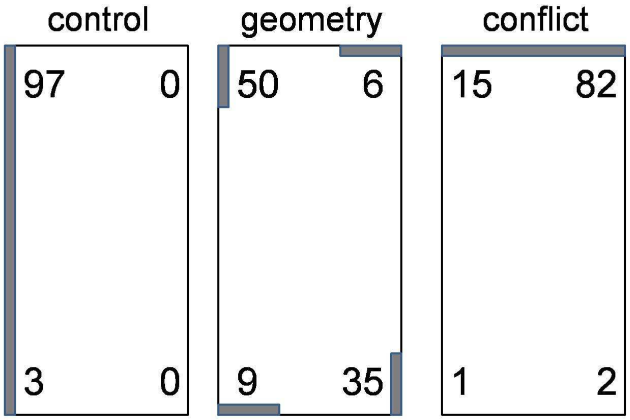
Figure 2-3. The mean percentages of choices to each corner on each type of test for (a) wild-caught black-capped chickadees, (b) hand-reared black-capped chickadees and (c) wild-caught mountain chickadees trained in the *Near-Feature* condition. The correct corner is shown as the top left, however the actual correct corner was counterbalanced across birds.

Near-Feature Condition

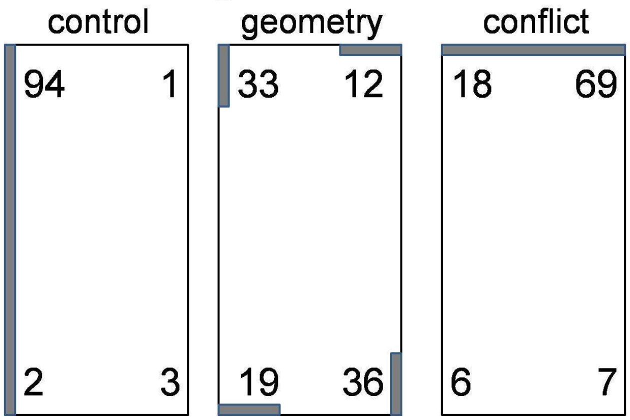
a. Wild-caught black-capped chickadees



b. Hand-reared black-capped chickadees



c. Wild-caught mountain chickadees



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Chapter 3

Rats’ use of geometric, featural and orientation cues to locate a hidden goal

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Introduction

Over the past 20 years, a substantial amount of research has focused on animals' abilities to use the geometric properties of an environment to reorient (see Cheng & Newcombe, 2005, for a review). In particular, a growing number of studies have examined how animals use the metric cues provided by either the walls of an environment or the configuration of landmarks to re-establish a directional frame of reference, or *determine heading* (Gallistel, 1990). In one common paradigm, pioneered by Cheng (1986), a disoriented animal is placed in a rectangular apparatus and is reinforced for locating a target corner. In a rectangle, however, geometric cues create an ambiguous situation where the two opposite corners within the rectangle share the same geometric properties (e.g., short wall on the left, long wall on the right). Featural information can be used to disambiguate the environment.

Cheng (1986) first used this paradigm to study how rats used geometric properties to determine heading. Rats were trained in both working memory and reference memory tasks. In the working memory task, the rats were allowed to find food that was partially hidden within the rectangular apparatus with distinctive featural information. Before consuming all of the food, the rats were removed for a retention interval, during which an identical test apparatus was rotated randomly to make orientation cues unreliable. After the retention interval, the rat was placed in the test apparatus and allowed to search for the remaining food. The rats searched at the rotationally equivalent corner (i.e., the location that maintained the same geometric relationship between apparatus and goal, but was featurally incorrect) almost as often as they searched at the correct location. In the reference memory task, food was always located at one corner of the rectangular environment. Rats learned to use featural information to distinguish between geometrically equivalent corners, but still made significantly more rotational errors than other errors. Cheng concluded that rats orient according to the geometric shape of the environment and that featural information is later "pasted" onto this metric frame of reference.

Use of geometry to orient has since been found with a variety of species including human children and adults (Hermer & Spelke, 1994, 1996), rhesus monkeys (Gouteux, Thinus-Blanc & Vauclair, 2001), fishes (Brown, Spetch & Hurd, 2007; Sovrano, Bisazza & Vallortigara, 2002, 2003; Vargas, Lopez, Salas & Thinus-Blanc, 2004) and ants (Wystrach & Beugnon, 2009). Avian species have also been found to use geometric information to orient, though they seem to rely more heavily upon featural information (pigeons: Kelly, Spetch & Heth, 1998, chicks: Vallortigara, Zanforlin & Pasti, 1990).

In addition to being an orienting strategy used by a wide variety of species, use of geometry also seems to be a very robust strategy; it has been shown to be resistant to cue competition effects, such as overshadowing by beacon landmarks (Pearce, Ward-Robinson, Good, Fussel & Aydin, 2001) and blocking (Wall, Botly, Black & Shettleworth, 2004). That is, although cue competition frequently occurs in the spatial domain (e.g., Biegler & Morris, 1999; Diez-Chamizo, Sterio & Mackintosh, 1985; Roberts & Pearce 1999; Rodrigo, Chamizo, McLaren & Mackintosh, 1997; Spetch, 1995), in many cases featural information does not block learning of geometric information. For example, Pearce et al. (2001) found that placing a beacon at the target location did not prevent rats from learning about the shape of a geometrically unambiguous environment. That is, rats predominantly searched at the target location even when the beacon was removed. Similar results have also been found in geometrically ambiguous environments (Hayward, McGregor, Good & Pearce, 2003).

There is, however, a growing body of evidence suggesting that cue competition does occur between geometric and featural information in some instances. For example, mountain chickadees trained with a distinctive feature near the target location were less likely (and sometime unable) to use geometric information in the absence of the feature (Gray, Bloomfield, Ferry, Spetch & Sturdy, 2005). In contrast, a closely related species of chickadee, the black-capped chickadees, do learn to use geometric information in similar training conditions (Batty, Bloomfield, Spetch & Sturdy, 2009), suggesting that mountain chickadees' reliance on featural information is a species-specific strategy. Additionally, although Pearce et al. (2001) found that beacons did not overshadow learning of geometric information, subsequent research from the same lab has shown that featural information in the form of differently coloured walls can overshadow or block geometric learning in rats during a water maze task (Pearce, Graham, Good, Jones & McGregor, 2006). Conversely, blocking was not found in a similar, but appetitively motivated, task (Wall et al., 2004).

Despite this growing body of research on the use of geometric information to orient, fewer studies have examined the use of geometric information to find a goal location within an already established directional frame of reference. In a study with children, Lourenco & Huttenlocher (2006), found that, when disoriented, children were able to use geometric information to re-orient and locate a target location. However, if the environment was rotated while the children maintained their initial frame of reference, they were less able to use geometric information to locate the target. This study suggests that geometric information may primarily be a tool for reorientation, and may not be as valuable for navigating when orientation is maintained.

Margules and Gallistel (1988) tested rats' use of both geometric and orientation cues in a working memory task similar to that of Cheng (1986). The rats were trained to find a partially uncovered target location within a rectangular apparatus. For some of the rats, distinctive panels in each corner of the apparatus provided local featural information. Unlike Cheng's (1986) study, the apparatus was located within a normally lit room and rats' were not disoriented. All rats had access to the distal featural information provided by the room cues. After finding the target location, rats were removed for a 75s retention interval, then returned to the apparatus and allowed to search for the "remaining" food. In the first experiment, the apparatus remained in the same orientation for both the initial and retention phases. Under these conditions, rats did not make rotational errors, suggesting that rats were able to retain heading information from extramaze cues.

In a second experiment, Margules and Gallistel (1988) manipulated the orientation of the apparatus between initial presentation and retention. The rats still searched in the correct location significantly above chance levels, but their performance declined substantially from the first experiment, suggesting that a stable frame of reference was an important factor in their ability to match locations. Only one of the rats made a significant number of rotational errors, indicating that most of the rats were not relying solely on the metrics of the apparatus to orient. That is, since most of the rats did not make rotational errors, they must have been using other orientation or featural cues to disambiguate the geometry of the environment.

In the current study, I aimed to answer some of the remaining unresolved questions about how rats use geometric information within a stable frame of reference, and how learning about geometry and other orientation cues may interact. First, in a reference memory task, will oriented and disoriented rats learn about featural information differently? Since featural and orientation cues will provide redundant information, oriented rats may be less likely to learn about the featural cues. Indeed, past research has shown that when rats are allowed to maintain a stable directional frame of reference, orientation cues (e.g., internal compass sense) are used in preference to visual featural cues (Huxter, Thorpe, Martin & Harley, 2001).

The current study also addresses the question of whether rats prefer geometric cues or other orientation cues (e.g., internal compass cues) when both are available. Margules and Gallistel (1988) showed that at least some rats were able to use geometric information to locate a target location when orientation cues were present but were made unreliable. However, the working memory task did not easily permit for orientation and geometric cues to be placed directly in conflict. In particular, since the goal location varied throughout the apparatus, it would be more difficult to locate on the basis of orientation cues, such as internal compass sense, alone. As well, since the rats had visual access to distal cues of the room, when the apparatus was rotated, *both* distal visual cues and internal orientation cues conflicted with the geometric information. In the current study, some groups of rats were not disoriented, but visual access to room cues was blocked. As well, the target location was always in one corner of the apparatus, making it easier to define on the basis of orientation cues alone (e.g., always search in the north-west corner). Therefore, by rotating the apparatus by 90° on test trials, I was able to place geometric cues and the rat's internal compass sense in conflict without confounding internal orientation sense with the distal visual cues. Moreover, I looked at whether initial training affects rats' preference for geometric or internal orientation cues.

Materials and Methods

Subjects

The subjects were 16 experimentally naive Sprague-Dawley rats (*Rattus norvegicus*). The rats were individually housed on a 12:12h light schedule. Training and testing sessions took place at approximately the same time each day, 5-6 days per week, at a time during which the lights in the holding room were on.

The rats were kept between 90-95% of the free-feeding weight and were allowed free access to water throughout the experiment.

Apparatus

The training and test apparatus was a Plexiglas rectangular chamber (60 cm × 120 cm × 47 cm) with a white bottom, clear walls and an open top. The walls were covered on the outside with white poster board to a height of 35.5 cm. The floor of the arena was covered with approximately 1 cm depth of aspen chips. The apparatus was placed on a metal cart with four wheels to allow for easier rotation of the apparatus during test trials. White, opaque curtains hung from the ceiling down to the floor around the perimeter of the apparatus to cover the extra-maze environment. A video camera was mounted on the ceiling above the center of the apparatus to allow viewing of the rat while in the apparatus and recording of the test trials. The feature, used in feature conditions, was a brightly colored rectangular, striped towel (50 cm × 70 cm) that could be hung from the surrounding white curtains with binder clips; the towel provided high contrast with the surrounding curtain. The dishes used to hold the food (Kellogg's Froot Loops) during training and testing were clear, circular plastic containers with a diameter of approximately 5 cm. The dishes were one-half to three-quarters filled with a mixture of sand and Froot Loops crumbs.

Procedure

Shaping, habituation, and pretraining. Rats were shaped in their home cages to dig in sand dishes to obtain a Froot Loop or Froot Loop piece. Shaping continued until the rats readily dug in the dishes with the Froot Loop completely covered.

Following shaping, rats were randomly assigned to one of four conditions: geometry-orientation training (GOT), geometry-disorientation training (GDT), feature-orientation training (FOT) or feature- disorientation training (FDT). Rats in the feature groups (FOT and FDT) had the feature affixed to the curtains at a constant location, whereas rats in the geometry groups had no distinctive featural information available within the apparatus. Rats were also assigned to a 'correct' corner which was always in the same location of the room (e.g., the northwest corner); the correct corner was counterbalanced across rats. Before each trial (for both habituation and training), rats were placed in an opaque holding container (20 cm × 24 cm × 15 cm). A lid was placed on the container while the experimenter set up the apparatus. For rats in the 'oriented' groups, the lid was removed before the rats were moved inside the curtained area and placed in the apparatus. For rats in the 'disoriented' groups, the lid was kept on the holding container and the container was slowly rotated (6-8 rotations per minute) for one minute. The lid remained on the container until it was brought into the curtained area. The experimenter always entered the curtained area along a long wall of the apparatus, but the side of entry varied randomly from trial to trial. Once inside the curtained area, the lid was removed (if necessary) and the container was placed in the center of the apparatus. The rat was lifted from the container and placed randomly facing one of the four walls. The experimenter then exited the curtained area from the point of entry and monitored the rat's behaviour on a TV monitor.

Rats were given one or two sessions of habituation to the apparatus. One sand dish was placed in the correct corner with one Froot Loop buried and one Froot Loop placed on the top of the sand. Froot Loop pieces were also scattered throughout the apparatus. Rats were allowed to explore and eat the Froot Loops for 30-60 minutes.

During subsequent pre-training sessions, rats received five to eight trials. Each trial during pre-training began as previously described with the rat being placed in the holding container and oriented or disoriented as necessary. During pre-training sessions, one sand dish was placed in the correct corner with the Froot Loop placed on top of the sand. Rats were allowed a maximum of five minute to obtain and eat the Froot Loop. Upon finding the Froot Loop, the rat was given approximately 30 seconds to eat, then was removed from the apparatus and returned to the holding container. Over trials the Froot Loop was gradually covered beneath the sand until it was completely buried within the sand dish. Between trials, the aspen chip was swept and any feces were removed. The rims of the goal dishes were wiped and the dishes were placed in different corners at random. As well, the apparatus was rotated by 180° every 2-3 trials; the correct corner maintained the same location within the room (e.g., the northwest corner) regardless of the rotation of the apparatus. Once the rat consistently obtained fully buried Froot Loops, it was moved onto training.

Training. During training sessions, rats always received eight trials. Training trials proceeded as pretraining trials, except that in this phase, a sand dish was placed in all four corners, although only the correct corner was baited with a Froot Loop. Rats were allowed to make as many choices as necessary to find the Froot Loop; however, only trials during which the rat made its first choice to the correct corner were counted as ‘correct’.

Once the rat reached a criterion of 8/10 correct trials (counted across sessions), the reinforcement was decreased to 62.5% (i.e., the correct corner was baited on 5/8 trials per session). When the rat reached criterion of 8/10 correct trials on this final phase, it was moved onto testing.

Testing. During testing, rats received five reinforced training trials and three non-reinforced probe trials. During the probe trials, the featural, orientation and geometric cues were systematically placed in conflict or removed. All groups of rats received three types of tests: (1) geometry+orientation probes, in which the apparatus remained in the same orientation as during training and the rat was not disoriented prior to the trial, (2) geometry vs. orientation probes, in which the apparatus was rotated by 90° and the rat was not disoriented prior to the trial, and (3) geometry-only probes, in which the rat was disoriented prior to the trial and the apparatus remained at the training orientation for half of these probes and was rotated by 90° for the other half. Rats received four trials of each probe type.

The groups trained with featural information (FOT and FDT) also received several additional tests. Two additional probe tests were conducted in the absence of orientation cues (i.e., the rat was disoriented prior to the trial): (1)

geometry+feature probes, in which both the geometric properties of the apparatus and featural information indicated the same correct corner and (2) geometry vs. feature probes, in which the geometric and featural information provided conflicting information. Finally, four probe types contained all three types of information (rats were not disoriented prior to these trials): (1) geometry+orientation+feature, the feature and apparatus were in the same position as during training, (2) orientation vs (geometry+feature), the apparatus and feature were rotated by 90°, (3) (orientation+geometry) vs feature, only the feature was rotated by 90°, (4) (orientation+feature) vs geometry, the apparatus only was rotated by 90°. A schematic of all the probe trials is shown in Figure 3-1.

Data Analysis

During many of the probe trials, more than one source of information could indicate the correct corner. To account for this overlap, I used the number of cues available and the rat's choice on each trial to assign a weighting to each cue type. The total weighting available for each trial was equal to the number of cues available. For example, in the (orientation+feature) vs geometry probes, all three types of cues were available to the rat, so the weighting available for that trial would be three. On trials in which the feature was removed and/or the rat was disoriented prior to the trial, the total weighting available would be less than three. The rat's choice on the trial determined how the weightings were assigned. For example, on the (orientation+feature) vs geometry probes, if the rat chose the corner indicated as correct by orientation and featural cues, the total weighting (3) would be divided between orientation and feature, yielding a weighting of 1.5 for orientation, 1.5 for feature and 0 for geometry (since the choice would be geometrically incorrect). In all cases, the weighting for geometry was divided by 2 to account for the higher chance of choosing geometrically correct corners (i.e., 2 corners are always geometrically correct). In other words, the total weighting was divided among the cues that indicated the chosen corner as 'correct'.

To compare the choices at each corner, I used replicated G-tests for Goodness of Fit (Sokal & Rohlf, 1995), which is distributed as a chi-square but allows one to pool data from several subjects (pooled G: G_P) and separate variance due to individual subjects (test for homogeneity: G_H) from variance due to choice locations. The Goodness of Fit tests allowed me to compare choices at particular corners to an expected ratio of responding, thus allowing me to compare whether rats used information from each cue equally. I used t-tests to compare specific conditions.

Results

Use of Featural Information

I first analyzed whether rats in the groups trained with the feature cue (FOT and FDT) used the feature to disambiguate the geometrically equivalent corners. In particular, I compared the proportion of choices to the correct corner to the proportion of choices made to the rotational equivalent on two types of probe trials: (1) geometry+feature probes when the rats were disoriented and (2) the (geometry+feature) vs orientation probes. In both of these cases, only featural information would disambiguate the two geometrically equivalent corners. There were no significant differences between choices to the correct or rotational corner (t(7)=1.53, p=0.170), suggesting that rats did not use the feature to discriminate between corners.

I used replicated Goodness of Fit G-tests on the weighted choices to examine search patterns on (1) trials during which the featural and geometric information conflicted and (2) trials during which featural and orientation cues conflicted. When featural and geometric information conflicted, the FOT group chose the geometrically correct corners significantly more than the featurally correct corner ($G_P(1)=6.91$, $p=0.009$) and there were no significant differences between rats ($G_H(3)=2.04$, $p=0.563$). The FDT group also chose the geometrically correct corners significantly more than the featurally correct corner ($G_P(1)=11.25$, $p=0.001$) and there were no significant differences between rats ($G_H(3)=6.16$, $p=0.104$).

When featural and orientation cues conflicted, the FOT group chose the orientation-correct corner significantly more than the featurally correct corner ($G_P(1)=14.79$, $p<0.001$), but there were significant differences between rats ($G_H(3)=11.06$, $p=0.011$). Two of the four rats showed a significant preference for the orientation-correct corner whereas two rats did not show a significant preference (individual G values: 18.71, 5.94, 1.02, 0.17). The FDT group did not choose the orientation-correct corner significantly more than the featurally correct corner ($G_P(1)=0.23$, $p=0.631$), but there were significant differences between rats ($G_H(3)=26.59$, $p<0.001$). One rat showed a significant preference for the orientation-correct corner (G=16.64), one rat showed a significant preference for the featurally correct corner (G=7.59) and two rats did not show a significant preference (G= 1.02, 1.57).

Finally, training with featural information did not appear to affect use of geometric or orientation cues. There were no differences between FOT and GOT groups in their proportion of geometrically correct choices (t(6)=0.35, p=0.741) or proportion of orientation correct choices (t(6)=0.14, p=0.897). There were also no differences between FDT and GDT groups on their proportion of geometrically correct choices (t(6)=1.28, p=0.247) or proportion of orientation correct choices (t(6)=0.39, p=0.713). I therefore collapsed the orientation-trained groups (FOT and GOT) into one group and the disorientation-trained groups (FDT and GDT) into another.

Use of geometric and orientation cues

On geometry-only probe tests (i.e., when rats were disoriented and no featural information was available), the orientation-trained group made their first choice at a geometrically correct corner 91% of the time and the disorientation-trained group made their first choice at a geometrically correct corner 72% of the time (Figure 3-2). Both were significantly above chance levels (oriented: t(7)=8.80, p<0.001, disoriented: t(7)=2.50, p=0.041). There were no significant differences between the two groups (t(14)=1.90, p=0.079).

I next analyzed whether rats in each group used orientation cues (when available) to disambiguate the geometrically equivalent corners. In particular, we compared the proportion of choices to the correct corner to the proportion of choices made to the rotational equivalent on two types of probe trials: (1)

geometry+orientation probes when no featural information was available and (2) the (geometry+orientation) vs feature probes (results are shown in Figure 3-2). In both of these cases, only orientation cues would disambiguate the two geometrically equivalent corners. The orientation-trained rats chose the correct corner 75% of the time and the rotational equivalent 14% of the time. In this group, the correct corner was chosen significantly more than expected by chance ($t(7)=8.00$, $p<0.001$) and also significantly more often than the rotational corner ($t(7)=5.11$, $p=0.001$). The disorientation-trained rats chose the correct corner 53% of the time and the rotational equivalent 20% of the time. Again, the correct corner was chosen significantly more than expected by chance ($t(7)=4.02$, $p=0.005$) and significantly more often than the rotational corner ($t(7)=2.42$, $p=0.046$). A comparison between the two groups revealed that the orientation-trained group chose the correct corner significantly more often than the disorientation-trained group ($t(14)=2.33$, $p=0.035$).

For trials in which geometric and orientation cues were in conflict, I used replicated Goodness-of-Fit G-tests on the weighted choices to determine how each group of rats used the geometrical and orientation cues. The proportion of choices and the average weighted choices on these conflict trials are shown in Figure 3-3. As a group, the orientation-trained rats showed a marginally significant preference for the orientation correct corner ($G_P(1)=3.81$, $p=0.051$). There were significant differences between rats ($G_H(7)=44.33$, $p<0.001$). Two rats showed a significant preference for the orientation correct corner ($G= 29.80$, 8.32), two rats showed a marginal preference for geometrically correct corners

(G=3.40, 2.77; p's<0.1) and the remaining four rats did not show any preference (G=2.29, 1.16, 0.20, 0.20; p's>0.1). The disorientation-trained group showed a significant preference for the geometrically correct corners ($G_P(1)=13.87$, $p<0.001$). However, there were significant differences between rats ($G_H(7)=24.71$, $p=0.001$). Five rats significantly preferred the geometrically correct corners (individual G values: 16.64, 6.02, 5.55, 4.28, 4.16) and three did not show a preference for either corner (individual G values: 1.93, 0.01, 0.00).

Finally, I compared orientation-trained and disorientation-trained groups on the proportion of choices to the orientation correct corner across all trials. The proportion of choices and the average weighted choices to geometrically and orientation correct corners across all trials are shown in Figure 3-4. The orientation-trained group chose the orientation correct corner 56% of the time whereas the disorientation-trained group chose it 36% of the time. The difference between groups was marginally significant ($t(14)=2.12$, $p=0.053$).

Discussion

Both orientation-trained and disorientation-trained rats were able to use the geometry in the absence of other cues and chose the geometrically correct corners significantly more than chance on the geometry only tests. The finding that the orientation trained rats learned as much about geometry as the disorientation-trained rats is interesting because these rats clearly used orientation cues. Specifically, on tests in which both geometry and orientation cues were available, the orientation-trained rats were able to use orientation to distinguish the correct corner from the rotational equivalent corner and did so significantly more than the disorientation-trained group. Thus, the presence of orientation cues during training did not overshadow learning about geometry.

When geometric cues and orientation cues were placed in conflict, the orientation-trained rats split their choices or showed a preference for the orientation correct corner. Disorientation-trained rats, on the other hand, most often preferred the geometrically correct corners. This suggests that the training procedures, and not simply the presence of orientation cues during testing, create the preference for geometric cues. Specifically, although the disorientation-trained were sometimes able to use orientation cues to disambiguate the correct corner from its rotational equivalent when the cues were not in conflict, these rats rarely used orientation cues during the conflict tests.

That the preferences seem to be created through the training procedures may also be reflected in working memory tasks, such as those used by Margules and Gallistel (1988) and Lourenco and Huttenlocher (2006). In working memory tasks, the subject is oriented during the initial presentation of the goal – most similar to my orientation-trained groups of rats. In Margules and Gallistel's study, the decrement in the rats' performance on trials when the apparatus was rotated could reflect this preference for orientation cues. Similarly, in the space-disorientation procedure (the environment is rotated while the subject maintains their sense of direction) used by Lourenco and Huttenlocher, children may have been less likely to use geometry because of a preference for orientation cues. In the viewer-disorientation procedure (the subject is disoriented), children effectively use geometric cues; this is most similar to my finding that orientation-trained rats did use geometric cues on trials when they were disoriented.

However, unlike Lourenco and Huttenlocher's (2006) study, I did not directly examine rats' use of geometric and orientation cues in a space-disorientation procedure. In particular, my orientation-trained group was not subjected to a disorientation procedure at all during training and my disorientation-trained group was subjected to a viewer-disorientation procedure. Since the training procedures apparently affected cue preference in my study, and use of geometric cues in Lourenco and Huttenlocher's study, it would be useful to test a space-disoriented group in a reference memory task. That is, a third group could be included in which the rats maintain their sense of direction, but the apparatus is rotated randomly between trials such that orientation cues do not effectively predict the location of the target corner. This would allow me to determine whether preference for orientation cues is persistent or whether rats can learn to ignore their sense of direction when it becomes irrelevant.

A second aim of my study was to determine whether oriented and disoriented rats would use featural information differently. However, the featural information did not appear to exert much control over the rats' behaviour, regardless of whether the rats were trained with or without a stable directional frame of reference. On trials in which there was no conflict between geometric and featural information, neither group of rats showed control by the featural information and they both made rotational errors in their choices. Additionally, on trials in which the featural information and geometric information were placed in conflict, all rats predominantly used the geometric information to guide their search.

During training, the rats were required to visit the correct corner first on 80% of the trials before continuing to testing. Use of geometric information alone would result in rotational errors and would not allow the rats to reach the criterion for testing. For rats trained in the disorientation group (FDT group), only the featural information could be used to disambiguate the geometrically correct corners. Thus, this group presumably used featural information during training but showed little control by featural information during testing. It is possible that the feature had low salience to begin with, and that probe trials in which the feature moved or was absent made it seem unstable which further reduced its salience (see Biegler & Morris, 1996).

On trials in which the featural information conflicted with other orientation cues, rats trained in the oriented conditions were more likely to search on the basis of orientation cues, whereas rats that were trained in the disoriented condition tended to split their searches between the featurally correct corner and orientation correct corner. Because geometric information was available in all tests, during the orientation vs. feature conflict tests, the geometrically correct corner was also featurally correct on half of the trials and correct according to orientation cues on the other half. Thus, the splitting of choices by the disoriented-trained group on this test seems to suggest a lack of preference for either orientation or featural cues, and a reliance on geometric cues. In contrast, the oriented-trained group clearly preferred orientation cues over featural cues.

Future research could expand on these findings by using more salient landmarks or featural information. Research with monkeys has shown that the size of the feature can affect the degree to which featural information is used (Gouteux et al., 2001), so it could be useful to use different features to determine saliency. Additionally, to more closely examine whether disoriented and oriented animals learn about featural information differently, animals could be trained to use featural information in the absence of polarizing geometric cues (e.g., a square arena instead of a rectangle).

Overall, my results have interesting implications for the study of the neurological basis of geometric processing. The hippocampus of the rat has been shown to play an important role in spatial learning in general, and the use of geometry in particular (Pearce, Good, Jones & McGregor, 2004; Jones, Pearce, Davies, Good & McGregor, 2007). Individual neurons within the hippocampus, called *place cells*, will respond selectively when the rat is in a specific area of the environment (O'Keefe & Burgess, 1996). As well, head-direction (HD) neurons in brain regions that project to the hippocampus, such as the entorhinal cortex and postsubiculum, are involved in encoding specific directions within an environment (Taube, Muller & Ranick, 1990a, 1990b).

In regards to how place cells map environments and direct explorative behaviour, O'Keefe and Speakman (1987) used a plus maze with a single baited arm to study how rats' place cells mapped the choice of the goal arm. Rats were trained with a variety of featural cues which maintained a constant spatial relationship with the baited arm but were rotated in conjunction with the baited arm across trials. During some tests, rats initially had visual access to the cues and were then required to locate the baited arm in the absence of the cues. On these “memory trials”, the place cells mapped correctly even though the rats no longer had visual access to the featural information. On some control tests, the rats were placed in the maze without initially having visual access to the featural cues and thus chose at random. On these trials, however, the place cells mapped to the rats’ chosen location as if it were the baited arm. That is, the place cells mapping was coupled with the rats’ choice behaviour. Thus, place cell mapping may be linked to the perceptual orientation of the rat; that is, the rat forms a directional frame of reference (that may be influenced by or coded by the HD cells) and the place cells map according to that frame.

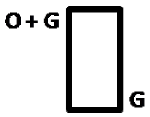
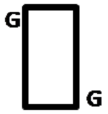
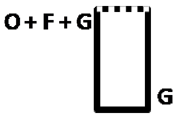
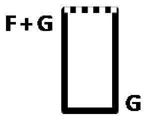
In one study examining how HD cell system measures direction, Dudchenko and Zinyuk (2005) measured the firing of rats’ HD cells in a T-maze. Rats were required to make a forced choice in a T-maze and then were carried to an adjacent identical T-maze, which could either be parallel to the initial T-maze or rotated by 90°. The behaviour of the HD cells was found to be linked to the T-maze itself; that is, when placed in the rotated maze, the firing direction of the cells also shifted by nearly 90° despite the fact that the rats were not disoriented between mazes.

Dudchenko and Zinyuk’s (2005) findings provide for an interesting perspective of my results. In particular, it would be interesting to note whether there were any differences between HD cell firing between the orientation-trained and disorientation-trained rats. Perhaps the extended training with a stable frame of direction would have allowed for the HD cells in the orientation-trained group to align with an allocentric (world-based) directional frame of reference. Conversely, since the disorientation-trained rats had less experience using orientation cues to locate the target corner, I would expect the HD cells to respond similarly to Dudchenko and Zinyuk's findings, and thus, orient on the basis of the geometry regardless of rotation. However, how the HD cell system interacts with place cells and place field firing remains a question for future research.

The hippocampus (and presumably place cells) seems to play an important role in discriminating between comparable locations within an environment (Jones et al., 2007). Jones et al. found that hippocampal-lesioned rats could find the target location at unambiguous locations (e.g., the apex of kite-shaped apparatus) but could not distinguish between a right-angled corner and its mirror image. Importantly, Dudchenko (2007) has suggested that HD cells may orient on the basis of a corner within a rectangular or square environment. If a rat has maintained a stable frame of direction throughout training (as in my orientation-trained group), I would expect the HD cells to consistently orient according to one specific corner. In contrast, the HD cells of a disoriented rat may switch orientation between trials. Moreover, if a disoriented rat were unable to distinguish between comparable shaped corners due to damage to place cells within the hippocampus, the HD cells may orient according to a random corner within the apparatus. An extension of my current study would then be to study the behaviour of hippocampal-lesioned rats, both oriented and disoriented, in a similar paradigm. On trials in which geometric information and orientation cues conflict, I might expect the orientation-trained rats to show a stronger preference for orientation cues based on the directional information of the HD cells. On the other hand, disorientation-trained rats may either respond at chance, or, since rats were able to use orientation cues to some degree in my study, I might expect them to show some preference for the orientation cues.

In summary, my results provide several different avenues for future research regarding the behavioural and neurological bases of geometric learning. The differences in preferred cues between the disorientation-trained rats and orientation-trained rats suggest that training procedures must be carefully controlled when studying control by geometry. Moreover, new hypotheses about the neurological basis of geometric processing can be formed by more closely attending to the distinction between forming a sense orientation by geometry and use of internal orientation sense.

Figure 3-1. A schematic of each probe-trial type. Dashed lines represent the location of the feature which was affixed to the surrounding curtains and not the apparatus itself. The letter 'F' indicates that a corner was correct according to featural information, 'O' indicated the corner was correct according to orientation cues and 'G' indicates that the corner was correct according to geometric properties.

Training Conditions
 *Geometry-Oriented*
 *Geometry-Disoriented*
 *Feature-Oriented*
 *Feature-Disoriented*

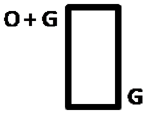
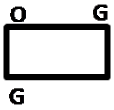
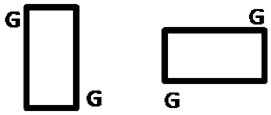
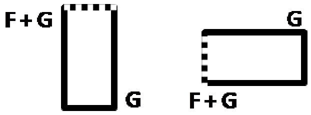
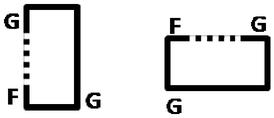
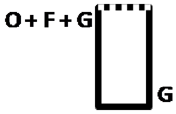
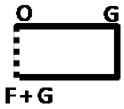
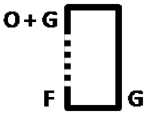
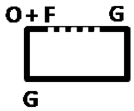
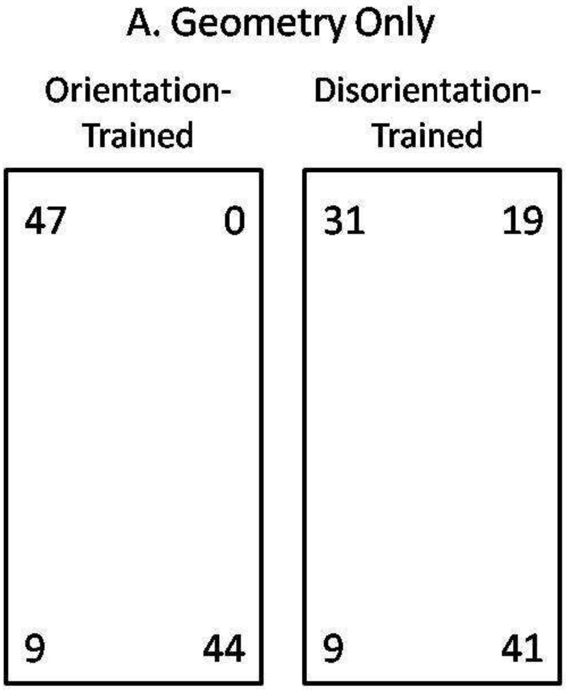
Probe Type	**Disoriented before probe?**	**Schematic**
Orientation + Geometry	no	
Orientation vs Geometry	no	
Geometry Only	yes	
Geometry + Feature	yes	
Geometry vs Feature	yes	
Geometry + Orientation +Feature	no	
Orientation vs (Geometry + Feature)	no	
(Orientation + Geometry) vs Feature	no	
(Orientation + Feature) vs Geometry	no	

Figure 3-2. The mean percentages of choices to each corner for orientation-trained and disorientation trained rats during A. Geometry-only probes and B. Geometry+Orientation trials (including both geometry+orientation probes when no featural information was available and (geometry+orientation) vs feature probes). The correct corner is shown as the top left, however the actual correct corner was counterbalanced across birds.


A. Geometry Only

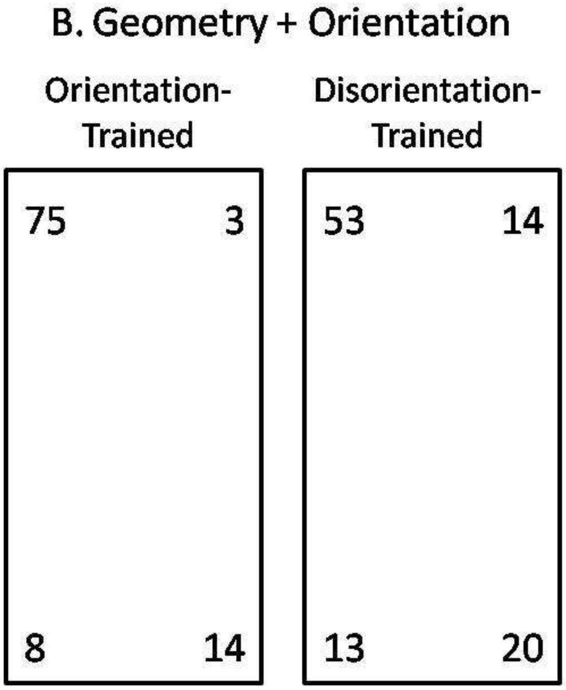

B. Geometry + Orientation

Figure 3-3. (A) Mean proportion of choices and (B) mean weighting of choices per trial to geometrically and orientation correct corners by orientation-trained and disorientation-trained rats on trials in which geometric and orientation cues conflicted.

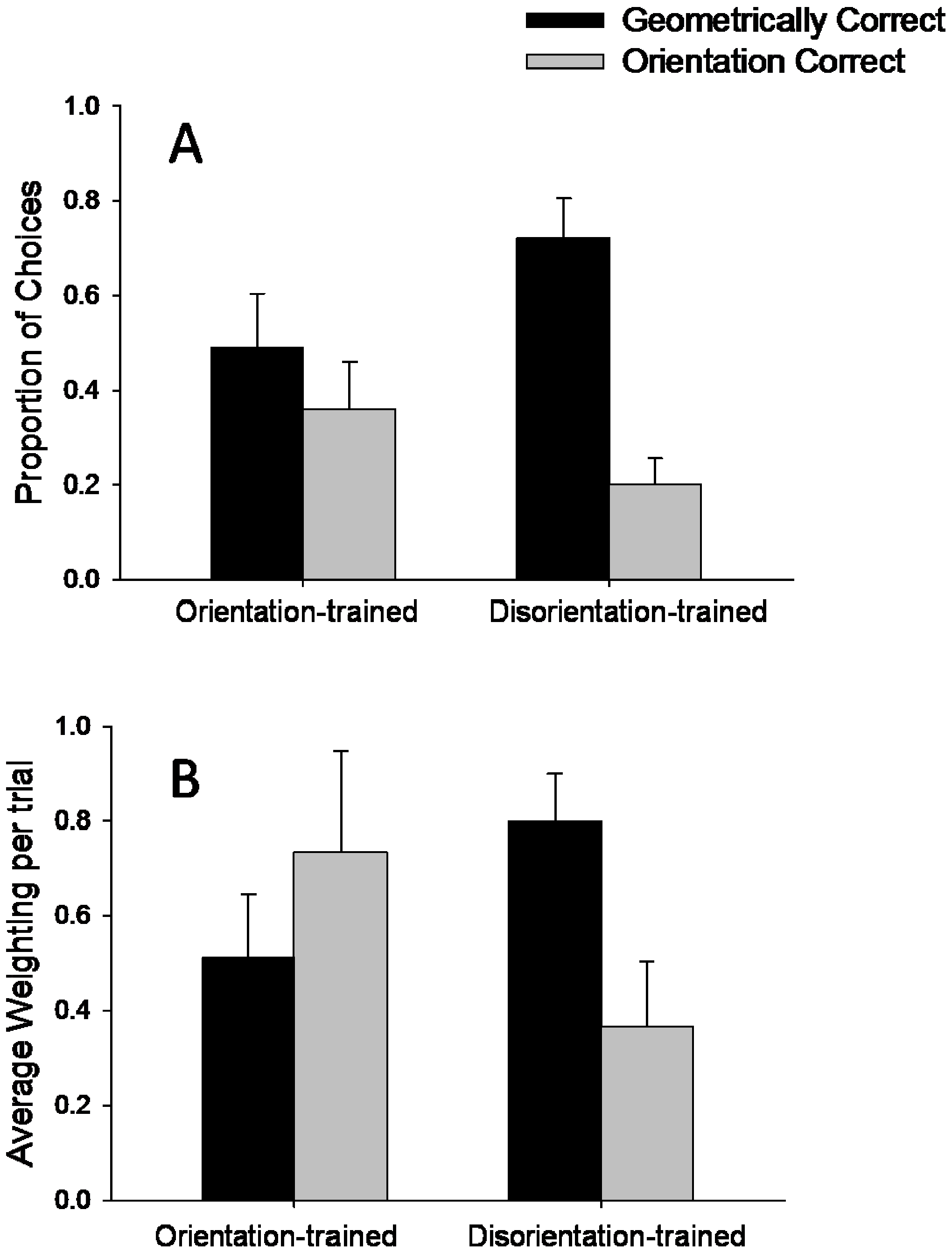
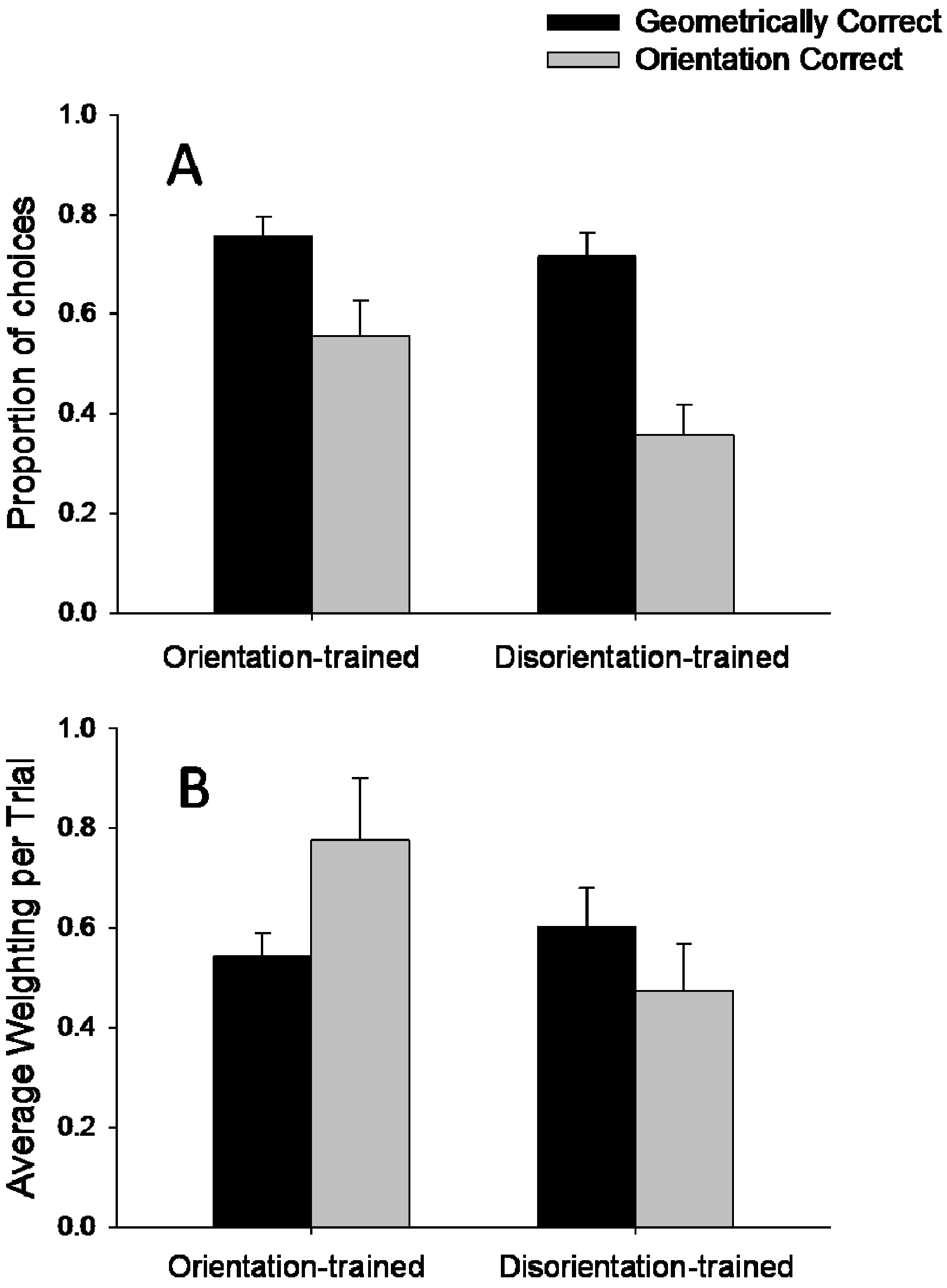


Figure 3-4. (A) Mean proportion of choices and (B) mean weighting of choices per trial on all trials. On some trials, the correct corner was both geometrically and orientation correct, therefore proportions do not sum to one.



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Chapter 4

Prior experience affects encoding of directional information from discrete landmarks

This chapter is being prepared for publication: Batty, E.R. & Spetch, M.L.

Introduction

The ability to return to a previously visited location is an important aspect of everyday life. One common mechanism for solving this problem is the use of landmarks near or surrounding the target locations (Cheng & Spetch, 1998). Navigation based on landmarks, also called piloting, is the process by which an organism determines position and orientation based on objects within the environment (Gallistel, 1990). Specifically, when piloting, an animal must be able to use the landmarks to determine both distance and directional information to pin-point a goal location. How an animal determines this distance and directional information is often described in terms of two specific strategies: an absolute strategy, wherein the animal learns a specific distance and/or direction from a single landmark, or a relational strategy, in which the animal learns the location of the goal based on its relationship to two or more landmarks. The latter strategy can be thought of as learning spatial "rules" such as 'in the middle'.

Although use of an absolute strategy is sometimes thought of as learning a specific vector from a landmark to a goal, evidence has suggested that animals encode distance and direction independently (Cheng, 1994). It follows that animals may also use separate strategies for remembering distance and direction to a goal; for the remainder of the paper, we therefore will refer to distance and direction strategies separately. For example, an absolute distance strategy would involve learning a specific distance from a landmark to a goal. An absolute direction strategy, on the other hand, would involve learning a specific angle between a landmark and goal based on global, or allocentric, directional cues (e.g., cardinal directions, such as the goal is to the east of the landmark). Relational distance or direction strategies involve learning the location of the goal relative to multiple landmarks, and do not rely on specific metrics.

Most research has suggested that, with the exception of human adults, oriented animals tend to prefer an absolute distance strategy when searching for a hidden goal. For example, Spetch, Cheng and MacDonald (1996) studied the types of search strategies used by human adults and pigeons when searching for a hidden goal. Humans and pigeons were trained to find a goal in the center of a square array of landmarks and were then tested with an expanded array. Humans used a relational distance strategy and continued to search in the center of the array. In contrast, pigeons mainly searched at the absolute learned distance from one landmark. Search strategies were found to be consistent across open field, table-top and computer tasks for humans, and across open field and touchscreen tasks for pigeons (Spetch et al., 1996; Spetch et al. 1997). Other animals that have also been shown to use absolute distance strategies include Clark's nutcrackers (Kelly, Kippenbrock, Templeton & Kamil, 2008), gerbils (Collett, Cartwright & Smith, 1986) and nonhuman primates (MacDonald, Spetch, Kelly, & Cheng, 2004; Poti, Bartolommei, & Saporiti, 2005; Sutton, Olthof, & Roberts, 2000).

In contrast, some evidence suggests that, in the absence of orientation cues, animals may be more likely to use relational distance strategies. For example, pigeons (Gray, Spetch, Kelly & Nguyen, 2004) and chicks (Tommasi & Vallortigara, 2000; Tommasi, Vallortigara & Zanforlin, 1997) will sometimes use relational distance strategies when searching for the center of an enclosed arena. Additionally, Sturz and Katz (2009) trained pigeons to search for a hidden goal in the center of a two landmark array. When pigeons were trained and tested in the presence of conspicuous orientation cues, pigeons searched according to an absolute distance strategy on large expansion tests. However, when pigeons were trained and tested in the absence of orientation cues, they searched according to a relational distance strategy, suggesting that the ability to maintain a stable directional frame of reference may play a role in strategy selection or preference.

Research on directional strategies, however, has yielded mixed results. For example, Kamil and Jones (2000) trained Clark's nutcrackers to use relational distances from two landmarks to find a goal, then tested the birds with rotated arrays. When the array was rotated by 90°, most birds searched according to an absolute direction strategy. That is, the birds did not use the relationship between the landmarks to determine direction to the goal. Quite the opposite, Sturz and Katz (2009) found that pigeons used a relational direction strategy when trained to search in the center of a two landmark array. The stark contrast between these two sets of results may be due to the different procedures used in each study. Specifically, in the experiments by Sturz and Katz (2009), pigeons were trained with two separate landmark arrays that were spatially identical (i.e., both contained two landmarks 60cm apart) but used visually different landmarks; in one study, identical red landmarks were used and in another, distinct blue and yellow landmarks were used. This repeated training with similar landmark relations, but different landmarks, could have caused the pigeons to ignore the identity of the landmarks and focus exclusively on the spatial relation. In contrast, the nutcrackers in Kamil and Jones' (2000) study were always trained with two distinct landmarks, and thus may have learned more about landmark identity. It could be that animals are more likely to use an absolute strategy when the individual landmarks are identifiable.

Strategy use may also be affected by the number of landmarks used in the array. For example, gerbils have been shown to use both absolute and relational direction strategies when trained to find the center of a three-landmark array (Collett et al., 1986). Gerbils were trained to search at the center of three identical landmarks placed in an equilateral triangle and were tested with trials in which the array was rotated by 60°. The gerbils primarily searched in the center of the rotated array, but showed secondary search peaks at locations corresponding to an absolute direction strategy. However, Gray and Spetch (2006) performed a similar experiment with pigeons, but used a four-landmark array. They found that the pigeons used only a relational direction strategy on rotation tests. Based on these different patterns of results with different landmark arrays, Gray and Spetch (2006) suggested that search strategy preference may depend on the number, distinctiveness and arrangement of landmarks within the array. However, most evidence to support this suggestion comes from comparisons of results between experiments and sometimes between species.

In the current study, I examined more closely how the number of landmarks in an array might affect search strategies in pigeons. Here, I used a within subject design to directly compare whether the number of landmarks within an array will affect search strategies. Additionally, I tested whether landmark distinctiveness may play a role in strategy preference. In particular, Spetch, Kelly and Lechelt (1998) found that pigeons tended to develop a preference for particular landmarks and that removal of the preferred landmark disrupted search accuracy, even when other landmarks were available. Thus, distinct landmarks may encourage pigeons to base their search on only one landmark, biasing the birds towards an absolute strategy. Conversely, with identical landmarks, landmark identity must first be determined by the overall configuration of the landmarks.

Since birds in the present study were presented with multiple landmark arrays, I also examined whether the order of array presentation would affect pigeons' search strategies. In particular, I investigated whether repeated training with a 'center' rule would affect pigeons' search strategies or whether pigeons would maintain an initially preferred strategy. Specifically, since pigeons may be more likely to use an absolute direction strategy on the two-landmark array (based on proximity to non-target landmarks, as discussed above), if a bird is trained with that array first, I hypothesized that the bird might 'stick' with the same strategy on subsequent arrays. In contrast, a bird trained with the four-landmark array first may be observed to maintain a relational direction strategy.

Methods

Subjects

Twelve adult pigeons (Columbia livia) with varied experience served as subjects. None had any previous experience searching with arrays of landmarks.

The birds were maintained between 85% and 90% of their free-feeding weights by pigeon pellets obtained during experimental sessions and supplemental feedings in the home cages. They were housed in large individual cages under a 12:12-h light:dark cycle (with light onset at 6:00 a.m.). Grit and water were freely available in the home cages.

Design

Pigeons were divided into four groups depending on the order of presentation of the landmark arrays and distinctiveness of the landmarks. For half of the birds, the landmarks arrays were presented in increasing numerical order (i.e., two-landmark array, three-landmark array, four-landmark array) and for the other half, the arrays were presented in decreasing numerical order (i.e., four-landmark array, three-landmark array, two-landmark array). Birds were trained and tested with one array before moving onto the next. For three birds in each group (six birds total), the landmark arrays were composed of identical landmarks and for the others, the landmarks arrays were composed of distinct landmarks. Specific landmarks were always different for the different arrays (i.e., the landmarks used in the two-landmark array were not the same as the landmarks used in the three-landmark or four-landmark arrays).

Apparatus & Stimuli

The experiment was conducted in custom-built operant chambers, equipped with a color LCD screen and an infrared touch frame that recorded the location of the pigeons’ pecks. The chambers contained two solenoid-type bird feeders, one on each side of the monitor. Lamps within each feeder illuminated feeder presentations, and photocells measured head entries into the hoppers for timing of feeding durations. Food rewards consisted of one to two seconds of feeding duration, depending on the weight of the bird. Computers located in an adjacent room controlled the experimental contingencies and recorded the responses.

The landmarks were approximately 1 cm × 1 cm variously shaped and coloured graphic stimuli, presented on a grey background. The goal was an approximately 2 cm × 2 cm white square. For all arrays, the center of the goal was approximately 3.5 cm from the center of each landmark. The landmark arrays were always presented in the same orientation during training, but were presented at a random location on the screen. For the two-landmark array, the landmarks were presented in a horizontal line. The three-landmark was presented as an equilateral triangle with the point facing up, and the four-landmark array was presented as a square.

Procedure

Pretraining. Birds were first given several sessions of autoshaping to establish reliable pecking behaviour. Autoshaping trials began with presentation of the white goal square at a random location on a grey background. The goal was presented for 8 s or until a peck in the goal area was recorded, at which point a randomly selected food hopper was raised for 2 s. Trials were separated by a 60 s intertrial interval (ITI), during which the monitor was illuminated only with the grey background. Autoshaping continued until the bird pecked on 80% of the trials for two consecutive sessions.

Search Training. During search training, pigeons were gradually trained to find the goal on the basis of landmarks. The graphic landmarks were introduced, but the goal square was still visible. The landmarks and goal were presented for 20 s and the intertrial interval was decreased to 30s. The number of landmarks presented depended on the bird's assigned array presentation order (increasing or decreasing). The goal square was gradually faded out within and between sessions at a rate that depended on the bird's accuracy.

Once the birds reached a criterion of two consecutive days at or above 80% accuracy on trials when the goal was completely invisible, the number of pecks required to the goal area was increased to three pecks. A consecutive peck requirement was also added so that the last two pecks had to be in the goal area. Pecks outside the goal area reset the consecutive peck counter. Once the bird met the criterion of 80% accuracy for five consecutive days at this level, it moved to the testing phase.

Testing. Each block of 20 trials during test sessions consisted of 14 reinforced training trials and 6 test trials. Test trials lasted for 20s and the co-ordinates of up to 30 pecks were recorded. Test trials were not reinforced. There were six types of test trials: Control, Small Rotation, Large Rotation, Expansion, Single Landmark, and Landmark Switch (for birds trained with distinct landmarks only). Figure 4-1 shows a schematic of Control, Rotation and Expansion tests. Control tests were visually identical to training trials, but terminated without food after 20s, in the same manner as for test trials. During Small and Large Rotation tests, the array of landmarks was rotated around the goal location; the amount of rotation depended on the number of landmarks in the array. For the two-landmark array, the array was rotated by 45° on Small Rotation tests and 90° on Large Rotation tests. The three-landmark array was rotated by 30° or 180° and the four-landmark array was rotated by 15° or 45° for Small and Large Rotation tests, respectively. On Expansion tests, the distance from the goal to each landmark was increased from 3.5 cm to 7 cm. A randomly chosen landmark was presented in the absence of the other landmarks in the Single Landmark tests. On Landmark Switch tests, (presented only for birds trained with distinct landmarks), the array maintained the same shape and orientation as during training trials, but the specific landmarks were placed in a different arrangement. Testing continued for five days then the bird began training with the next array in the series.

Retesting. Once the birds had completed training and testing on all three landmark arrays, they were given a brief retesting phase to examine whether their strategies changed based on extensive experience. During the retesting phase, the arrays were presented in decreasing order for all birds (i.e., four-landmarks, three-landmarks, two-landmarks). Birds were first given refresher training sessions. Once the birds completed two consecutive training sessions with 80% accuracy, they were give three days of testing. During the retesting phases, only Control, Small Rotation and Large Rotation tests were presented.

Data Analysis

In most cases, I examined the proportion of searches in an approximately 2.4 cm × 2.4 cm area that corresponded to absolute (i.e., defined by distance and direction to individual landmarks) and relational (i.e., center) strategies. I chose an area that was slightly larger than the training goal area in order to include search coordinates that were close to or on the edge of the goal. Proportions were compared using a mixed model ANOVA with array type (i.e., two-, three- and four-landmark arrays) as a within-subjects factor and landmark distinctiveness and presentation order as between-subjects factors.

Results

Control Tests

For Control tests, I compared the proportion of searches falling within the goal area across array types. Main effects of array type, landmark distinctiveness and presentation order were all non-significant. There was a significant interaction between array type (i.e., number of landmarks) and order of presentation (F(2,16)=10.61, p=0.001).

In order to compare the differences, I used independent sample t-tests to compare presentation order for each array type. For the two-landmark arrays, birds in the increasing group had an mean proportion of 0.39 (SEM=0.04) searches in the goal area and birds in the decreasing group had a mean proportion of 0.36 (SD=0.05); these proportions were not significantly different (t(10)=0.49, p=0.635). For the three-landmark arrays, birds in the increasing group were less accurate (M=0.34, SEM=0.06) than the birds in the decreasing group (M=0.49, SEM=0.05), but this difference failed to reach significance (t(10)=1.95, p=0.080). Finally, in the four-landmark arrays, birds in the increasing group were significantly less accurate (M=0.33, SEM=0.03) than birds in the decreasing group (M=0.49, SEM=0.04; t(10)=2.88, p=0.016).

Rotation Tests

For the purpose of visualizing search patterns, the response density of searches on Control and Rotation tests was calculated and graphed. Figures 4-2 and 4-3 show the response density of searches for birds in the increasing group and decreasing group, respectively.

An ANOVA comparing the proportion of searches in the center of the array on the Small Rotation tests revealed a significant main effect of array type (F(2,16)=14.09, p<0.001). There was no effect of landmark distinctiveness or presentation order, and no significant interactions. Pairwise comparisons revealed that birds searched significantly less in the center area on the two-landmark arrays (M=0.17, SEM=0.02) than on the three-landmark arrays (M=0.24, SEM=0.03), and significantly less on three-landmark arrays than on four-landmark arrays (M=0.31, SEM=0.03).

The ANOVA on proportion of searches in the center of the array during the Large Rotation tests revealed a significant main effect of array type (F(2,16)=18.904, p<0.001) and a significant interaction between array type and presentation order (F(2,16)=5.15, p=0.019). Main effects of landmark distinctiveness and presentation order were not significant. Pairwise comparison on the main effect of array type revealed that birds searched significantly less in the center area on the two-landmark arrays (M=0.05, SEM=0.01) than on the three-landmark arrays (M=0.11, SEM=0.01), and significantly less on three-landmark arrays than on four-landmark arrays (M=0.19, SEM=0.02).

I used independent sample t-tests on presentation order for each array type to examine the interaction between array type and presentation order. For the two-landmark arrays, birds in the increasing group had a mean proportion of 0.03 (SEM=0.01) searches in the goal area and birds in the decreasing group had a mean proportion of 0.06 (SD=0.02); these proportions were not significantly different (t(10)=1.10, p=0.296). Similarly, on the three-landmark array, there was no difference between birds in the increasing group (M=0.11, SEM=0.04) and the birds in the decreasing group (M=0.12, SEM=0.08; t(10)=0.28, p=0.787). However, in the four-landmark arrays, birds in the increasing group searched significantly more in the center (M=0.25, SEM=0.08) than birds in the decreasing group (M=0.13, SEM=0.05; t(10)=2.97, p=0.014).

Finally, I ran additional tests to compare the proportion of relational searching in each type of Rotation test to the Control tests. For each array type, I used a mixed model ANOVA with trial type as a within-subjects factor and order of presentation and landmark distinctiveness as between-subjects factors. For all three array types, there was a significant main effect of trial type (two-landmarks: F(2,16)=57.59, p<0.001; three-landmarks: F(2,16)=29.81, p<0.001; four-landmarks: F(2,16)=12.68, p=0.001). In all cases, birds searched more in the center on Control tests than Small Rotation tests (p’s < 0.03) and searched more in the center on Small Rotation tests than Large Rotation tests (p’s < 0.02).

Expansion Tests

On the expansion tests, birds only rarely searched in the center of the array (M=0.04, SEM=0.01), so I conducted an ANOVA comparing the proportions in the absolute areas only. Main effects of array type (F(2,16)=3.12, p=0.072) and landmark distinctiveness (F(1,8)=0.92, p=0.366) were not significant. However, there was a significant main effect of presentation order (F(1,8)=9.08, p=0.017), and a significant interaction between array type and presentation order (F(2,16)=5.39, p=0.016). Independent samples t-tests revealed that birds in the decreasing group searched in the absolute regions significantly more than birds in the increasing group on both the three-landmarks array (decreasing, M=0.37, SEM=0.04; increasing, M=0.24, SEM=0.03; t(10)=2.34, p=0.042) and the four-landmark array (decreasing, M=0.33, SEM=0.04; increasing, M=0.16, SEM=0.02; t(10)=3.53, p=0.005). The groups did not differ on the two-landmark array (decreasing, M=0.30, SEM=0.04; increasing, M=0.30, SEM=0.02; t(10)=0.00, p=1.000).

Since birds in the increasing group searched less at the absolute regions on later arrays, I conducted a second ANOVA on the proportion of searches in the relational region. Specifically, I wondered if birds in the increasing group were searching more in the relational region, and whether this would account for the fewer searches in the absolute regions. There were no significant differences between array types (F(2,16)=0.58, p=0.573), presentation order (F(1,8)=0.17, p=0.689) or landmark distinctiveness (F(1,8)=0.768, p=0.406). There were no significant interactions.

Single Landmark and Landmark Switch Tests

To compare performance on the Single Landmark tests, I calculated the proportion of searches in the goal area. For birds trained with distinctive landmarks, I used only the training goal area. Since birds trained with identical landmarks would have no directional reference when presented with a single landmark, I visually examined the search patterns to determine if the bird's peak area of responding corresponded to a trained distance and direction from one of the landmarks and coded that area as the 'correct' area. For example, if a bird mostly searched to the left of a landmark, the area to the left of the presented landmark was counted as 'correct' regardless of whether the left or right landmark had been presented. Although birds generally had high proportions of searching in the correct area (M=0.26, SEM=0.02), their proportion of searching in the goal area was significantly less than on Control trials (F(2,16)=25.38, p=0.001). There was no effect of array type (F(2,16)=0.49, p=0.622), presentation order (F(1,8)=3.70, p=0.091) or landmark distinctiveness (F(1,8)=0.32, p=0.59).

The birds trained with distinctive landmarks made few searches in the center of the arrays during landmark switch tests (M=0.11, SEM=0.02). There were no significant differences for array type (F(2,8)=1.52, p=0.276) or presentation order (F(1,4)=1.93, p=0.238), and no interaction between the two factors (F(2,8)=1.01, p=0.405).

Retesting

The response densities on the retests are shown in Figures 4-4 and 4-5 for the increasing and decreasing groups, respectively. I used paired t-tests to compare the birds' retesting results with the initial patterns of responding. On Control tests, there was no difference between the proportion of response in the center on initial and retesting trials for any of the array types (two-landmarks:

t(11)=1.21, p=0.252; three-landmarks: t(11)=1.11, p=0.290; four-landmarks: t(11)=1.28, p=0.228). Similarly, on the Small Rotation tests, there were no significant differences between initial tests and retests for any of the array types (two-landmarks: t(11)=0.81, p=0.433; three-landmarks: t(11)=1.64, p=0.130; four-landmarks: t(11)=1.81, p=0.097). On the Large Rotation tests, there was no difference between the proportion of responses in the center on two-landmark tests (t(11)=1.53, 0.154). There was a significant difference between initial tests and retests on the three-landmark array (t(11)=3.00, p=0.012); this was largely driven by an increase in relational searches by the birds trained in the decreasing group (t(5)=3.05, p=0.028). Overall, there was no significant difference between initial tests and retests on the four-landmark array (t(11)=1.85, p=0.092), however, birds in the decreasing group searched in the center significantly more during retests (t(5)=3.19, p=0.024).

Discussion

The pigeons' search patterns on both the Expansion tests and Single Landmark tests revealed use of an absolute distance strategy. This strategy seemed to be strongly preferred by all birds, regardless of whether the birds were trained with distinctive or identical landmarks and the number of landmarks in the array. In particular, on the Single Landmark tests, all birds were able to use the landmark to search appropriately. Interestingly, this pattern of results did not depend on the distinctiveness of the landmark. In particular, birds were able to search in a correct learned distance and direction from a single landmark regardless of whether they were trained with identical or distinctive landmarks.

This suggests that landmark distinctiveness does not increase search accuracy. Moreover, that the pigeons trained with identical landmarks were as accurate in searching on the basis of a single landmark indicates that distinctive landmarks are not necessary for choosing a preferred landmark.

Although distinctive landmarks did not increase search accuracy on Single Landmark tests, it did play a role during the Landmark Switch tests. Specifically, the birds did not search in the center on the Landmark Switch tests, suggesting that the spatial relationship between their 'preferred' landmark and the goal was more important than the overall configuration of the landmarks.

On the Expansion tests, all birds showed high levels of responding in areas that correspond to an absolute distance strategy and low levels of responding at the center of the array. This pattern of results is consistent with previous findings that oriented animals tend to prefer absolute distance strategies (e.g., Spetch et al. 1996, 1997). Moreover, this preference seemed to be quite consistent despite the extensive experience with different arrays. In particular, as the birds progressed through the array types, the birds did not increase their relational searching on Expansion tests.

Although the birds did not increase relational distance searching with experience, training with multiple arrays may have provided some interference in learning the spatial relationships on later arrays. In particular, birds in the increasing group had smaller proportions of absolute distance searches on Expansion tests than birds in the decreasing group. In other words, if the four-landmark array was the first array that birds were presented with, they searched quite accurately according to absolute distances on Expansion tests. In contrast, when the four-landmark array was the last array presented, birds were not as accurate. However, the birds in the increasing group were also less accurate on Control tests on the later arrays, suggesting that they may have learned less about the overall spatial relationship than birds with no prior experience with the landmark arrays.

Although birds in the increasing group appeared to suffer from some interference, this pattern of results was not seen in the opposite direction. That is, birds in the decreasing group were as accurate as birds in the increasing group on the two-landmark arrays – both on Control tests and Expansion tests. Although birds in the decreasing group were less accurate on the two-landmark array than they had been on the three- and four-landmark arrays, this is consistent with Kamil and Cheng's (2001) multiple-bearing hypothesis, that increasing the number of landmarks can increase search accuracy.

In contrast to the Expansion tests (which indicate the strategy used for distance information), the results of the Rotation tests suggest that previous experience with other landmark arrays influences how pigeons encode directional information. This influence of past training can be seen most clearly in the search patterns on the Large Rotation of the three-landmark array. The birds in the increasing group, who had previously been trained to search in the center of two horizontally aligned landmarks, made the majority of searches between and slightly above the top two horizontally aligned landmarks in the rotated three-landmark array (Figure 4-2, left center panel). In contrast, the birds in the decreasing group had previously been trained to search in the center of a square array of landmarks, which could be considered as searching at the center of two sets of diagonally placed landmarks. On the rotated three-landmark array, these birds predominantly concentrated their searches between but slightly offset of the diagonally placed landmarks (Figure 4-3, left center panel). In both cases, the search patterns corresponded most closely to an absolute direction strategy. However, the differences between the two groups indicate that the birds seemed to preferentially encode the directional information in a way that was consistent with their previous experience.

Further evidence that previous experience can affect directional search strategies comes from the Large Rotation of the four-landmark array. In this case, the birds in the decreasing group, who had no previous experience at this point, searched according to an absolute direction strategy. Conversely, birds in the increasing group searched mainly according to a relational direction strategy. However, in the rotated four-landmark array, two of the landmarks of the square become horizontally aligned. Thus, birds in the increasing group may have been able to transfer strategies from their initial training with the two-landmark array. There was a slight trend towards this pattern of results on the Small Rotation of the two-landmark array, as well. Specifically, when the two-landmark array when it was rotated by 45° (consistent with training in the four-landmark array), birds in the decreasing group searched more in the center than birds in the increasing group, although not significantly so.

The retesting on the rotational tests was conducted to help clarify these results. Specifically, I examined whether both groups would display similar search patterns after they had experience on all three arrays. On the retests, birds in the decreasing groups changed their search patterns on the Large Rotation of both the three- and four-landmark arrays; in both cases, the birds made more searches in the center of the array. The change in the search pattern on the four-landmark array supports the idea that previous experience can affect search strategies. That is, for birds in the decreasing group, the most recent experience before the retesting of the four-landmark array would be learning the two-landmark array, suggesting that the experience of learning to peck in the center of two horizontally aligned landmarks could encourage the birds to use this strategy on following tests.

The increase in relational searching on the rotated three-landmark array, however, is less clear. The increase in relational responding may seem to suggest that birds were learning to transfer a relational rule across spatial arrangements. Alternatively, the change in responding on the rotated three-landmark array could be explained in terms of the birds past experience. Specifically, results from the initial rotation tests seemed to indicate a preference based on which array the birds were trained with first (i.e., above the horizontal place landmarks for the increasing group, and along the diagonals for the decreasing group). During retesting, birds did not seem as likely to follow one particular previously learned strategy, but rather spread searches to the absolute regions more equally between multiple absolute areas. That is, birds in the decreasing group searched more between the two horizontal landmarks than they had previously, and birds in the decreasing group search more along the diagonals. This may also account for the increase in relational responding since searches were more spread out among the absolute locations; the birds may have also made more searches in the center as they switched search locations.

The preference for an absolute direction strategy on a large rotation of a two-landmark array is consistent with the results of Kamil and Jones' (2000) study with Clark's nutcrackers, but inconsistent with previous findings with pigeons by Sturz and Katz (2009). The presence of strongly orienting cues may account for the discrepancy between these sets of results. Specifically, by using a vertical touchscreen, birds in my study had gravity as a strongly polarized orientation cue. Indeed, there is considerable and growing evidence that gravity may create a "privileged-axis" (e.g., Cartwright & Collett, 1982; Legge, Spetch & Batty, 2009; Kelly & Spetch, 2004a, 2004b; Rossel & Wehner, 1986). It may be the case that training pigeons with a two-landmark array along a cardinal axis encouraged the birds to preferentially using an absolute direction strategy. The three- and four-landmark arrays may be less influenced by biases created by the cardinal axes since the spatial relationships between the goal and landmarks were most often along a diagonal angle. One exception to this pattern is the top point of the equilateral triangle of the three-landmark array. Interestingly, the pigeons trained with the landmarks presented in a decreasing order all seemed to prefer this spatial relationship; the birds trained with identical landmarks most often searched according to the learned direction from the top landmark on single landmark tests and birds trained with distinctive landmarks searched proportionally more when the top landmark was the one presented (on average, birds search 19 more times when the top landmark was presented than any other landmark). In contrast, birds trained in the increasing group did not show this preference. This supports the idea that searching along a cardinal axis may influence search strategy preference. Specifically, the birds that had already been trained to search along the horizontal axis (i.e., the increasing group) were less likely to show a preference for searching along a vertical axis. Conversely, birds in the decreasing group, who had no prior experience searching along the cardinal axis, showed a strong preference for the spatial relationship along the vertical axis.

In summary, my results show that past experience can affect spatial encoding and search strategies. Experience with multiple landmark arrays may interfere with later learning in some cases; specifically, birds trained with arrays presented in an increasing order were less accurate on control trials and searched less according to an absolute distance strategy than birds without past experience. My results further show that past experience can affect the way pigeons encode directional information and can bias the pigeons towards certain response strategies.

Figure 4-1. Schematic representation of the Control, Rotation and Expansion tests.

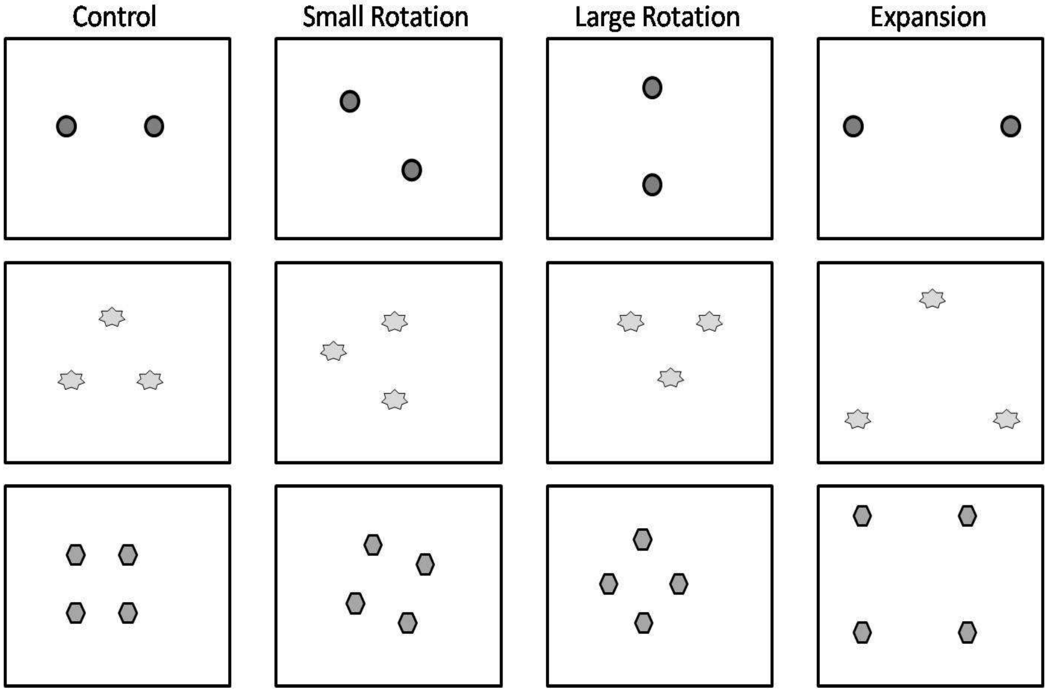


Figure 4-2. Response densities on initial control and rotation tests for birds in the increasing group. Darker regions indicate higher proportion of searches. White circles represent the relational goal location and white triangles represent the absolute goal location.

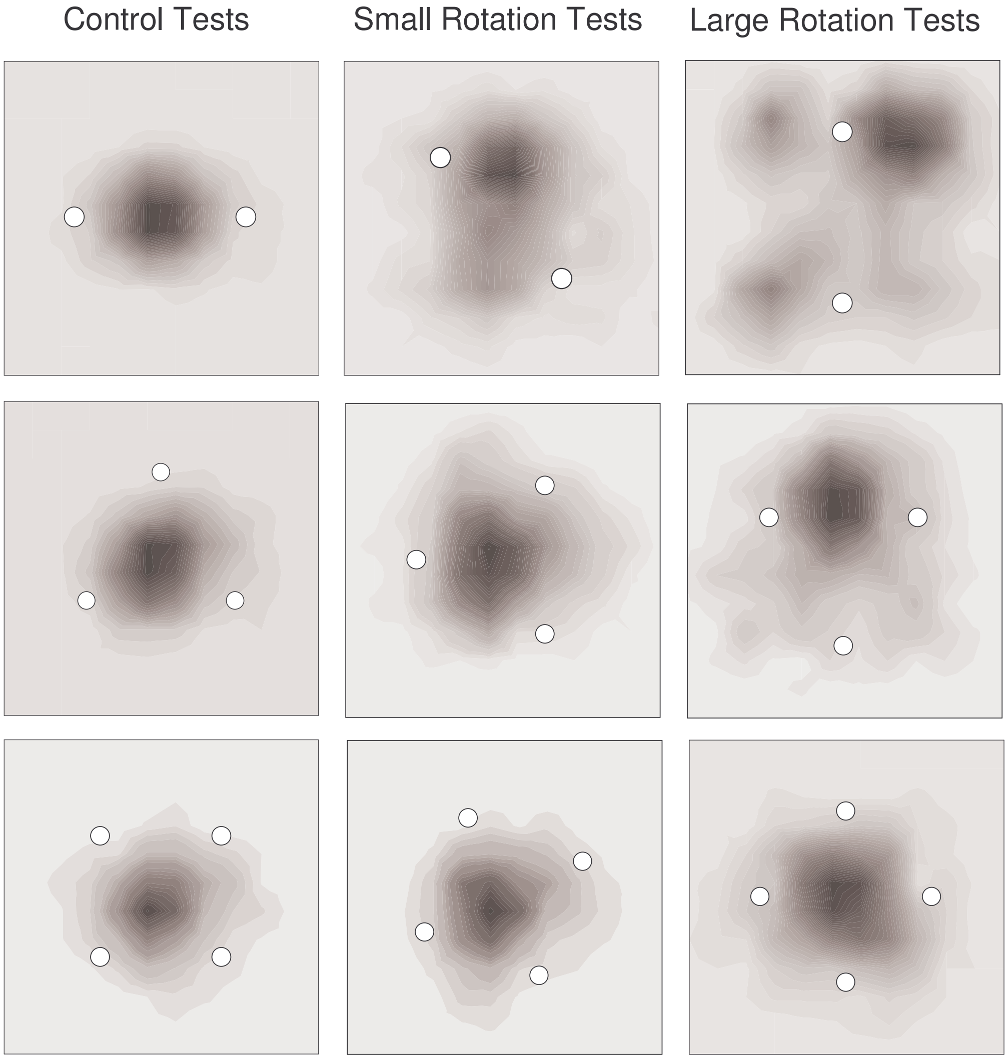
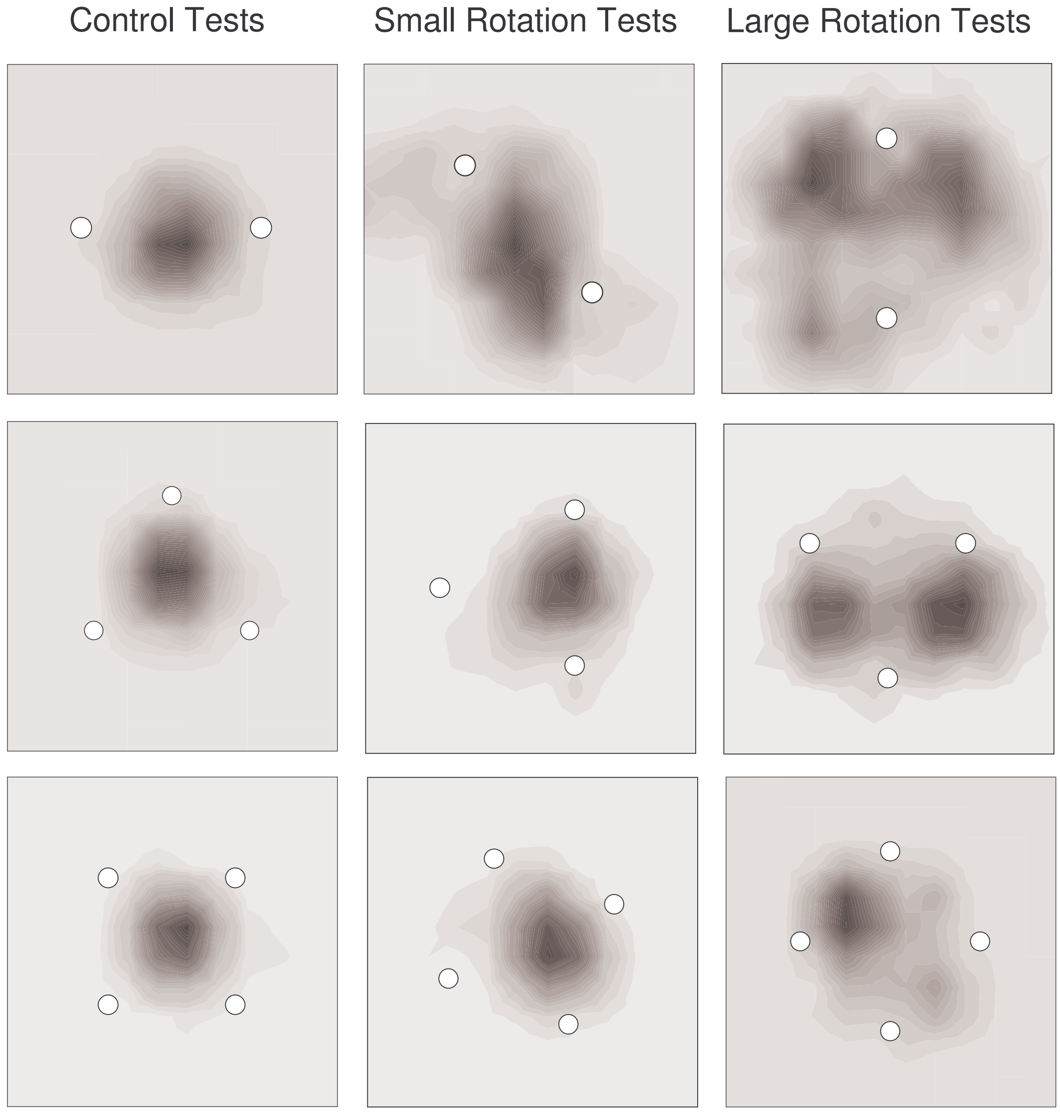


Figure 4-3. Response densities on initial control and rotation tests for birds in the decreasing group. Darker regions indicate higher proportion of searches. White circles represent the relational goal location and white triangles represent the absolute goal location.



Control Tests

Small Rotation Tests

Large Rotation Tests

Figure 4-4. Response densities on control and rotation tests during retesting for birds in the increasing group. Darker regions indicate higher proportion of searches. White circles represent the relational goal location and white triangles represent the absolute goal location.

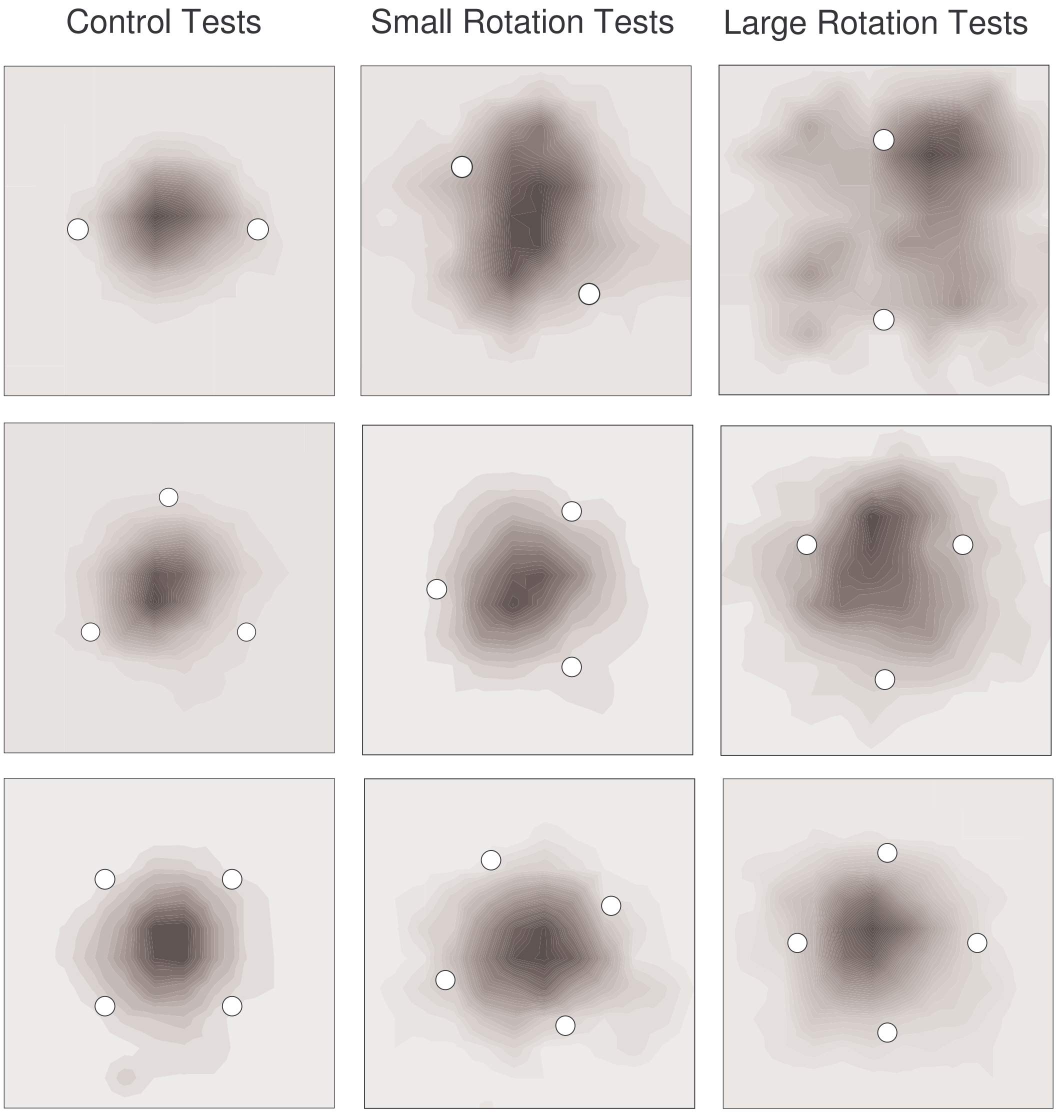
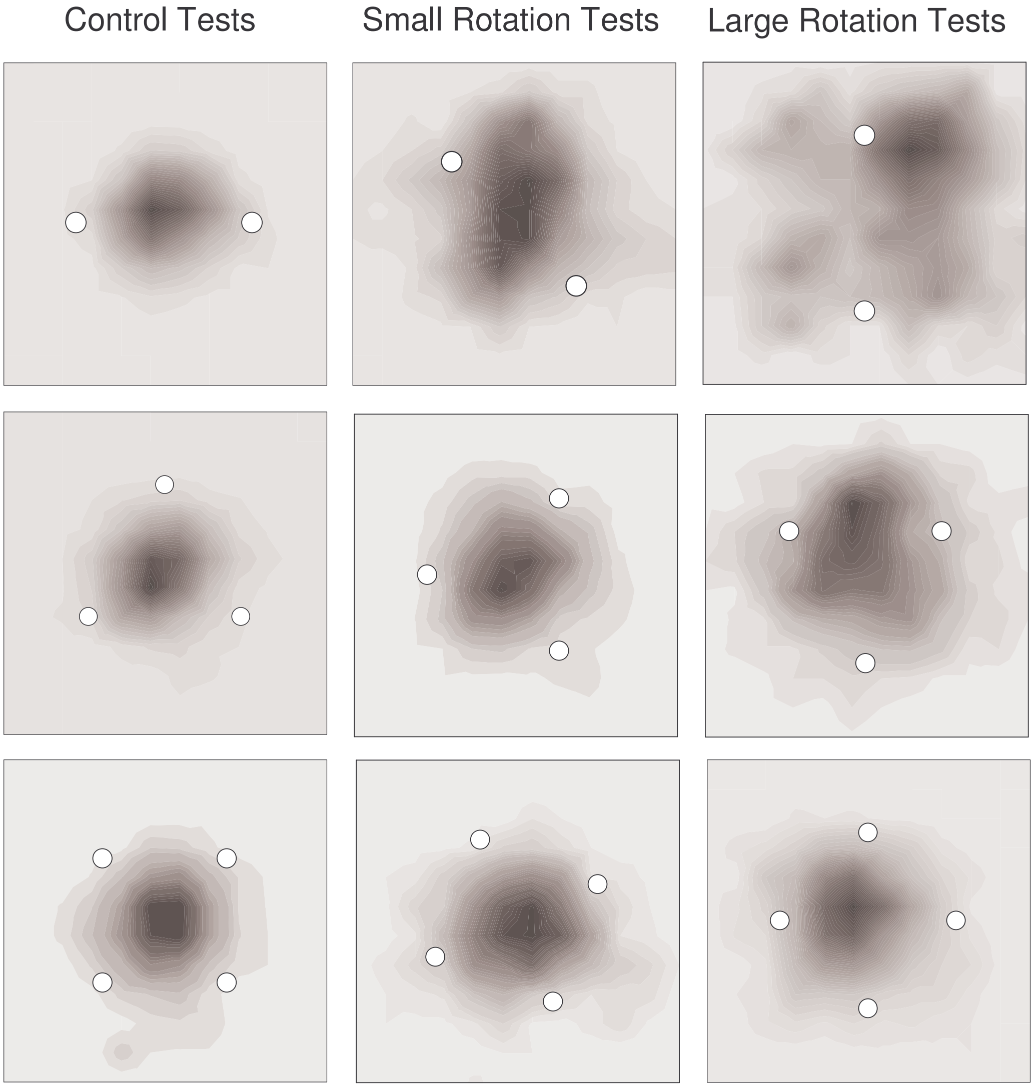


Figure 4-5. Response densities on control and rotation tests during retesting for birds in the decreasing group. Darker regions indicate higher proportion of searches. White circles represent the relational goal location and white triangles represent the absolute goal location.



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Chapter 5

Proximity to an edge affects choice of search strategy in adults and children

This chapter is being prepared for publication: Batty, E.R, Spetch, M.L. & Parent, M.

Introduction

The ability to remember places is an important aspect of everyday life, and as such, researchers have spent a great deal of time examining different strategies that can be used to remember and return to previously visited locations. There are several different ways in which organisms can navigate effectively, including path integration, beaconing, use of celestial cues and landmark-based navigation or *piloting* (Gallistel, 1990). When piloting, organisms must be able to learn and remember both distance and directional information from one or more landmarks. If multiple landmarks are available, an organism can either encode the location of the goal as a specific distance and direction from a single landmark or in terms of the goal's spatial relationship to two or more landmarks. Search pattern based on the former is often referred to as an absolute strategy whereas the latter is referred to as a relational strategy.

Spetch, Cheng and MacDonald (1996) used a comparative approach to examine whether pigeons and adult humans use absolute or relational strategies when searching for a hidden goal. Both pigeons and humans were trained to search for a goal in the center of a square array of landmarks. On pivotal test trials, the landmark array was expanded either horizontally, to create a rectangular shape, or diagonally, creating a larger square. On both types of expansions, humans continued to search in the center of the array, suggesting use of a relational strategy. In contrast, pigeons searched at locations that matched the learned distance and direction from a single landmark, suggesting use of an absolute strategy. This pattern of results was consistent across open field, table-top and computer tasks for humans, and across open field and touchscreen tasks for pigeons (Spetch et al., 1996; Spetch et al., 1997). Other non-human animals, such as Clark's nutcrackers (Kelly, Kippenbrock, Templeton & Kamil, 2009), gerbils (Collett, Cartwright & Smith, 1986) and nonhuman primates (MacDonald, Spetch, Kelly, & Cheng, 2004; Poti, Bartolommei, & Saporiti, 2005; Sutton, Olthof, & Roberts, 2000) have also been shown to use absolute strategies when searching within landmark arrays.

The use of absolute strategies by non-human animals seems to reflect a preference rather than a limitation of ability. For example, both pigeons (Jones, Antoniadis, Shettleworth, & Kamil, 2002; Spetch, Rust, Kamil, & Jones, 2003) and Clark's nutcrackers (Kamil & Jones, 1997, 2000) will use the spatial relationship between landmarks to find a goal if they are trained with multiple exemplars. Additionally, pigeons (Gray et al., 2004) and chicks (Tommasi et al) will sometimes use relational strategies when searching for the center of an enclosed arena.

Orientation cues, or an animals' ability to maintain a stable directional frame of reference, may play a role in strategy preference or selection. Gray and Spetch (2006) trained pigeons to search in the center of either a square array of landmarks or a set of short walls that did not block external cues. On expansion trials, both groups of pigeons searched according to an absolute distance strategy, indicating that strategy preference is not dependent on cue type (i.e., landmarks or continuous surfaces). In another study, Sturz and Katz (2009) found that disoriented pigeons would use a relational strategy to find the middle of a two landmark array. That is, when trained in the absence of orienting cues, pigeons continued to search in the middle of the array on expansion trials rather than at the absolute learned distance. Overall, these results suggest that, although animals may prefer to use an absolute strategy, they are capable of learning and using relational strategies in some situations.

When it comes to the preferred strategy of human children, however, the results are mixed. MacDonald et al. (2004) examined children's (age 5-9 years) search strategies when searching for the center of a square array of landmarks. In one study, participants (children and adults) were presented with a grid of discrete locations; the landmarks formed a square around the goal location and were diagonally adjacent to it. On expansion trials, adults searched at the center location of the array. On the other hand, children tended to choose locations that were directly adjacent to the landmarks, indicating that they used the landmarks as beacons. In a follow-up experiment, MacDonald et al. used a continuous search space and landmarks that were further from the goal. However, this proved to be a difficult task for the children to learn. Approximately half of the children were able to learn the task, and of those, only a few searched according to a relational strategy on expansion tasks.

In contrast, Uttal, Sandstrom and Newcombe (2006) found that children (age 4-5 years) readily used spatial relationships in larger scale open-field task. In their study, children were required to search for a toy between two landmarks that were 6 meters apart in a field. On expansion trials, children continued to search in the middle of the two landmarks. Additionally, when tested with only one landmark, children searched at the learned distance and direction from the available landmark. In this case, children seem to have learned the location of the goal according to both absolute and relational strategies, but preferred the relational strategy on expansion tests.

Spetch and Parent (2006) found age and sex differences in how easily children were able to acquire a similar, but smaller-scale, task. Children (age 3-5 years) were asked to look for a sticker hidden between two landmarks spaced approximately 15 cm apart. As in the MacDonald et al. (2004) study, this seemed to be a difficult task for the children to learn; only 37% of the children acquired the task within 20 training trials. Older children (i.e., the five year olds) and boys tended to acquire the task more easily than young children and girls. On the expansion test, most children chose the middle location; however, several children still chose a location based on an absolute strategy.

Despite these many studies examining the use of a 'center' or 'middle' relation, few studies have looked at other goal-landmark relationships or, more specifically, how search strategies may change based on the goal location. In particular, although studies have shown that animals are capable of using other spatial relationships, such as 'quarter-way' or triangular shapes (Kamil & Jones, 2000; Spetch et al., 2003), there is little research examining how an individual's search strategy may change according to different spatial relations. One study that has looked at this topic was conducted by Hartley, Trinkler and Burgess (2004). In their study, they used a video-game-like virtual environment to study how adults remember different locations in a working memory task. Participants explored a virtual environment of a square or rectangular open arena, with distal visual cues for orientation. Participants were required to locate a cue item within the arena; after finding the item, they were briefly removed from the arena. They were then returned to a test arena, which, on some trials, was expanded or contracted along one or both axes. Participants were asked to place a marker object where they had found the (now absent) cue item. On expansion trials, participants tended to place the marker according to an absolute strategy when the goal location was near the boundary of the virtual arena. However, if the cue item had been closer to the center of the arena, participants were more likely to use a relational strategy. Their results support the idea that preference for absolute or relational strategies can vary according to situation.

In the current studies, I wanted to extend the findings of Hartley et al. (2004) and determine whether similar strategies are used on a smaller scale and with simpler, non-immersive stimuli. The use of simple stimuli to study strategy preference can help me to determine whether search strategies may differ based on the scale and complexity of the environment, as well as provide a base for comparative studies with children, as discussed in Experiment 2, and future studies with animals.

Experiment 1

In Experiment 1, I investigated the strategies used by adults in a working memory task similar to that of Hartley et al. (2004). In this study, I used simple stimuli and a larger variety of goal locations than Hartley et al. Participants were trained to remember the location of a goal within a simple white square presented on a computer screen. The precise location of the goal varied from trial to trial so that I could compare how search strategies may change based on the goal's proximity to the boundary of the square. That is, if closer boundaries exert more influence, I would expect search patterns to differ according to the different goal locations.

Methods

Participants

The participants were 60 undergraduate students from the University of Alberta, Edmonton, Canada. They received course credit in their introductory psychology class for their participation. Participants were randomly assigned to one of two conditions with the constraint that each condition have an equal number of participants: Big Expansion group (20 females, 10 males) and Small Expansion group (22 females, 8 males). Ages ranged from 18 to 31 years old, with a mean age of 19.8.

Apparatus, Stimuli and Procedure

Participants were seated in front of a 17-in monitor with a resolution of 1280 × 1024 pixels. Participants were instructed that they would be required to remember the location of a target, a red star, within a limited search space, a white square. They were told that a white square with a red star somewhere in it would appear on the computer screen at the beginning of each trial. Their task was to remember where the red star was within the square. The experimenter explained that they should click on the star once they had memorized its location, and the star and square would then disappear and the white square only would appear somewhere else on the screen. Participants were instructed to click on the location within the square where they thought the star had been. They were told that on some trials, the star would reappear to show them how close their guess had been. Participants were informed that their participation was voluntary, and consent was obtained before continuing with the experiment.

Following the verbal instructions, participants read an additional set of instructions on the computer screen that re-stated the procedure. At the beginning of each trial, a white display square (10cm × 10cm) appeared on a grey background in a random location on the screen. A red star (1cm × 1cm) marked the goal location within the display square. The goal location varied from trial to trial on a 5x5 grid (25 possible goal locations). The goal locations were categorized according to the goal's distance to the x- and y- axes to create 6 distinct locations: edge/edge, edge/intermediate, edge/center, intermediate/intermediate, intermediate/center, center/center (see Figure 5-1A). The participant was required to click on the red star before proceeding to the test display. If the participant did not click the red star within 10 seconds, the trial was terminated and a screen appeared with text reminding the participant that they must click on the red star in order to continue. Participants failed to click the red star on less that 1% of all trials.

After clicking the red star, the display square (and red star) disappeared from the screen. The screen was blank for 1s before a white test square appeared at a different random location on the screen. The goal location was not marked in the test square. A schematic of the training and test trials is shown in Figure 5-1B and 5-1C.

During training trials, the test square was the same size as the display square. Once the participants clicked at a location within the test square, a small black circle appeared to mark their choice location. After a 500ms delay, the red star would reappear at the same grid location that it had appeared at during the display screen. If the participant's choice was within 1.5 cm of the center of the red star, it was counted as a 'correct' trial and the participant scored 1 point. A screen displaying the point tally was displayed every 5 trials. All participants received at least 12 training trials in which the goal location appeared twice in each of the six distinct locations. If the participant did not reach a criterion of at least 75% correct after the first 12 training trials, they repeated the training trials before moving onto the testing phase.

During the testing phase, 36 probe test trials were intermixed with 72 training trials for a total of 108 trials. No feedback was available on the probe test trials; as in the training trials, a small black circle appeared when the participants clicked the mouse button, however, the red star would not reappear and no point was scored. On test trials, the display square was the same size as on training trials, but the test square was expanded in one of three ways: diagonally (in which both the horizontal and vertical dimensions were expanded), horizontally or vertically.   In the Big Expansion group, the affected sides of the test square were increased to double the length of the display square. In the Small Expansion group, the sides were increased to 1.5 times the length of the display square.

Participants received two of each type of expansion trial for each of the six distinct locations, although the specific location was randomized (i.e., an edge/edge goal location could be any of the four corners).

Data Analysis

Each search was recorded as a set of x and y coordinates, which were then converted to a percent of the total length of the sides in order to compare across conditions. In order to examine whether subjects may have been organizing their search according to the goal's proximity to the edge, I collapsed the search coordinates across 3 different proximities: edge, intermediate and center. For edge proximity, I measured the straight line distance from each search to the edge of the search space for (1) x and (2) y coordinates for the Edge/Edge location, (3) the x coordinate for the Edge/Intermediate Location, and (4) the x coordinate for the Edge/Center location. For intermediate proximity, I measured the straight line distance from each search to the edge of the search space for (1) y coordinate for the Edge/Intermediate location, (2) the x and (3) y coordinates for the Intermediate /Intermediate Location, and (4) the x coordinate for the Intermediate/Center location. For the center proximity, I measured the straight line distance from each search to the edge of the search space for (1) y coordinate for the Edge/Center location, (2) the y coordinates for the Intermediate /Center Location, and (3) the x and (4) the y coordinates for the Center/Center location.

Results

Control performance

I first calculated the median search distance and inter-quartile range of searching at each proximity on training trials in order to ensure that participants learned the task. Since training trials were identical for both conditions, I used the data from both the Big Expansion and Small Expansion groups for this analysis. At the edge proximity, the distance from the edge of the search space to the goal was 10% of the total length of the search space. Participants were remarkably accurate at locating the goal location when there was no change between the display and test square. The median search distance was 10.0%, with an interquartile range of 0.75. At the intermediate proximity, the goal was located at a distance of 30%. The median search distance was 30.0% with an interquartile range of 0.75. At the center proximity, the goal was located at a distance of 50%. Again, the median search location was 50.0%, and the interquartile range was 0.75.

Response Density by Location

For the purpose of visualizing search patterns, the response density of searches for each group was calculated by counting the number of responses in each bin of a 21 × 21 grid, measuring from -2.5% to 102.5% of the search area (i.e., grid sections were 5 × 5 percent units). The size of grid sections was chosen such that the goal according to absolute and relational strategies would fall into different grid sections. The search density for each of the six distinct goal locations for the Big Expansion Group is shown in Figure 5-2. For the Small

Expansion group, the search density for each of the six distinct goal locations is shown in Figure 5-3.

Absolute vs. Relational Searching

The median distance and spread of all search distances at each proximity for each group can be seen in Figure 5-4. To compare the frequency of choices in the area corresponding to the absolute distance with the frequency of choices in the area corresponding to the relational distance at each proximity, I used replicated G-tests for Goodness of Fit (Sokal & Rohlf, 1995). The G-test is distributed as a chi-square but allows one to pool data from all subjects (pooled G: G_P), as well as to separate variance due to individual groups (test for homogeneity: G_H), in this case, males and female.

Edge proximity. For the edge proximity, the absolute goal location would be at a distance of 5% for the Big Expansion group and 6.7% for the Small Expansion group. The relational goal location would be at a distance of 10% for both groups. The median search distance was 7.8% for the Big Expansion group and 9.3% for the Small Expansion group. I used a G-test to compare the number of searches falling in the absolute range (2.5-7.5) to the number of searches within the relational range (7.5-12.5) using each sex in each group as separate samples (i.e., males in the big expansion group, females in the big expansion group, males in the small expansion group and females in the small expansion group were all compared against each other). The G-test revealed significant differences between the four samples ($G_H(3)=35.24$, $p<0.001$). Further comparisons revealed that there were no significant differences between the males in the Big Expansion group and males in the Small Expansion group ($G_H(1)=0.13$, $p=0.721$), but there were significant differences between the females in each group ($G_H(1)=34.95$, $p<0.001$). Men in both groups tended to split their searches equally among both ranges ($G_P(1)=0.19$, $p=0.660$). Women in the Big Expansion group made significantly more searches within the absolute range ($G_{Big}(1)=18.53$, $p<0.001$) whereas women in the Small Expansion group made significantly more searches within the relational range ($G_{Small}(1)=16.42$, $p<0.001$).

In the Big Expansion group, searches in both regions combined accounted for 86% of all searches for women and 96% for men. For the Small Expansion group, searches in both regions combined accounted for 85% of all searches for women and 81% for men.

Intermediate proximity. At this proximity, the absolute goal location would be at a distance of 15% for the Big Expansion group and 20% for the Small Expansion group. The relational goal location would be at a distance of 30% for both groups. For the Big Expansion group, the median search distance was 24.6%. The median search distance for the Small Expansion group was 26.4%. I compared the number of searches falling in the absolute range (Big Expansion: 12.5-17.5, Small Expansion: 17.5-22.5) to the number of searches within the relational range (27.5-32.5) for each sex and group. Again, there was a significant difference between the four samples ($G_H(3) = 8.15$, $p=0.043$). Further comparisons revealed that, again, there were no significant differences between the males in each group ($G_H(1)=0.25$, $p=0.620$). Men continued to split their searches equally among both ranges ($G_P(1)=0.40$,$p=0.529$). There were significant differences between the females in each group ($G_H(1)=4.96$, $p=0.026$), however, both groups of women made significantly more searches within the relational range ($G_{Big}(1)=17.65$, $p<0.001$; $G_{Small}(1)=4.40$, $p=0.036$).

Searches in both regions combined account for only 30% for men and 34% of all searches for women in the Big Expansion group., In this group, for males, the interior range between the absolute and relational area (17.5-27.5) contained the bulk of searches (61%). Within this interior range, the searches were spread fairly evenly with 29% falling in the 17.5-22.5 area range and 32% in the 22.5-27.5 range. Females made 46% of their searches within the interior range, with 18% falling in the 17.5-22.5 area range and 28% in the 22.5-27.5 range.

In the Small Expansion group, searches in both the absolute and relational regions accounted for 61% of all searches for men and57% for women. For this group, there was only one bin between the absolute region and relational region (22.5-27.5). Males made 27% of their searches and females made 26% of the searches within the interior bin.

Center proximity. At this proximity, the absolute goal location would be at a distance of 25% and 33.3% for the Big and Small Expansion groups respectively, and the relational goal location would be at a distance of 50%. The median search distance at the center locations was 50.1% for the Big Expansion Group and 49.8% for the Small Expansion group. I compared the number of searches falling in the absolute range (Big Expansion group: 22.5-27.5, Small Expansion group: 32.5-37.5) to the number of searches within the relational range

(47.5-52.5) for each sex and group. Here, there were no differences between the four samples ($G_H(3)=1.97$, $p=0.578$) and searches were highly concentrated within the relational range ($G_P(1)=471.48$, $p<0.001$). There were only four total searches in the absolute range.

Females in the Big Expansion group made 75% of their searches and men made 81% of their searches within the relational area. In the Small Expansion group, females made 76% of their searches and males made 78% of their searches within the relational area.

Spread

I examined the spread of searches at each proximity in two ways. First, I calculated an average search distance and standard deviation for each subject at each proximity. I compared the standard deviations for each subject as a measure of within-subject variability. That is, if subjects switched search strategies between trials (sometimes searching at the absolute location and sometime searching at the relational location), subjects would have a larger standard deviation around their mean search distance. Second, I calculated the absolute deviation between the subject's average and the overall average as a variance score to measure between-subject variability. Specifically, if a subject consistently used one strategy (e.g., always searched at the absolute location), they may have a small standard deviation, but may vary more widely from the overall mean.

The comparison of within-subject standard deviations revealed a significant main effect of proximity ($F(2,112)=14.726$, $p<0.001$) and of gender

(F(1,56)=4.50, p=0.038), but no effect of expansion size (F(1,56)=0.01, p=0.981). Females had larger standard deviations than males (females: M=3.84, SD=0.209, males: M=3.03, SD=0.322). Pairwise comparisons on the three proximities (using Bonferroni adjustments) revealed that the spread at the intermediate level (M = 4.85, SD=0.299), was significantly different from both the edge proximity (M=2.62, SD=0.262; p<0.001) and the center proximity (M=2.84, SD=0.397; p<0.001). Spread at the edge and center proximities did not differ from each other (p=1.000).

A comparison of the variance scores also revealed a significant main effect of proximity (F(2,112)=10.91, p<0.001) with no effect of expansion size (F(1,56)=1.01, p=0.319) or gender (F(1,56)=0.29, p=0.590). There were no significant interactions. Pairwise comparisons (using Bonferroni adjustments) again revealed that the spread at the intermediate level (M = 2.82, SD=0.329), was significantly different from both the edge proximity (M=1.83, SD=0.206; p=0.033) and the center proximity (M=1.18, SD=0.198; p<0.001). There was a marginally significant difference between the variance scores at the edge and center proximities (p=0.060).

Comparison to Horizontal and Vertical Expansions

In order to determine whether subjects used similar strategies as above when searching on the horizontal and vertical expansions, I used a mixed model ANOVA at each proximity to compare subjects' average search distance on diagonal expansion and horizontal or vertical expansions. That is, for each subject, I determined their average search distance from the edge of the search space (for each proximity) on diagonal expansions and on horizontal and vertical expansions. For these comparisons, I collapsed across horizontal and vertical expansions, and looked only at the search proximities along the expanded axis. The median distance and spread of all search distances at each proximity for the horizontal and vertical expansions can be seen in Figure 5-5.

At the edge proximity, there was no difference between subjects' average search distance on diagonal (*M* = 8.78, SD=0.328) and horizontal/vertical expansions (*M* = 8.74, SD=0.524; F(1,56)=0.01, p=0.938) and no effect of gender (F(1,56)=0.07, p=0.799). There was, however, a significant main effect of expansion size (F(1,56)=4.89, p=0.031). Participants in the Big Expansion group tended to search closer to the edge (M=8.01, SD=0.464) than participants in the Small Expansion group (M=9.51, SD=0.495). There were no significant interactions.

At the intermediate proximity, there was a significant main effect of the expansion type (diagonal or horizontal/vertical, F(1,56)=10.20, p=0.002), as well as a significant interaction between expansion type and gender (F(1,56)=4.69, p=0.035). Overall, subjects tended to search closer to the edge on horizontal/vertical expansions (M=23.40, SD=0.654) than on diagonal expansions (M=25.27, SD=0.517). For males, the difference between search distances on the two expansion types was smaller than for females (diagonal search distance – horizontal/vertical search distance: males = 0.60, females = 3.14).

Finally, at the center proximity, there was no difference between subjects' average search distance on diagonal (*M* = 49.95, SD=0.256) and horizontal/vertical expansions (*M* = 50.20, SD=0.391; F(1,56)=0.42, p=0.518) and no effect of gender (F(1,56)=0.37, p=0.544) or expansion size (F(1,56)=0.04, p=0.851).

Discussion

The results of this study reveal several interesting findings. First, although participants all readily used a relational strategy when the goal was in the center of the search space, they did not use purely relational strategies when the goal was located at other proximities. Moreover, the search patterns at proximities other than the center varied by gender. In particular, the search patterns of women at the edge and intermediate proximities differed significantly from the search patterns of men. Specifically, at both the edge and intermediate proximities, men searched equally in both the absolute and relational ranges. On the other hand, women searched significantly more in the relational region at the intermediate proximity. At the edge proximity, women's search strategies depended on the expansion size; with smaller expansions, they tended to search most at the relational region whereas with larger expansions, they searched most in the absolute region.

Second, women's search patterns tended to be more affected by expansion size and type than men's. That is, men's search strategies seemed to be consistent across the Big and Small Expansion groups. In contrast, women's search strategies showed significant differences between the Big and Small Expansion groups at both the edge and intermediate proximities. Additionally, at the intermediate proximity, there was a larger difference between women's search patterns on diagonal and horizontal/vertical expansion than was observed for men.

Finally, there were significant differences in measures of both within subject and between subject variability at the different proximities. Participants displayed more varied searching, both within and between subjects, at the intermediate proximity than at the edge and center proximities. In particular, at the intermediate proximity, the larger spread of searching and the high frequency of searches between the absolute and relational regions suggests that participants may be averaging strategies or switching between strategies. Although women were more likely to search in the relational range, they also displayed higher within-subject standard deviations of searching. That is, women tended to be more variable in their searches across trials.

Overall, my results partially replicate those of Hartley et al. (2004). In particular, the pattern of results found here and by Hartley et al. suggest that strategy preferences are flexible, situation specific, and more complex than a simple "relational rule". In contrast to Hartley et al's results, I found several significant differences between the search strategies employed by men and women. Additionally, search patterns reflected an absolute strategy only in the case of women searching for a goal near an edge.

Experiment 2

In Experiment 2, children were tested in a similar paradigm to determine how their search strategies may change based on boundary information. In particular, previous results have been mixed as to whether children prefer absolute or relational strategies (e.g., MacDonald et al., 2004; Uttal et al., 2006). However, previous work has concentrated on the use of a ‘center’ rule with reference memory tasks. In the current study, I examined how children’s search strategies may change based on the goal’s proximity to an edge. Moreover, I used a working memory paradigm similar to Experiment 1.

Methods

Participants

40 children, aged 41-62 months (M=52.8 months) completed the study. The children were recruited from two daycare centers in Atlanta, through letters sent to parents. The Georgia State University Institutional Review Board and the University of Alberta Human Ethics Committee approved the recruitment and experimental procedures. All of the parents signed a consent form on behalf of their children. The children were asked if they wanted to “play the game” after it was explained to them, and they were told that they could stop playing at any time.

Apparatus, Stimuli and Procedure

The children were tested individually in a private location within the day-care centers. The experiment was conducted on a portable tablet computer with a widescreen 12.1 inch display and resolution of 1280 × 800 pixels. The display could swivel 180° and fold down to be laid flat on a table. The children interacted with the computer using a stylus pen.

The program began with an instructional phase during which the children were shown how to use the stylus and given time to practice using it. After this instructional phase, the experimenter advanced the program to show a picture of cat. The experimenter told the child that the cat liked to be petted with the stylus; the child was allowed to practice “petting” the cat and a sound (either a “purr” or “meow”) was played when the stylus contacted the picture of the cat.

The experimenter then explained that the cat liked to hide in the “garden” (a 10 × 10 cm black square on a green background). A picture of the cat (1.5 × 1.5 cm) was shown within the black square and the child watched as it faded away. The experimenter told the child that it was their job to remember where, within the garden, the cat was hiding and that although the garden might move about on the computer screen, the cat would be in the place in the garden that they last saw it hide.

The children then completed a second practice phase. In this phase, a display screen appeared with the cat (goal) visible within the garden (search space). The child was required to tap the cat with the stylus, at which point the cat and search space would disappear. After 1s, a test square (without the cat) appeared somewhere else on the screen. The child was asked to use the stylus to “dig” in the garden where they thought the cat was hiding. A small white circle appeared at the location where they pressed the stylus. After one search, the cat reappeared. If their search was not within 2 cm of the center of the goal, the child was allowed to correct their choice after the cat reappeared (i.e., they used the stylus to tap the now visible cat). If their initial search was within 2 cm of the goal, a “meow” would sound when the cat reappeared, the experimenter said “Good job! You found him!” and the program advanced to a training phase.

Trials during the training phase proceeded similarly to the practice trials except that the children were not allowed to correct their choices after the cat appeared. If the initial search was not within 2 cm of the goal area, no “meow” was sounded when the cat reappeared and the experimenter said “There he is. Let’s try again”. Children received at least 6 training trials, with the goal appearing once in each of the 6 distinct locations as described in Experiment 1. If the child was correct on at least 4/6 of the training trials, they moved on to the testing phase. If they did not get a minimum of 4/6 trials correct, they repeated the 6 training trials.

During the testing phase, 6 probe trials were intermixed with 9 regular training trials. During test trials, the size of the ‘garden’ increased to 15 × 15 cm after the cat hid and the cat did not reappear after the child made a choice. On these trials, the experimenter said that the cat was still hiding. The children received one test trial for each of the 6 distinct locations.

Data Analysis

Search coordinates were coded and divided into proximities using the same procedures as in Experiment 1.

Results

Control Performace

The task proved to be difficult for the children to learn. Only 21 of the 40 children reached the testing phase, and of those only 14 completed the testing phase. However, upon reaching the testing phase, the main reason for not completing the testing phase appeared to be fatigue rather than inability, so partial data from the children who did not complete testing were included in the results.

The children tended to have more variable responses than the adults, so to measure control performace, I calculated the iterated median search distance and inter-quartile range (of the iterated range) of searching at each proximity on training trials in order to ensure that children learned the task. At the edge proximity, the distance from the edge of the search space to the goal was 10% of the total length of the search space. The median search distance was 9.1%, with an interquartile range of 5.23. At the intermediate proximity, the goal was located at a distance of 30%. The median search distance was 32.7% with an interquartile range of 14.42. At the center proximity, the goal was located at a distance of 50%. The median search location was 50.0, and the interquartile range was 13.58.

Response Density by Location

As in Experiment 1, each search was recorded as a set of x and y coordinates, which were then converted to a percent of the total length of the sides in order to compare across conditions. Response densities were calculated and graphed in order to provide a visual display of search patterns. For the edge proximity, the response density of searches was calculated by counting the number of response in each bin of a 21 × 21 grid, measuring from -2.5% to 102.5% of the search area (i.e., grid secions were 5 × 5 percent units). Since responding was more variable for the intermediate and center proximities, the response density of searches was calculated by counting the number of responses in each bin of a 11 × 11 grid, measuring from -5% to 105% of the search area (i.e., grid sections were 10 × 10 percent units). The size of grid sections was chosen such that the goal according absolute and relational strategies would fall into different grid sections. The search density for each of the six distinct goal locations is shown in Figure 5-6.

Absolute vs Relational Searching

As in Experiment 1, I collapsed the search coordinates across 3 different proximities: edge, intermediate and center. The median distance and spread of all search distances at each proximity can be seen in Figure 5-7. Frequency of choices in the areas corresponding to the absolute distance and relational distance at each proximity were compared using a replicated G-tests for Goodness of Fit (Sokal & Rohlf, 1995), using males and females as separate groups. Values that were more than 3 standard deviations from the mean were excluded from analysis; this resulted in the removal of 5 values at the edge proximity and 2 values at the center proximity.

Edge proximity. The median search distance at each of the locations collapsed into the edge proximity (as described in the Data Analysis section of Experiment 1) were 6.71, 6.50, 8.71, and 10.70, respectively. At this proximity, the absolute goal location would be at a distance of 6.7 and the relational goal location would be at a distance of 10. Since most of the searches were concentrated in the corners, for this analysis I used smaller grid sizes of 5 × 5 to compare the number of searches falling in the absolute range (2.5-7.5) to the number of searches within the relational range (7.5-12.5). There were no significant differences between males and females ($G_H(1) = 0.16$, $p=0.685$) and children searched equally in both regions ($G_P(1)=0.58$, $p=0.445$). Overall, 63% of searches fell into these two regions.

Intermediate proximity. The median search distance at each of the locations collapsed into the intermediate proximity were 38.42, 26.02, 35.59, and 16.73, respectively. At this proximity, the absolute goal location would be at a distance of 20 and the relational goal location would be at a distance of 30. I compared the number of searches falling in the absolute range (15-25) to the number of searches within the relational range (25-35). Again, there were no significant differences between males and females ($G_H(1) = 0.41$, $p=0.523$) and children searched equally in both regions ($G_P(1)=0.13$, $p=0.715$). At this proximity, searches in both regions combined account for only 38% of all searches.

Center proximity. The median search distance at each of the center locations were 45.53, 55.93, 42.14, and 49.15, respectively. At this proximity, the absolute goal location would be at a distance of 33 and the relational goal location would be at a distance of 50. I compared the number of searches falling in the absolute range (25-35) to the number of searches within the relational range (45-55). Although there was no significant difference between males and females ($G_H(1)=0.21$, $p=0.650$), males showed a marginally significant preference for searching in the relational region ($G=3.29$, $p=0.070$) whereas females did not show a significant preference ($G=1.33$, $p=0.249$). Overall, the pooled-G revealed significantly more searches in the relational region ($G_P(1)=4.42$, $p=0.036$).

Overall, males searched in the relational region 44% of the time and in the absolute region 19% of the time. They made only 9% of their searches in the interior range between the relational and absolute regions. Females made 28% of their searches in the relational range and 16% of their searches in the absolute region. They made 16% of their searches in the interior range between the relational and absolute regions.

Spread.

As in Experiment 1, I measured spread both by examining the standard deviations of each subject and the subjects' variance from the overall mean. The comparison of standard deviations revealed a significant main effect of proximity (F(2,24)=4.18, p=0.028) but no effect of gender (F(1,12)=1.58, p=0.223). Pairwise comparisons (using Bonferroni adjustments) revealed that the spread at the edge proximity (M=6.253, SD=1.805) was significantly different from the intermediate proximity (M=11.981, SD=1.519; p=0.014). The standard deviations at the center proximity (M=10.405, SD=1.203) did not differ from either the edge proximity (p=0.292) or the intermediate proximity (p=1.000). There were no significant differences between the variance scores at the different proximities (F(2,24)=2.32, p=0.120) or between genders (F(1,12)=0.01, p=0.907).

Discussion

Despite the difficulties in learning the task, children that did learn centered their searches around the correct goal location on training trials, although the spread was substantially higher than adults in Experiment 1. Both during training and expansion trials, children were most accurate when searching near the edge of the enclosure, suggesting that proximity to the boundary exerts a large influence on children's search patterns.

As with the adults, the spread of searches was highest at the intermediate proximity. However, unlike the adults, children continued to have a high spread of searches at the center region, indicating less adherence to a strict relational strategy. Additionally, for the children, the larger variability seemed to be predominantly within subjects; that is, children had higher standard deviations at the intermediate and center proximities, but there was no difference in the calculated variance scores across proximities. This suggests that children more frequently switched search strategies between trials (sometimes searching at the absolute location and sometime searching at the relational location), contributing to larger standard deviations around their mean search distance.

Although there was not a significant difference, males appeared to search in the center region more than females when the goal was at the center proximity. This trend is consistent with the findings of Spetch and Parent (2006) that boys were able to learn to search in the middle of two landmarks more easily than girls. Interestingly, the boys tended not to make many searches in between the absolute and relational regions, suggesting that boys may have search according to either an absolute or relational strategy. In contrast, girls were more likely to spread their search between the two regions, perhaps indicating that they averaged the two strategies more than the boys.

General Discussion

Overall, both children and adults tended to adjust their search patterns based on the goal's proximity to the boundary of the search space, indicating that search strategy preferences are flexible and may be situation-specific. The sex differences observed in Experiment 1 was a new and unexpected result. Although sex differences have previously been reported in a variety spatial navigation tasks (e.g Astur, Ortiz, & Sutherland, 1998; Dabbs, Chang, Strong, & Milun, 1998; Kelly & Bischof, 2005; MacFadden, Elias, & Saucier, 2003; Sandstrom, Kaufman, & Huettel, 1998; Saucier, Bowman, & Elias, 2003), most have focused on men and women's differential use of geometric and featural information. In particular, studies have shown that females tend to rely more upon featural or landmark information whereas men prefer more geometric-based information. What is interesting about the current findings is that sex differences were found in the absence of distinctive featural information.

The current study revealed that men tended to be less variable in their search patterns than women. This could be construed to support previous findings in that men were able to use geometric information to search more accurately. However, although women were more variable in their search patterns, they were also more likely than men to search according to a relational strategy at the intermediate proximity. In this way, women seemed more likely than men to rely on the overall (i.e., relational) shape of the search space. Overall, the sex differences appear to be somewhat mixed, and warrant further investigation.

Our results also provide some support for the sex differences in children observed by Spetch and Parent (2006). However, unlike the adults, sex differences in children appear to be in how well children are able to use a relational ‘center’ rule. In particular, boys tended to search in the center region more than girls.

Another notable result of my study was that the spread of searches for both children and adults was highest at the intermediate proximity. At this proximity, adults tended to mainly search in between the absolute and relational areas, suggesting that they may be averaging strategies or perhaps switching strategies across trials. However, with children, the visual representation (see Figure 5-7) of their searches shows such dramatic variability that the larger spread may simply represent a greater level of uncertainty. Specifically, the response densities at the Intermediate/Intermediate location show a pattern of searching that extends well beyond the relational goal location, and at both the Edge/Intermediate and Intermediate/Center locations, the peak areas of searching do not match with either the absolute or relational areas. Additionally, even during training trials, the intermediate proximity had the widest range of searches.

Studies with Clark’s nutcrackers have shown that some geometric relationships may be easier to learn than others (Kamil & Jones, 2000). With the nutcrackers, however, the easiest learned rule was a ‘quarter-way’ relation, which was learned more easily than either a ‘middle’ relation or triangular relations. In that case, the nutcrackers may have learned the quarter-way relationship most easily since the goal was close to a landmark. This would stand in contrast to my pattern of results. Specifically, at the intermediate proximity, the goal is closer to the boundaries and corners of the search space than at the center proximity. If the ease of learning the geometric relation was based only on proximity, children (and adults, for that matter) should have learned the intermediate proximity better than the center proximity and thus, would have had less uncertainty for these locations.

With the adults, the spread of searches reduced dramatically at the center proximity whereas children's spread of searches remained high at the center proximity. That the adults were much more accurate at the center locations is consistent with previous findings that adults tend to prefer relational strategies (Spetch et al., 1996, 1997; MacDonald et al. 2004). For children, although the spread remained high, the peak areas of responding (see Figure 5-7) for the Edge/Center and Center/Center locations does correspond with the relational goal area, which may indicate less uncertainty than at the intermediate proximity. Additionally, children made proportionally more responses in the 'appropriate' ranges for the center proximity (52% of searches were in the absolute or relational ranges) than for the intermediate proximity (38% of searches were in the absolute or relational ranges). Thus, although spread was high for both intermediate and center proximities, children seemed to learn the center relationship more easily than the intermediate relationship.

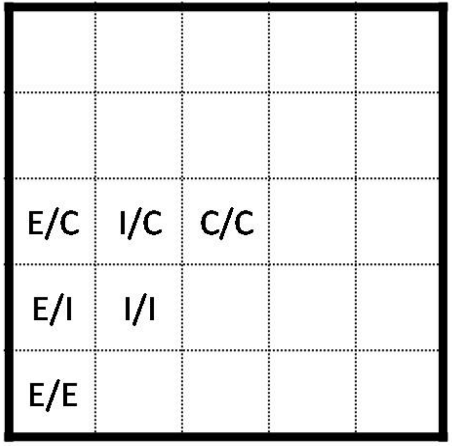
Children also tended to respond more in the center region than at the absolute distance for the center proximity, supporting the idea that children are able to use relational strategies (Spetch & Parent, 2006; Uttal et al., 2006). However, like MacDonald et al. (2004) and Spetch and Parent (2006), the task seemed difficult for the children to acquire. This difficulty in task acquisition may be an issue of scale; the studies by MacDonald et al. and Spetch and Parent, along with the current study, all used small-scale stimuli. In contrast, Uttal et al. (2006) tested children in an open-field with larger-scale landmarks. Perhaps immersion in the test environment may facilitate the use of relational strategies in children.

Indeed, immersion in the test environment could also help explain the differences between my results in Experiment 1 and the results of Hartley et al. (2004). Specifically, Hartley et al. found that adults' search patterns matched an absolute strategy when the goal was close to a boundary, whereas my results did not clearly show use of an absolute strategy. Specifically, males in Experiment 1 tended to split searches between the absolute and relational areas, and females search strategies at the edge proximity depended on the amount that the test environment was expanded. Although Spetch et al. (1996, 1997) compared adults in small scale, non-immersive tasks and large-scale open-field tasks, only a 'center' relationship was used. Both the current results and those of Hartley et al. (2004) support the previous findings and show that adults prefer a relational strategy when the goal is in the center. Future studies could help to determine whether the differences between the virtual environment used by Hartley et al. and the simple stimuli used in the current study can account for the different pattern of results at goal locations other than the center.

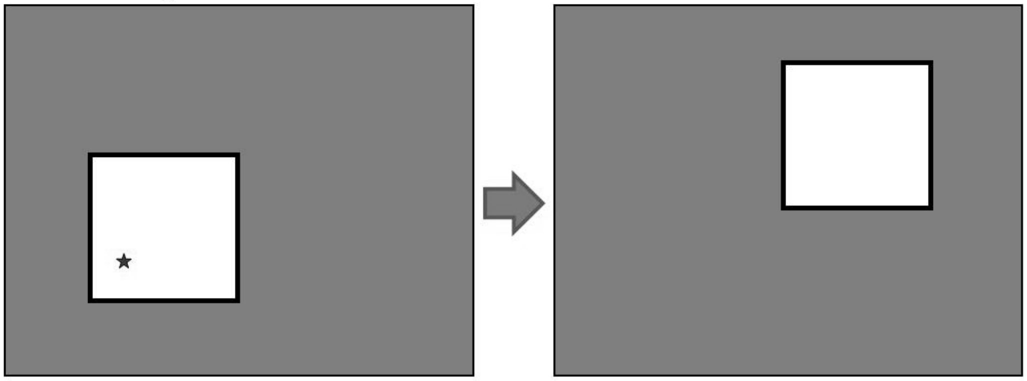
In sum, my results show that strategy use and preference is malleable, and varies according to the goal's proximity to a boundary of the search space. Both adults and children may change strategies based on a goal's specific location within a limited search space. Intermediate locations appeared to create the greatest amount of variability in search patterns for both adults and children, and may reflect an area where search strategies are averaged or an area of greater uncertainty. Additionally, there appear to be sex differences in strategy use for adults at non-center locations. my results also provide support for the sex differences in children found by Spetch and Parent (2006), where boys made more searches according to a relational strategy than girls.

Figure 5-1. (A) Schematic of the six geometrically distinct goal locations; “E” stands for edge, “I” stands for intermediate and “C” stands for center. Each distinct location is defined by its proximity to both the horizontal and vertical edges. (B) Schematic of a training trial. (C) Schematic of a diagonal expansion test trial in the Big Expansion group.

A. Locations Types



B. Training Trial



C. Test Trial: Diagonal Expansion (Big)

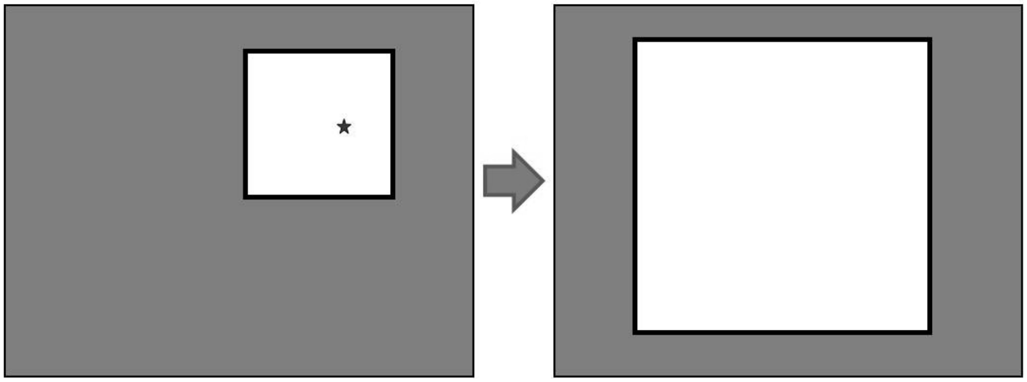


Figure 5-2. Response densities at each of the six distinct locations on Diagonal Expansion test trials for the Big Expansion group. Darker regions indicate higher proportion of searches. White circles represent the relational goal location and white triangles represent the absolute goal location.

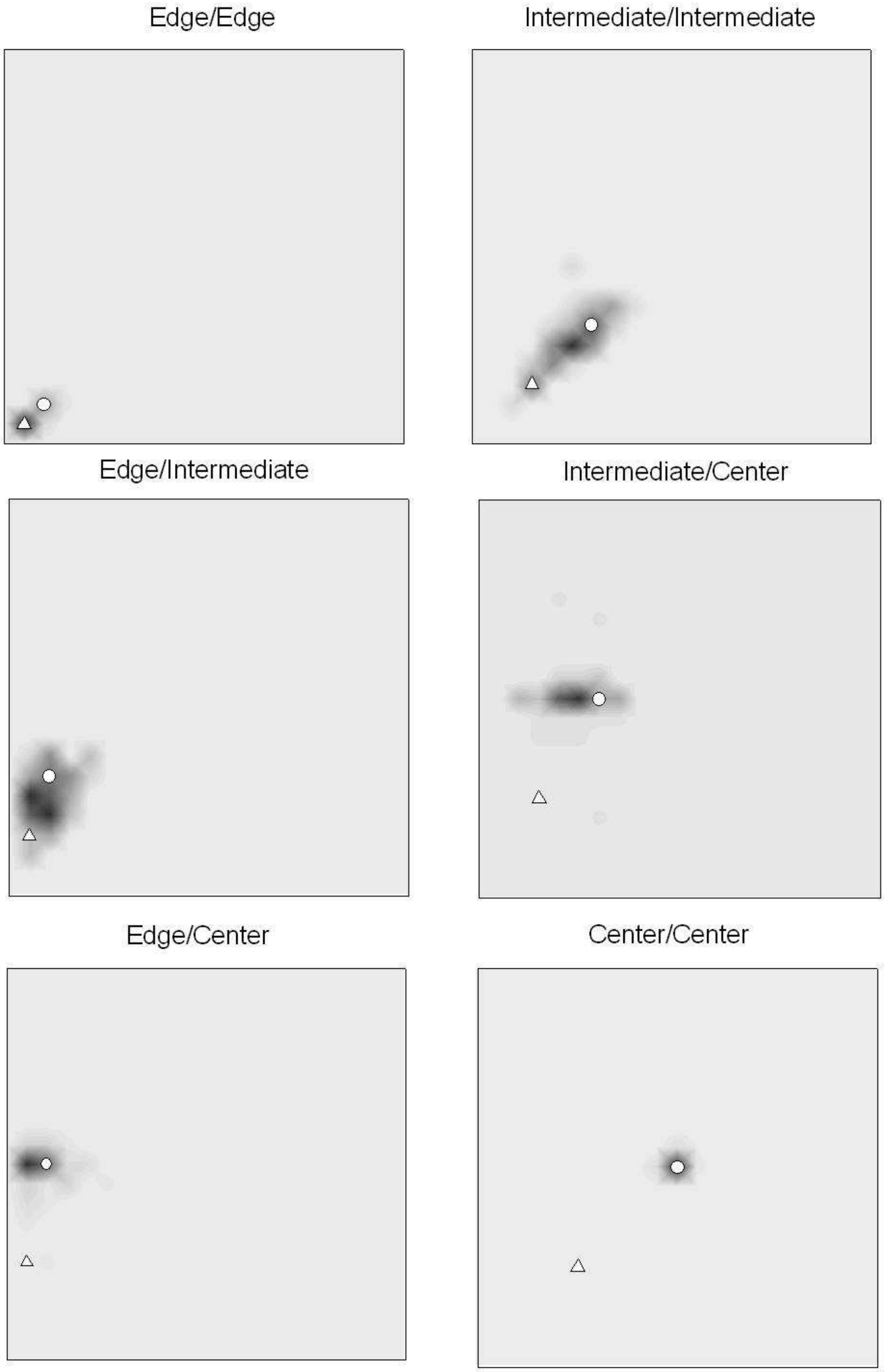
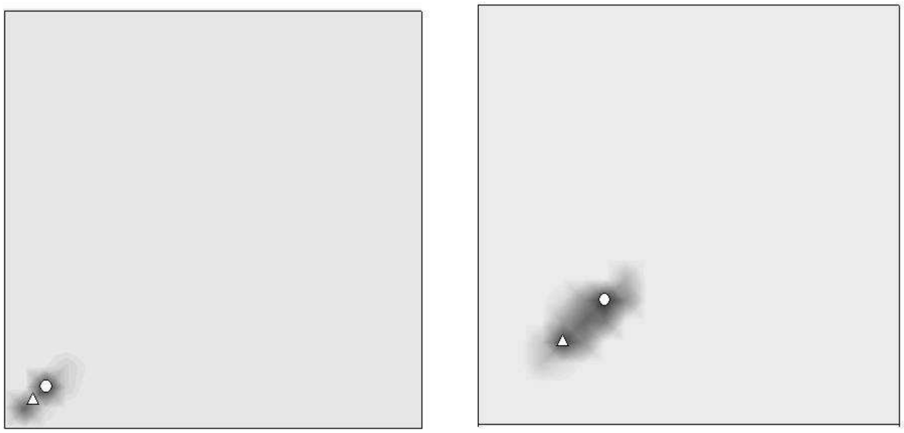
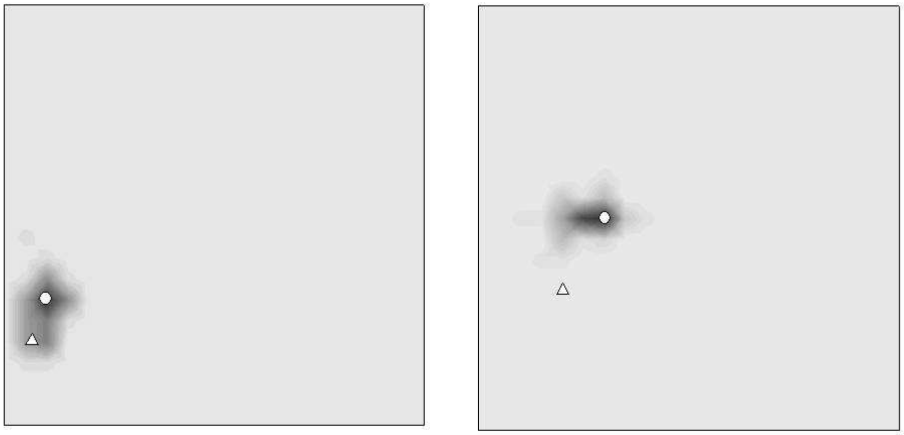


Figure 5-3. Response densities at each of the six distinct locations on Diagonal Expansion test trials for the Small Expansion group. Darker regions indicate higher proportion of searches. White circles represent the relational goal location and white triangles represent the absolute goal location.

Edge/Edge Intermediate/Intermediate



Edge/Intermediate Intermediate/Center



Edge/Center Center/Center

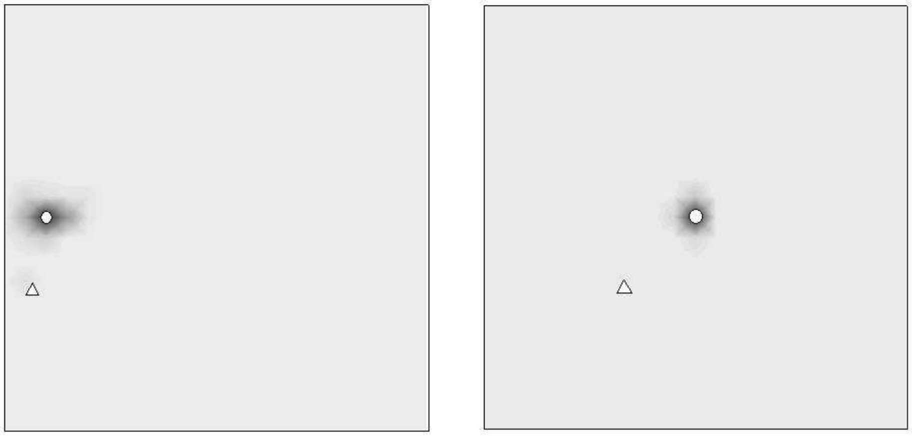


Figure 5-4. Median search distance and spread of searches at each proximity on diagonal expansion tests for the Big and Small Expansion groups. Spread is represented by the width of each bar, the line in the within the bar shows the median search distance and the whiskers extend to the 10th and 90th percentiles of search distances.

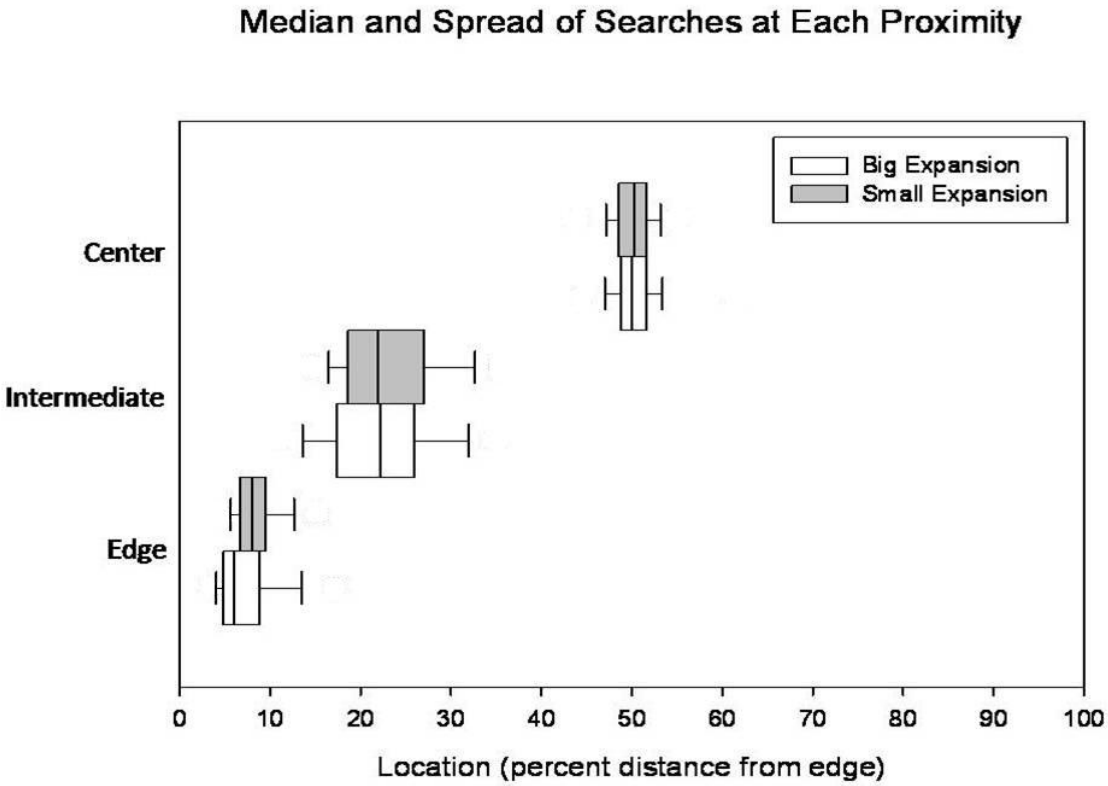


Figure 5-5. Median search distance and spread of searches at each proximity on horizontal and vertical expansion tests for the Big and Small Expansion groups. Spread is represented by the width of each bar, the line in the within the bar shows the median search distance and the whiskers extend to the 10th and 90th percentiles of search distances.

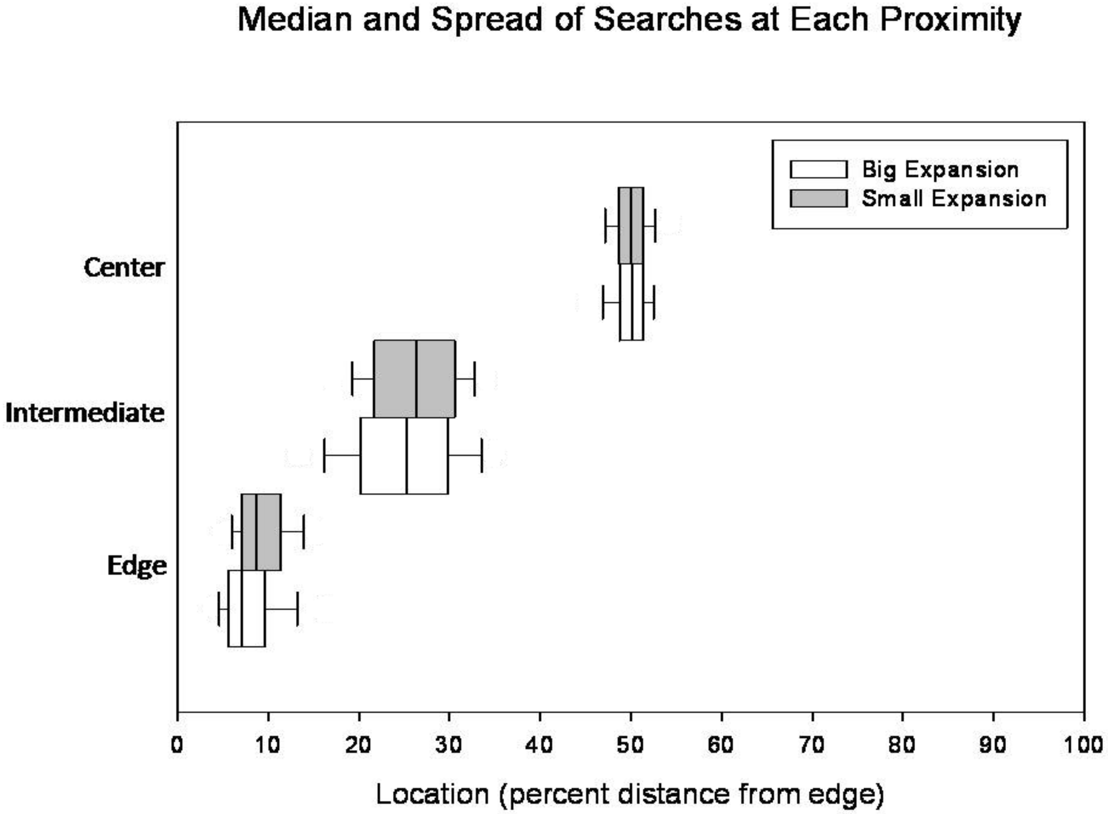
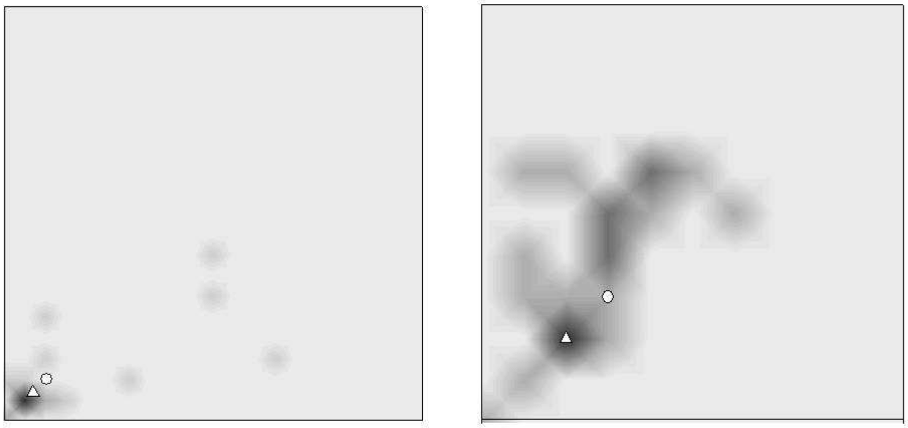
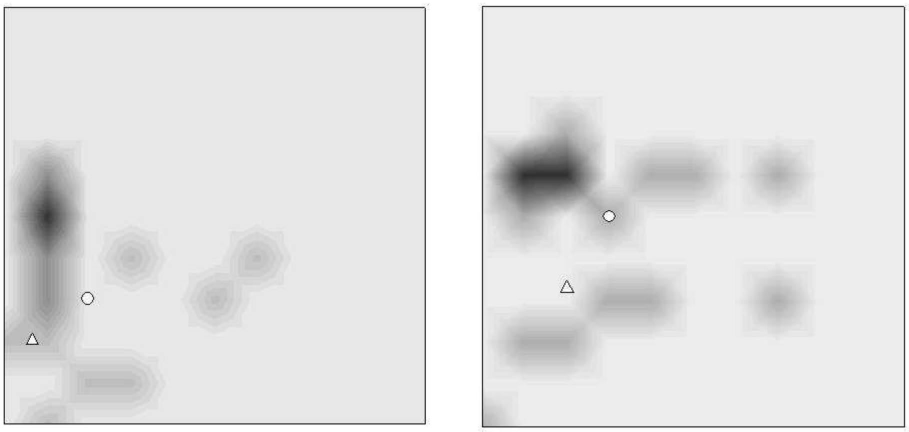


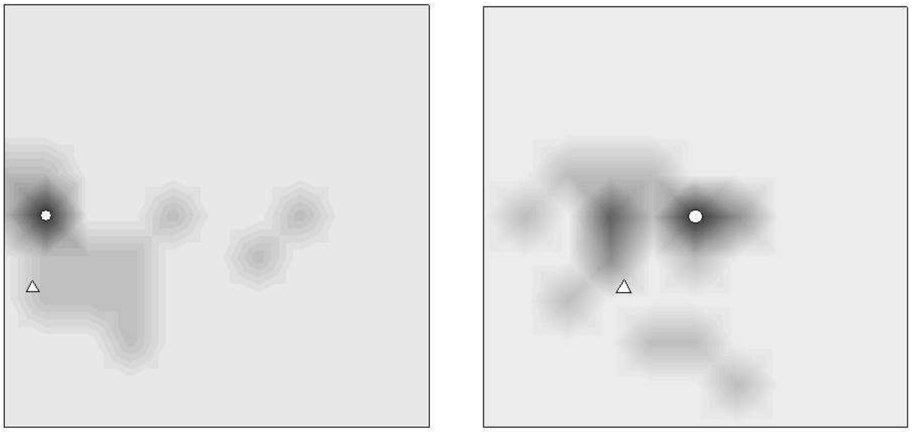
Figure 5-6. Response densities at each of the six distinct locations on expansion tests in Experiment 2. Darker regions indicate higher proportion of searches. White circles represent the relational goal location and white triangles represent the absolute goal location.


Edge/Edge

Intermediate/Intermediate

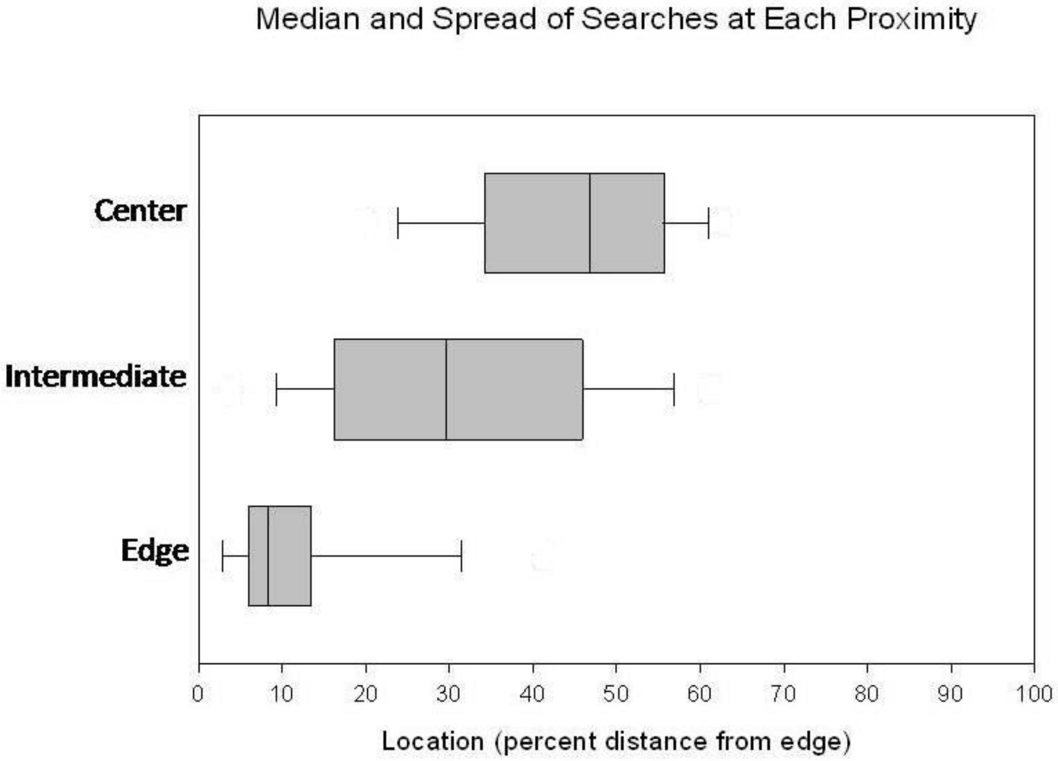

Edge/Intermediate

Intermediate/Center


Edge/Center

Center/Center

Figure 5-7. Median search distance and spread of searches at each proximity on expansion tests in Experiment 2. Spread is represented by the width of each bar, the line in the within the bar shows the median search distance and the whiskers extend to the 10th and 90th percentiles of search distances.



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Chapter 6

General Discussion

The purpose of this thesis was to examine factors that can affect the way in which animals use metric information to orient and navigate. Although there is no universally accepted theory regarding how animals represent spatial relations (see Bennett, 1996), the use of metric information is a common assumption across theories. Thus, determining how animals represent metric information is a fundamental part of understanding how animals navigate, and how navigational processes can differ across species (Cheng & Spetch, 1998). In this thesis, I have investigated several factors that can lead to differences in the way in which animals encode and use metric information to orient or to locate hidden goals. Specifically, in chapter 2, I examined how rearing environments and ecological factors affect the way in which chickadees use geometric properties of an environment to orient. In chapters three and four, I investigated how different training procedures and past experience can affect how rats and pigeons use metric information to locate a hidden goal. In chapter 5, I looked at the flexibility of search strategies in human adults and children, and focussed on how boundary cues can affect the way in which metric information is used.

Training and Past Experience

The idea that past experience, ranging from rearing environments to training procedures, can affect encoding and use of metric information was a focus in chapters 2, 3 and 4. First, in chapter 2, I investigated whether rearing environment affects use of geometric information to orient in black-capped chickadees. In a previous study with chickadees, Gray, Ferrey, Bloomfield, Spetch and Sturdy (2005) showed that featural information overshadowed learning of geometric information in wild-caught mountain chickadees. Based on this result, Gray et al. suggested that a lack of extensive early experience with right-angled environments could have affected the chickadees' ability or willingness to use geometric information.

Partially supporting this idea, Brown, Spetch and Hurd (2007) found that rearing conditions affected the degree to which fish (convict cichlids) preferred featural information. Specifically, fish reared in a rectangular tank were more reliant upon geometric information when geometric and featual information were placed in conflict than fish reared in a circular tank. However, both groups of fish were able to orient on the basis of geometric cues when featural information was absent. Similarly, Chiandetti and Vallortigara (2008) showed that domestic chicks' use of metric information to orient was not impaired when raised in environments lacking right-angled corners.

I investigated how rearing environment affected use of geometric properties in black-capped chickadees by comparing how wild-caught and lab-reared black-capped chickadees orient in a rectangular environment. If early experience with right-angled environments predisposed chickadees to prefer use of metric information, I would expect the lab-reared chickadees to be more likely to use geometric properties over featural information. However, in line with the findings of Brown et al. (2007) and Chiandetti and Vallortigara (2008), both groups of chickadees used geometric information to orient. In contrast to Brown et al., I did not find that rearing condition affected preference for featural information. Specifically, since the lab-reared birds did not show a greater preference for metric information than the wild-caught birds, my results support the idea that early experience with right-angled environments *does not* facilitate use of metric information to orient or inhibit use of featural information.

Although past experience may not affect use of metrics to orient, the results of chapters 3 and 4 suggest that it may affect use of metrics to navigate. In chapter 3, I examined how rats use the geometric properties of an environment to navigate, or determine location, when it is not necessary to establish heading. In a paradigm similar to that used with the chickadees, I investigated how the presence or absence of orientation cues during training affect rats' preference for metric cues during navigation. Specifically, rats were trained to find food in one corner of a rectangular environment under either oriented or disoriented conditions. During testing, geometric and orientation cues were placed in conflict. Results showed that although both groups of rats were able to use geometric information in the absence of orientation cues, rats trained in the disoriented condition preferred geometric cues to orientation cues whereas rats trained in the oriented condition showed a more equal preference for orientation and geometric cues. my results here indicate that experience gained through training can affect how metric information is preferentially used to navigate.

Chapter 4 extended this finding and showed that directional metrics, as well, can be influenced by past experience. Pigeons were trained to search in the center of three separate landmark arrays consisting of two, three or four landmarks that were presented in either an increasing or decreasing order. The pigeons' search patterns on rotational tests revealed that training on previous arrays influenced the way in which they encoded directional information on subsequent arrays. For example, when the arrays were presented in increasing order, the experience gained by searching in the center of two horizontally aligned landmarks seemed to encourage use of a relational directional search strategy on rotated four-landmark arrays; this was likely due to the fact that in the rotated four-landmark array, two of the landmarks of the square become horizontally aligned. Additionally, search patterns on the three landmark arrays also indicated that the previous training affected directional encoding preferences.

Overall, these three chapters indicate that past experience is more likely to affect use of metrics to navigate than to establish heading. Past experience, in the context of training procedures, affected rats' preference to use metric information over other orientation cues (such as internal compass sense) to navigate. Additionally, past experience with landmark arrays affected the way in which pigeons' encoded directional information. In contrast, early experience (i.e., rearing environment) did not affect chickadees' use of metrics to orient.

Ecological Considerations

In addition to studying rearing environment in chapter 2, I also showed that despite the close relation between black-capped and mountain chickadees, the two species use different strategies when orienting according to geometric or featural information. In particular, I trained both black-capped and mountain chickadees to search for food in one corner of a rectangular environment with a salient featural cue on the wall nearest the goal corner. On transformational tests, the feature was removed, forcing animals to rely only on geometric cues to orient.

my results showed that black-capped chickadees were more likely than mountain chickadees to orient on the basis of geometric cues. Specifically, only some of the mountain chickadees chose the geometrically correct corners when tested in the absence of the featural cue.

Differences in the way in which each species interacts with their natural environment can provide an account of why the two species would show different reliance on metric cues. In particular, although black-capped and mountain chickadees live in sympatry in some areas, they show very different patterns in their use of the environment, including foraging and nesting behaviours (Hill & Lein, 1988). Notably, mountain chickadees frequently reuse nest holes whereas black-capped chickadees do not. Featural information may play a significant role in encoding the location of specific nest holes and, as such, could explain an increased reliance on featural information for mountain chickadees.

Boundary Cues

Chapters 2, 3 and 4 examined factors that affect the way in which metric information is encoded and used, and thus demonstrate that use of metrics is malleable. Chapter 5 extends upon this idea and shows how search strategies can change across trials of a single training session based on the environmental cues, and more specifically, the goal's proximity to a boundary.

Recent research (Hartley, Trinkler & Burgess, 2004) used a simulated 3D environment to demonstrate that proximity to a boundary affects strategy choice. In particular, when searching close to an edge, human participants were more likely to use an absolute strategy whereas when searching at a central location, participants were more likely to use a relational strategy. In chapter 5, I extended these findings and examined how both adults' and children's search strategies change based on a goal's proximity to a boundary. Search strategies were affected by gender and by the proximity to the edge.

Sex Differences

Sex differences have been reported in a variety of spatial navigation tasks (e.g Astur, Ortiz, & Sutherland, 1998; Dabbs, Chang, Strong, & Milun, 1998; Kelly & Bischof, 2005; MacFadden, Elias, & Saucier, 2003; Sandstrom, Kaufman, & Huettel, 1998; Saucier, Bowman, & Elias, 2003), but have generally focused on men's preference for geometric-based information as compared to women's preference for featural or landmark-based information. Interestingly, I found sex differences in the absence of distinctive featural information, suggesting a gender difference in use of metric information. In particular, women tended to have more variable search patterns, but were also more likely than men to use relational search strategies when the goal was between an edge and center location.

Sex differences have also been found in the way children use metric information (Spetch & Parent, 2006); boys learn a 'middle' relationship more easily than girls. Spetch and Parent also found that boys tended not to make many searches in between the absolute and relational regions whereas girls were more likely to spread their search between the two regions. This finding provides an interesting parallel to my results showing increased search variability shown by adult women.

Proximity to Edge

In addition to gender, the goal's proximity to the edge was a factor that affected the way participants used metric information. Specifically, when the goal was at the center of the search area, participants mainly used a relational strategy. At intermediate proximities, however, there was an increased spread of searches for both children and adults. Adults, in particular, mainly searched between the absolute and relational regions, suggesting that they may have been averaging the distance to either area (i.e., averaging strategies). Children, in contrast, had such a dramatic increase in variability that it likely represented a greater level of uncertainty, rather than a distance averaging strategy.

Overall, the results of chapter 5 support the idea that use of metric information is flexible and situation specific. Moreover, both sex and goal location are factors which can affect how metrics are encoded and used for both adults and children.

Summary

The experiments presented in this thesis were designed to demonstrate the malleability of animals' use of metric information. The use of the transformational approach allows us to determine which aspects of metric information are preferentially used or encoded in different situations. Moreover, this thesis presents a comparative approach in order to illuminate both the similarities and differences in how various species represent metric information. Understanding how factors such as past experience and training, ecological differences, gender and boundaries influence use of metric information to orient and navigate provide a foundation for theories regarding how space is represented.

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