The important thing is not to stop questioning. Curiosity has its own reason for existing.

– Albert Einstein

University of Alberta

MULTIPLE CUE USE IN ANIMALS

by

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For my mother, Audrey, who always said
I could accomplish anything if I tried

Abstract

Animals often redundantly encode multiple cues to aid in navigation and goal localization. While encoding multiple cues can help animals navigate and localize goals, (e.g., using multiple cues can increase an animals' search accuracy and robustness), encoding multiple cues can also create problems when one or more cues become displaced. In such situations, the displaced cue(s) provide information that conflicts with other nearby cues (creating what is commonly referred to as cue conflict). Cue conflict is not uncommon in the natural world, as many animals use small, easily displaced objects as landmarks for localizing goals. As such, animals have developed a number of strategies to cope with cue conflict, and here I report four studies that investigates the use of these strategies in both pigeons (*Columba livia*) and desert ants (*Melophrous bagoti*). Overall, I report evidence that suggests both pigeons and desert ants can utilize similar strategies to resolve cue conflict, even when these strategies are complex.

Acknowledgements

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Sincerely,
Eric L. G. Legge, PhD
July 11, 2013

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Chapter 1

Introduction

Animals can encode and use many cues for navigation and goal localization. These cues can range from auditory (Gröhn, Lokki, & Takala, 2005; Rossier, Haeberli, & Schenk, 2000; Lokki & Gröhn, 2005; Poulet & Hedwig, 2005), olfactory (Wallace, Gorny, & Whishaw, 2002; Wallraff, 2004; Wolf & Wehner, 2000; Steck, Hansson, & Knaden, 2009) and visual cues (for reviews see: Cheng, 2012; Spetch & Kelly, 2006; Cheng, Narendra, Sommer, & Wehner, 2009), to ideoethic cues such as path integration (Wehner & Srinivasan, 2003; Loomis, Klatzky, Golledge, & Philbeck, 1999; Benhamou, 1997; Etienne & Jeffery, 2004), odometry (Srinivasan, Zhang, Lehrer, & Collett, 1996; Wittlinger, Wehner, & Wolf, 2006), and optic flow (Ronacher & Wehner, 1995; Esch & Burns, 1995; Wylie, Bischof, & Frost, 1998; Lee & Aronson, 1974). These cues often provide redundant information, which animals encode and use to locate important goals (e.g., food caches or a nest). Encoding multiple cues that provide redundant information is generally advantageous for animals, as it can increase search accuracy and robustness (Kamil & Cheng, 2001; Kamil, Goodyear, & Cheng, 2001). For example, having encoded multiple redundant cues, an animal will still be able to locate a goal when one cue is suddenly lost or unavailable (e.g., a tree used as a landmark fell down; a mountain range used as a beacon becomes obscured by fog).

However in some situations, encoding multiple redundant cues can also lead to problems, such as when one cue becomes slightly displaced, e.g., by the wind. In these situations, the displaced cue will provide information that conflicts with other nearby cues. Such cue conflict can cause animals to search inaccurately, thus wasting valuable time and energy required for other survival-related tasks (Shettleworth, 2010; Spetch & Kelly, 2006). Because of this, animals have developed a number of strategies to cope with cue conflict, ranging from relying on only a single preferred cue for goal localization, to integrating the information provided by many nearby cues to predict a location near enough to the true goal location for success. An investigation of the strategies two model species use to cope with spatial cue conflict, namely pigeons (*Columba livia*) and desert ants (*Melopherous bagoti*), is the focus of my dissertation.

1.1 Background:

Research on how animals utilize cues for navigation and goal localization has been an active area of investigation for over 60 years, arguably becoming an area of serious scientific inquiry with Tolman's seminal work on place learning in rats (e.g., Tolman, 1948; Tolman, Ritchie, & Kalish, 1946). In one of his classic studies, Tolman trained rats in an arena that contained a single exit that led along a path to a goal box some distance away (see Figure 1.1a). Notably, the arena walls did not prevent the rats from viewing the surrounding features of the room. Rats were trained until they immediately left the arena to travel along the goal path after being placed in the apparatus. After training, rats were tested using a similar apparatus in the same room that, instead of containing the goal path used in training, contained 18 paths that radiated outward from the location of the goal path in training (see Figure 1.1b). Results revealed that rats overwhelmingly chose the path that would bring them closest to the goal box's location (path 5 in Figure 1.1b), instead of selecting the paths that were closer to the goal path used in training (e.g., paths 9 and 10 in Figure 1.1b). Thus, Tolman found that rats could use extra-maze cues for navigation, and could integrate a direction using these cues when a learned route was no longer available. Subsequent studies have since manipulated extra-maze cues in various experimental contexts and shown that such cues are very important for successful goal localization in enclosed environments for a number of species (e.g., Astur, Tropp, Sava, Constable, & Markus, 2004; D'Hooge & De Dyen, 2001; Astur, Ortiz, & Sutherland, 1998; Morris, 1981).

Since Tolman's experiments with rats, research has found that animals can use a large number of cues for navigation and goal localization, including visual cues such as landmarks, landmark arrays, and environmental geometry, (for reviews see: Spetch & Kelly, 2006; Srinivasan & Zhang, 1999; Cheng et al., 2009) auditory beacons such as mating calls (Poulet & Hedwig, 2005; Hedwig & Poulet, 2004; Rossier et al., 2000), olfactory cues such as pheromone trails (Steck et al., 2009; Wolf & Wehner, 2000), as well as proprioceptive cues such as path integration (Wehner & Srinivasan, 2003; Etienne & Jeffery,

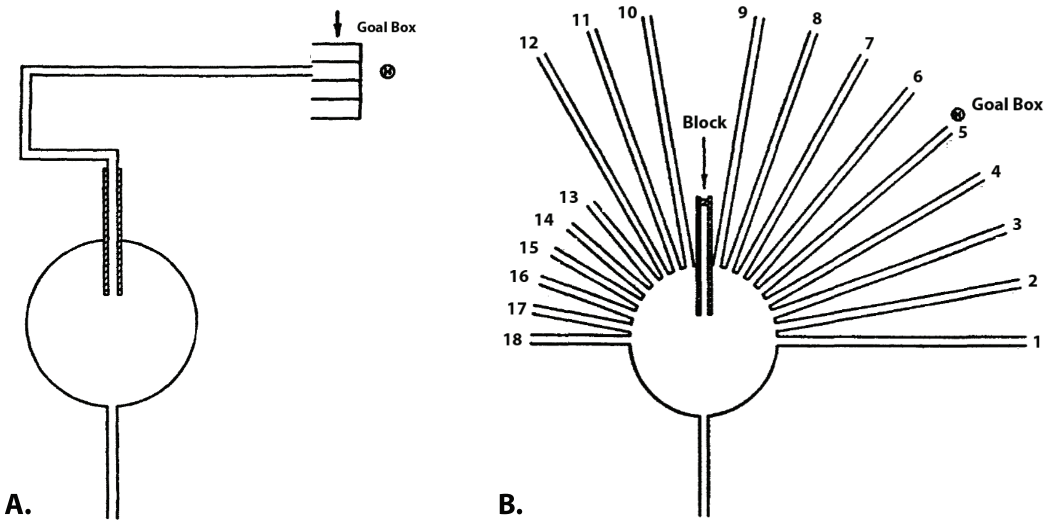

Figure 1.1: [**A**] The apparatus used by Tolman et al. (1946) in which rats were trained to run to a lighted goal box for food. [**B**] The apparatus Tolman et al. used to test rat's knowledge of the location of the goal box in the room. All available paths (labeled 1-18) were novel to test subjects. If a rat had knowledge of the goal box's location in the room, it should take the most direct route to the goal box (path 5). If the rat had only learned the specific route to the goal box provided in training, it should take the paths closest to the path used in training (paths 9 or 10). Figures depicted here have been reproduced with permission from Tolman et al. (1946) ©American Psychological Association 2012.

2004). Additionally, scientists have investigated navigational cue use across a wide range of species, from invertebrates such as arthropods (van Nouhuys & Kaartinen, 2007) and arachnids (Tarsitano & Jackson, 1997) to vertebrates such as birds (Gould-Beierle, 2000; Jones, Antoniadis, Shettleworth, & Kamil, 2002), fish (Cain & Malwal, 2002; Odling-Smee & Braithwaite, 2003), and mammals (Sutton, Olthof, & Roberts, 2000; Dolins, 2009).

Thus, while most animals must locate goals accurately and efficiently, many species have particular preferences for the type(s) of information they primarily rely on for goal localization. For example, while rodents rely heavily on olfactory cues for navigation, birds such as pigeons tend to rely on visual cues (rats: Wallace et al., 2002; pigeons: Spetch & Kelly, 2006). Often such cue preference is related to an animal's physiology (e.g., birds generally have excellent eyesight, whereas rodents do not, rats: Wiesenfeld & Branchek, 1976; Prusky, West, & Douglas, 2000; pigeons: Catania, 1964; Blough, 1971).

1.2 Multiple cue use and its adaptive significance:

To understand how animals use multiple cues to locate a goal, it is important to understand why using multiple cues would be adaptive in the wild. Generally, encoding multiple cues for goal localization has two primary benefits: decreasing the delay between beginning a search and locating a goal (search delay), and increasing search accuracy and robustness (Bossema, 1979; Kamil & Cheng, 2001; Kamil et al., 2001). Delay and inaccurate searching can have negative consequences for an animal trying to locate a goal, e.g., starvation; prolonged exposure to a harsh environment. Additionally, delay and inaccurate searching can jeopardize an animal's safety and the goal it is attempting to locate by increasing the chances that the animal will be observed by a predator or conspecific. Due to the severity of these negative consequences, strong selection pressure has led animals to adopt strategies to reduce search delay and increase their search accuracy. One such method is to encode multiple redundant cues.

An example of how redundantly encoding multiple cues can help animals survive can be seen by observing food-storing birds living at high latitudes during winter. For example, black-capped chickadees can survive winters in northern Alaska, even though the ground is often covered by deep snow and temperatures regularly reach $-30\,^{\circ}\mathrm{C}$ (Alaska Climate Research Center, 2012). To make matters worse, diurnal animals such as the black-capped chickadees only have approximately four hours of daylight in which to forage each day, thus creating a very narrow window for foragers to obtain enough food to survive until the next sunrise. Thus, recovering food quickly and efficiently is especially important for survival in these conditions, as failure to recover a food cache or to locate a nest before dark can result in death. In these conditions, relying on a single landmark is extremely risky, as high winds and sudden snow storms can quickly cover or displace low-lying terrestrial landmarks, and/or obscure prominent distal cues. Thus, it is logical that animals that inhabit these environments encode multiple cues for locating food caches and their nest (Roth, LaDage, & Pravosudov, 2010; Pravosudov, 2007). By encoding multiple landmarks, not only can animals better pinpoint their goal (Bossema, 1979; Kamil & Cheng, 2001; Kamil et al., 2001), but also have access to multiple cues in case some are obscured or lost. Thus, there would have been strong selection pressure for navigating animals living in such climates to encode multiple redundant cues for goal localization.

As evidenced by the previous example, encoding multiple redundant cues can often help animals survive. However, such encoding can occasionally create a unique problem for animals: cue conflict. Specifically, cue conflict occurs when a cue becomes slightly displaced relative to other nearby encoded cues, such as when a rock used as a landmark by a navigating ant is displaced by a large passing mammal. In this situation, the displaced cue will now provide information that conflicts with other nearby encoded cues, leading to multiple possible goal locations. It is often unreasonable for an animal to search at each possible goal location, and thus they must resolve the conflict another way. The methods by which animals have been found to cope with cue conflict will be the focus of the next section.

1.3 Strategies for coping with cue conflict:

While cue conflict is potentially hazardous for animals in the wild, it has provided researchers with an invaluable tool to study how animals use spatial information for navigation and goal localization: the transformational approach. This approach, which involves purposefully placing previously learned cues in conflict to observe how animals respond (Cheng & Spetch, 2001), is one of the main methods used by researchers to help identify the mechanisms by which animals navigate and locate goals in space.

The transformational approach was first used to evaluate the cues animals use for goal localization by Tinbergen in 1932 (as summarized in Tinbergen, 1972). Specifically, Tinbergen used the transformational approach to study how digger wasps were able to return to their burrow (a small hole in the sand) after foraging. In his experiment, Tinbergen placed pine cones around the entrance to a wasp's burrow while it was inside, and then, after the wasp had left to forage, moved the pine cones a short distance away. Thus, Tinbergen utilized the transformational approach to place the local cues that indicated the nest entrance (the pine cones) in conflict with the surrounding visual panorama. When the digger wasps returned to enter their burrow, they went towards the shifted pine cones. Thus, Tinbergen demonstrated that wasps memorized the location of their burrow relative to the local landmarks that surrounded it (see Figure 1.2).

Since Tinbergen, many studies of spatial cue use in animals have utilized the transformational approach to investigate the mechanisms animals use for goal localization and navigation (for reviews, see: Shettleworth, 2010; Spetch & Kelly, 2006; Cheng & Spetch, 1998; Roberts, 1998). From these investigations, researchers have identified a number of methods by which animals cope with cue conflict that can be broadly divided into three categories: hierarchical, independent, and integrative strategies. Each will be discussed in detail below.

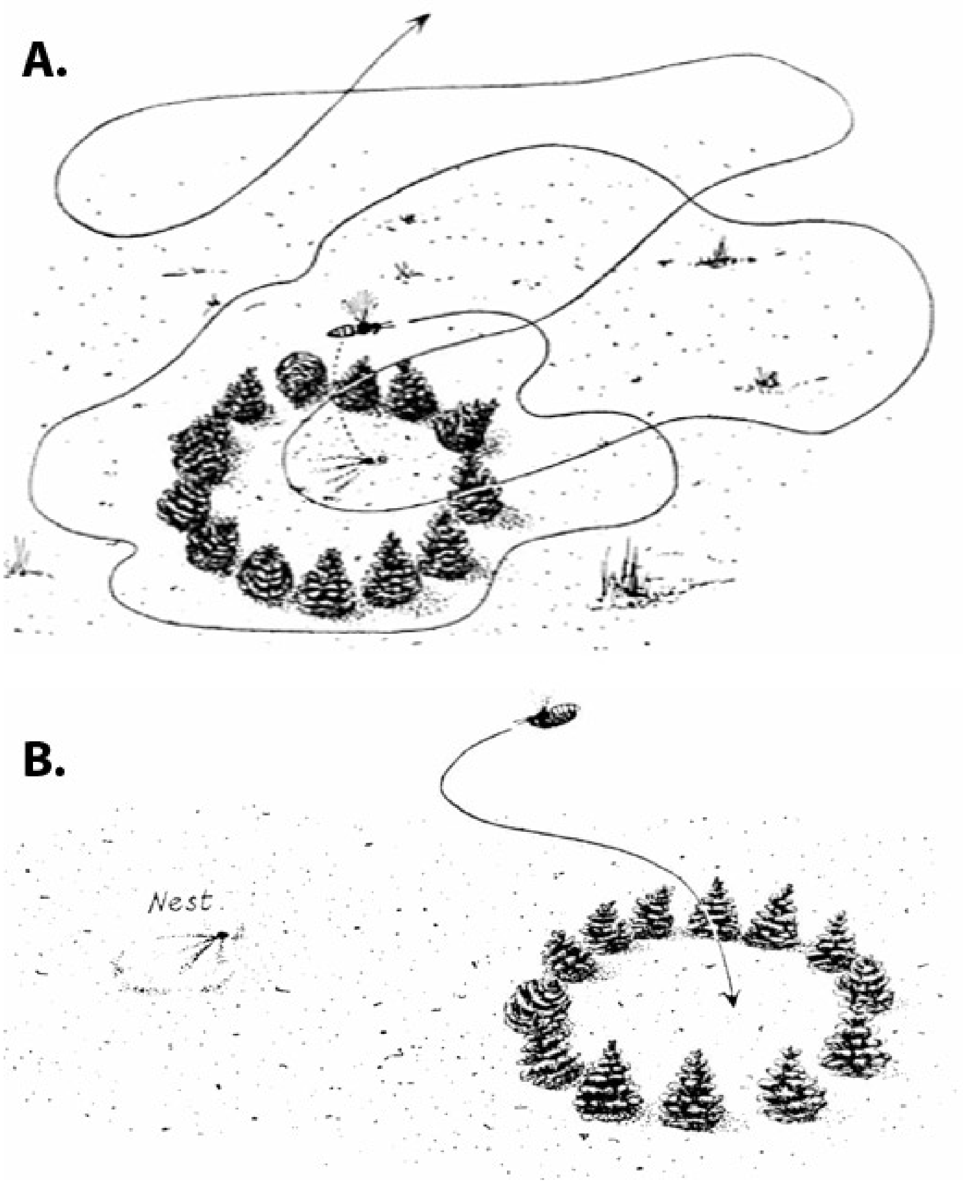

Figure 1.2: Figure illustrates how Tinbergen tested which cues digger wasps use to locate their nest. [**A**] An illustration of a digger wasp's initial flight path after emerging from its nest to find a circle of pine cones surrounding the entrance. During this flight, the wasp encodes the position of its nest relative to nearby landmarks. [**B**] An illustration of a transformation test, whereby the circle of pine cones that once surrounded the wasp's nest is moved to a nearby location while the wasp was foraging. The arrow indicates where the returning wasp initially landed to search for its nest. Figures depicted here have been reproduced with permission from Tinbergen (1969) ©Oxford University Press, 2013.

1.3.1 Hierarchical strategies

In hierarchical strategies (also referred to as winner-take-all or take-the-best strategies, Gigerenzer & Brighton, 2009; Gigerenzer & Goldstein, 1999; Morgan, Ward, & Castet, 1998; Palmer, 1994; Palmer, Ames, & Lindsey, 1993), cues are ranked according to preference. Thus, when cues provide conflicting information, only the cue at the top of the hierarchy is used to search for the goal (see Figure 1.3b). However, animals using hierarchical strategies still encode multiple cues to provide redundancy should the cue at the top of the hierarchy go missing (see Figure 1.3c). While hierarchical strategies have the advantage of being relatively simple (e.g., requiring very little computation prior to searching), they may not provide the optimal solution for coping with cue conflict. This is because hierarchical strategies require animals to discard potentially relevant information from nearby cues that are not at the top of the hierarchy. Additionally, hierarchical strategies may sometimes lead an animal to search in a incorrect location that is very far away from the actual goal location, such as when the cue at the top of the hierarchy is displaced.

Interestingly, even in light of these problems, many animals have been shown to use hierarchal strategies for coping with cue conflict in discrete choice tasks[1] (e.g., Clark's nutcrackers: Gould-Beierle & Kamil, 1996; hummingbirds: Hurly & Healy, 1996; squirrels: Nesterova, 2007; Vlasak, 2006b, 2006a; adult humans: Steck & Mallot, 2000). One classic example of an animal using a hierarchical strategy to cope with cue conflict was conducted by Spetch and Edwards (1988) with pigeons in an open field. In their study, Spetch and Edwards trained pigeons to locate a food source in the middle of an array of three objects. Notably, the array was always located in the same position in the open field during training, thus allowing pigeons to learn the location of the goal relative to distal room cues (see Figure 1.4). Furthermore, because the array always contained three objects during training, pigeons could also learn the location of the goal relative to the objects within the array. When tested, Spetch and Edwards found that pigeons redundantly encoded the goal relative to both the absolute location in the room, and relative to the objects

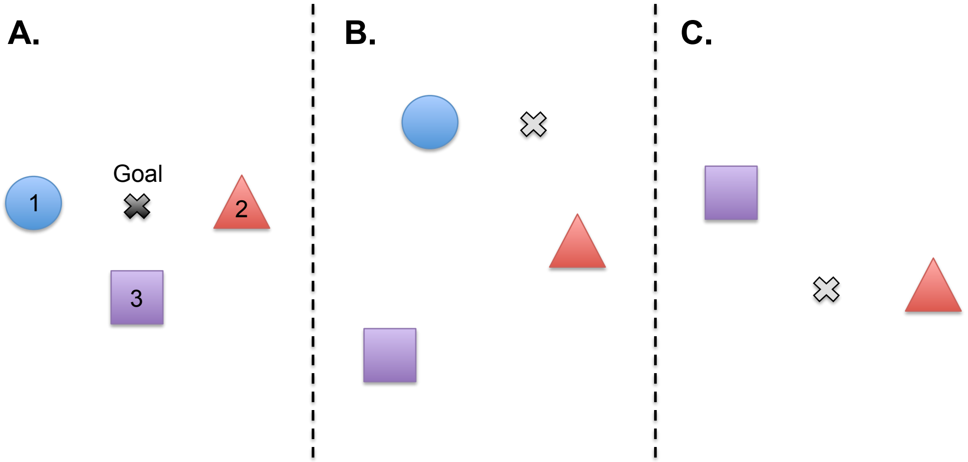

Figure 1.3: Illustration of hierarchical strategy use in a spatial localization task. [**A**] Position of landmarks during training. The numbers within each landmark indicate it's hierarchical rank. [**B**] A test trial in which the three landmarks now provide conflicting information. The × indicates the location where an animal would search given the hierarchical rankings depicted in panel A. [**C**] A test trial in which the blue circular landmark has been removed. In this situation, an animal using a hierarchical strategy would search using the next highest ranked landmark (the red triangle). The animal's search location is indicated by the ×.

in the array (Figure 1.4). Additionally, on critical test trials, both sources of information were placed in conflict. On these tests, pigeons were significantly more likely to search for the goal relative to objects within the array than in relation to distal room cues (Figure 1.4). Thus, Spetch and Edwards found that while pigeons clearly encoded both cues, they used a hierarchical strategy in which local, configural array cues were ranked higher than distal room cues.

Since Spetch and Edwards (1988), many studies have found behaviour suggestive of hierarchical cue use for goal localization using discrete choice tasks across a wide variety of species (black-capped chickadees: Brodbeck, 1994, dark-eyed juncos: Brodbeck & Shettleworth, 1995; squirrels: Nesterova, 2007; dogs: Fiset, Gagnon, & Beaulieu, 2000; among others) and across a number of experimental paradigms (e.g., use of geometric information: Batty, Bloomfield, Spetch, & Sturdy, 2009; Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005; Vallortigara, Feruglio, & Sovrano, 2005; foraging: Vlasak, 2006a; navigation and orientation tasks: Steck & Mallot, 2000; Jacobs & Shiflett, 1999; Vlasak, 2006b; Nesterova, 2007; as well as goal localization in open environments: Gould-Beierle & Kamil, 1996; Brodbeck, 1994; Brodbeck & Shettleworth, 1995; Hurly & Healy, 1996; and touch screens: Ushitani & Jitsumori, 2011; Legge, Spetch, & Batty, 2009). Unfortunately, this wealth of information has not made it easier to predict how an animal will rank a particular cue in a given situation. Instead, research has shown that the type of information animals rank highest is not fixed, and can differ according to a number of factors including species (e.g., black-capped vs. mountain chickadees Batty et al., 2009), individual (Vallortigara et al., 2005; Learmonth, Nadel, & Newcombe, 2002; Sovrano, Bisazza, & Vallortigara, 2005; Legge et

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[1] It is important to note that evidence supporting hierarchical strategy use in spatial tasks has only been demonstrated in discrete choice experiments. This point is important, as discrete choice tasks often do not offer animals the opportunity to respond to cue conflict by using either independent source or integrative strategies (discussed in sections 1.3.2 and 1.3.3). Thus, much of the reported evidence of animals using hierarchical strategies to cope with cue conflict in spatial tasks may be a product of the method in which animals were tested. While results from discrete choice tasks show that animals can use hierarchical strategies to cope with cue conflict, they do not provide evidence that animals will use hierarchical strategies when other options are available. We test whether pigeons use hierarchical strategies to cope with cue conflict when other strategies are viable in Chapter 5.

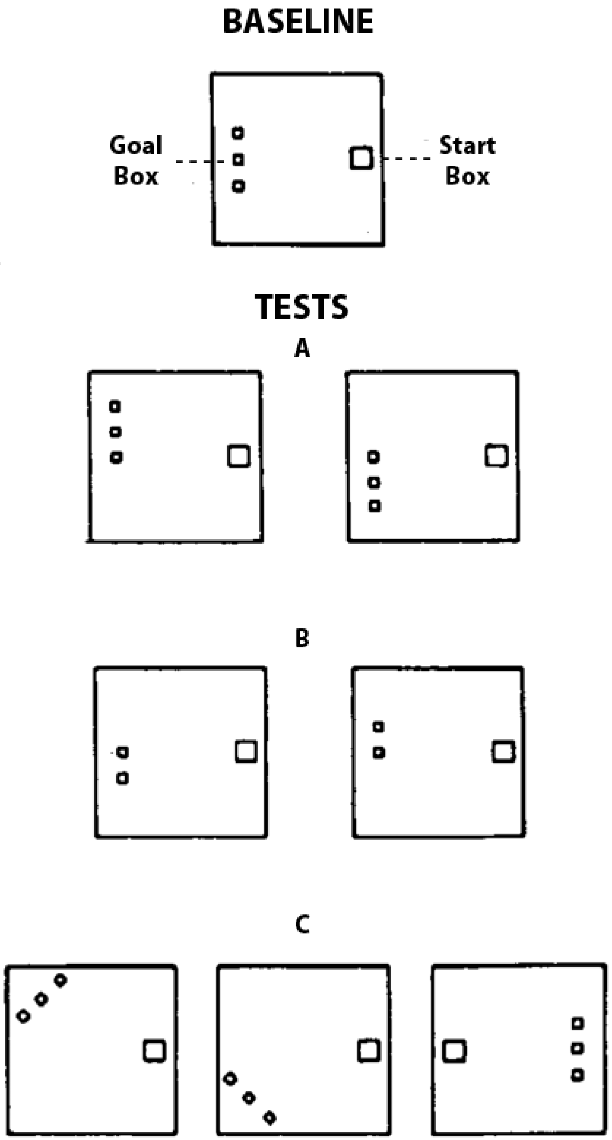

Figure 1.4: Trial types used in Spetch and Edwards (1988). [**Baseline**] The position of the start box and array within the experimental room during training. [**A**] Test trials in which the array was moved to place the local cues (position in the array) in conflict with the global cues (position in the room). [**B**] Test trials in which a box from the array was removed, thus preventing local cues from being used. [**C**] Test trials in which the arrays were displaced so that global cues were no longer informative for locating the goal. This figure was reproduced with permission from Spetch and Edwards (1988) ©American Psychological Association 2012.

al., 2009), developmental conditions (Brown, Spetch, & Hurd, 2007; Twyman, Newcombe, & Gould, 2012), and the properties of encoded cues (Vallortigara et al., 2005; Learmonth et al., 2002; Sovrano et al., 2005; Legge et al., 2009).

One of the best examples for highlighting the malleability of cue preferences in hierarchical strategy use comes from investigations into how animals use geometric information for goal localization[2]. In these experiments, geometric information, such as the length of walls and the angle of corners are encoded in conjunction with nearby featural cues such as a specific landmark (for reviews see: Vallortigara, 2009; Cheng & Newcombe, 2005; Cheng, 2008). When these cues provide conflicting information, animals often resolve the conflict by using a hierarchical search strategy. However, whether animals prefer to use featural or geometric information for resolving cue conflict can vary according to many factors, including species, individual, developmental conditions, and stimulus properties. To highlight this point, I provide an example of each below.

Species and individual differences. As previously stated, whether an animal will prefer featural or geometric information can vary according to species and individual. For example, Batty et al. (2009) showed that while black-capped chickadees reliably encode geometric information, even in the presence of a salient landmark, mountain chickadees did not. Specifically, Batty et al. found that, on tests where the feature was removed, only two of four mountain chickadees responded using geometric information (the other two chickadees responded randomly). Thus, these results demonstrate that not only are there differences in cue preference across species, but that some species can display differences in cue preference across individuals as well.

Developmental conditions. Whether an animal prefers to use geometric or featural information can also be influenced by the conditions in which they were raised. For example, Brown et al. (2007) reared convict cichlids in either

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[2] Studies investigating the role that geometric information plays in goal localization are generally designed as discrete choice tasks, whereby animals are unable to respond using integrative or independent source strategies.

circular or rectangular tanks prior to testing. Thus, cichlids raised in circular tanks were prevented from having previous experience with geometric information. While Brown et al. did not find evidence that being raised without geometric information prevented cichlids from using geometry as a cue, they did find that such rearing influenced the hierarchical ranking of geometric information in situations of cue conflict. Specifically, cichlids raised in circular tanks were less likely to prefer geometric information to featural information than cichlids raised in rectangular tanks. Since Brown et al.'s work with cichlids, rearing environment has also been shown to influence geometric and featural cue preference in mice (Twyman et al., 2012).

Stimulus properties. Lastly, stimulus properties such as enclosure size (Chiandetti & Vallortigara, 2008) have also been shown to affect whether animals' prefer featural or geometric information for resolving cue conflict. For example, in a study with chicks, Vallortigara et al. (2005) found that while geometric information was preferred for resolving cue conflict when tests were conducted in relatively small enclosures, chicks preferred featureal information to resolve the same cue conflict when tested in larger enclosures. This pattern of results has also been reported in both young children (Learmonth et al., 2002; Learmonth, Newcombe, Sheridan, & Jones, 2008) and fish (Sovrano et al., 2005; Sovrano, Bisazza, & Vallortigara, 2007).

Thus, even though hierarchical strategies are unlikely to provide the optimal solution for coping with cue conflict in many situations, there is strong evidence to suggest that, at least in discrete choice tasks, animals can use hierarchical strategies to resolve cue conflict.

1.3.2 Independent Source Strategies

As previously noted, hierarchical strategies have two main disadvantages: they require an animal to discard potentially relevant information from other nearby cues, and they may cause an animal to search in a drastically incorrect location if the cue at the top of the hierarchy is displaced. To overcome these disadvantages, some animals have adopted a different method for coping with cue conflict, namely using an independent source strategy (also known as win-shift/lose-shift or win-stay/lose-shift strategies) (Hodges, 1985; Kamil, 1983; Gaffan & Davies, 1981).

Similar to hierarchical strategies, animals using an independent source strategy will begin searching for a goal using information provided by a single, preferred cue (Pfuhl, Tjelmeland, & Biegler, 2011). However, unlike hierarchical strategies, animals using independent source strategies will shift from searching using information from a preferred cue, to searching using information provided by other encoded cues (e.g., Gaffan & Davies, 1981; Chalfoun & Martin, 2010; see Figure 1.5).

Like pure hierarchal strategies, independent source strategies require little computation to identify potential goal locations relative to encoded spatial cues (e.g., animals using an independent source strategy still only search relative to a single cue at any given time). However, compared to pure hierarchical strategies, animals using independent source strategies may be more likely to locate goals when multiple cues provide conflicting information. This is because independent source strategies allow animals to search using each cue independently. Thus, as long as all available encoded cues were not displaced in some way, an animal relying on an independent source strategy will eventually locate the goal by searching relative to a cue that was not displaced.

While independent source strategies are very effective in locating a goal over an extended period of time, they are unlikely to be the optimal solution for resolving cue conflict due to the time and energy cost associated with searching relative to many individual cues. Furthermore, the cost associated with searching relative to many cues individually will be compounded in cases where the goal an animal is searching for is no longer available (e.g., a food cache has been pilfered by another animal). In such cases, an animal relying on an independent source strategy will have to rule out many more possible goal locations than an animal relying on either hierarchical or integrative strategies. Even in light of these problems, many animals have been observed to use independent source strategies when foraging, including birds (Burke & Fulham, 2003; Sulikowski & Burke, 2007), bees (Demas & Brown, 1995;

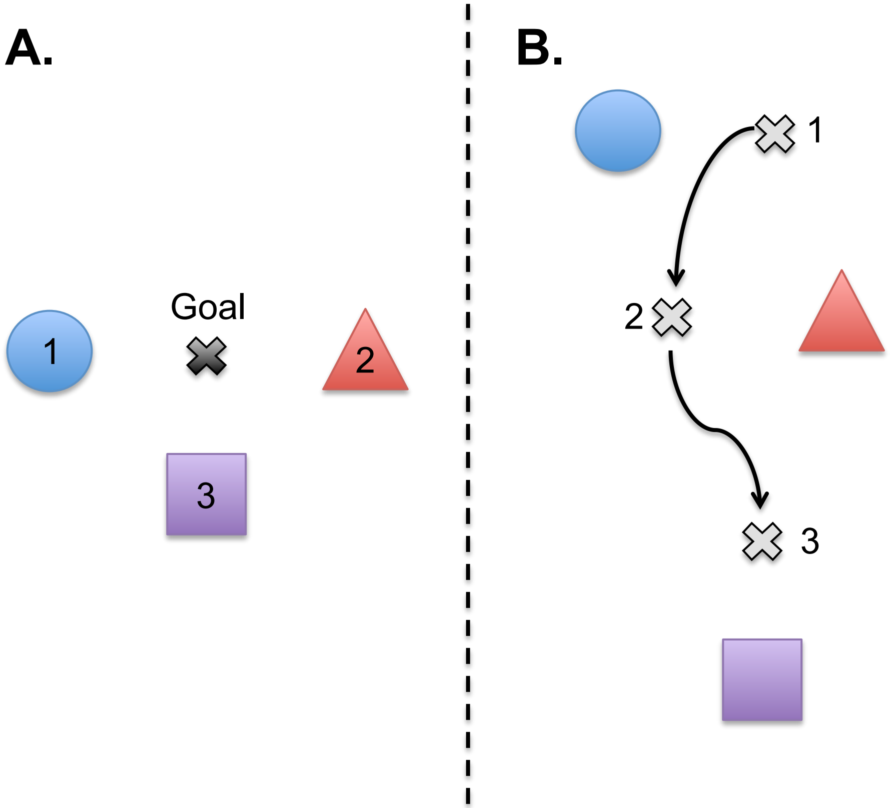

Figure 1.5: Illustration of independent source strategy use in a spatial localization task. [**A**] Position of landmarks during training. The numbers within each landmark indicate it's hierarchical rank. [**B**] A test trial in which the three landmarks now provide conflicting information. The ×s indicate the locations where an animal would search relative to each landmark. Furthermore, the numbers next to each × indicate the order in which an animal will search for the goal. The back arrows indicate the travel path an animal would take from one search location to another, given the search order indicated by the numbers next to each ×.

Hodges, 1985), rats (Comer & Means, 1989; Means, 1988; Evenden & Robbins, 1984), pigs (Laughlin & Mendl, 2010; Mendl, Laughlin, & Hitchcock, 1997), monkeys (Bicca-Marques, 2005; MacDonald, Pang, & Gibeault, 1994), Great apes (MacDonald & Agnes, 1999; MacDonald, 1994) and fish (Hughes & Blight, 1999), among others (e.g., Winter & Stich, 2005; Burke, Cieplucha, Cass, Russell, & Fry, 2002; Hosoi, Rittenhouse, Swift, & Richards, 1995; Hosoi, Swift, Rittenhouse, & Richards, 1995).

1.3.3 Integrative Strategies

In addition to hierarchical and independent source strategies, animals may also employ integrative strategies to cope with cue conflict. As the name suggests, integrative strategies require animals to combine information from multiple sources, including those that are displaced, to identify a "best guess" location that is close enough to the true goal for success. Integrative strategies are computationally more complex than hierarchical or independent source strategies because they require vector information to be combined from multiple sources. However, because information from many sources are used, integrative strategies can potentially provide a more accurate estimate of a goal's location than other strategies that only rely on information from a single cue to predict where a goal would be.

Integrative strategies can vary widely in complexity, depending on how cues are combined and the type of information used to form the integration. For example, a relatively simple integrative strategy is Pure Averaging, where a straight average is taken between the locations predicted by each available cue (e.g., if two cues predict two different locations, Pure Averaging would predict that the goal would be in the intermediate location between the two goal locations predicted by each cue individually; see Figure 1.6b). Use of a Pure Averaging strategy has been demonstrated in experiments where animals searched in the middle of an array after the array was expanded or contracted (e.g., adult humans: Spetch et al., 1997; MacDonald, Spetch, Kelly, & Cheng, 2004, pigeons: Gray, Spetch, Kelly, & Nguyen, 2004; Sturz & Katz, 2009, chicks: Tommasi & Vallortigara, 2000). Specifically, in such experiments, ani-

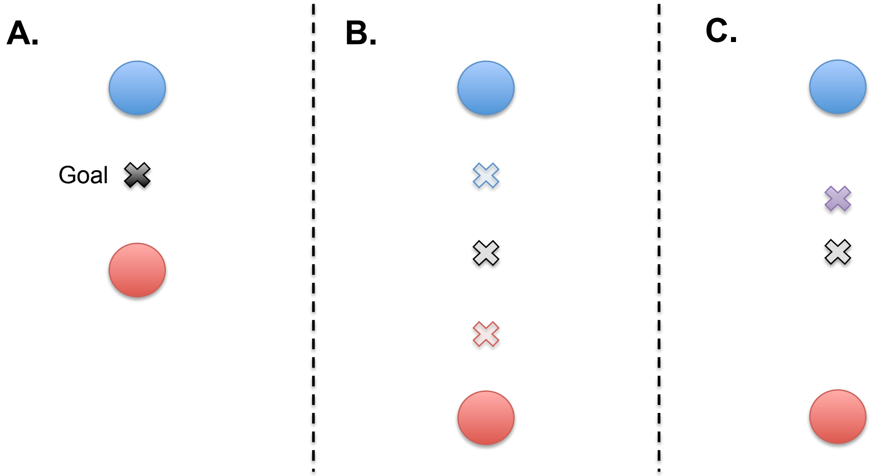

Figure 1.6: Illustration of two integration strategies in a spatial localization task. [**A**] Position of landmarks during training. [**B**] A test trial in which the two landmarks are experimentally separated and thus provide conflicting information. The ×s indicate the search location if an animal was using a hierarchal strategy with the blue (blue ×) or red (red ×) landmark as the highest ranked cue. The grey × indicates the search location if the animal weighted each cue equally. [**C**] Another test trial where the landmarks were experimentally separated and thus provide conflicting information. The grey × indicates the animal's search location if it weighted both cues equally. The purple × indicates the animals search location using a Bayesian integration strategy, assuming the blue landmark was more reliable than the red landmark, and thus was weighted more heavily. In this example, the search location predicted using a Bayesian strategy assumes the weight of the blue landmark to be 0.75, while the weight of the red landmark is assumed to be 0.25.

mals were trained to find a hidden goal in the centre of an array of landmarks or an enclosure. On critical tests, the array or enclosure was either expanded or contracted so that the absolute metric information from individual elements conflicted with the learned position within the array relative to all cues (e.g., the middle of the array or enclosure). In cases where animals responded to the relative location in the array, the results could be interpreted as relying on an integrative, Pure Averaging strategy that used all elements from the expanded/contracted array or enclosure (e.g., Gray et al., 2004).

While an integrative strategy such as Pure Averaging may be relatively simple to implement, it may not be the best strategy to use in all situations. In particular, if an animal had a great deal of experience with a particular set of cues over a number of exposures, it may be better served to use a more complex integrative strategy that would also take into account information derived from past experience. One such strategy, referred to as Bayesian Integration, has recently been proposed for spatial localization in animals (see Cheng, Shettleworth, Huttenlocher, & Rieser, 2007). This strategy assumes that an animal will use information from past experience to determine a cue's reliability relative to other nearby cues. A cue's relative reliability is then used to determine how heavily the information provided by the cue should we weighted. Specifically, the more reliable a cue, the more weight it is given (Cheng et al., 2007; Körding et al., 2007). For example, imagine two cues (A and B) are providing an animal with conflicting information. Based on past experience, the animal knows that cue B is very unreliable, being displaced almost every day. In such a situation, a Bayesian strategy would assume that the animal would not weight the information from cue B very heavily, and thus primarily rely on the information provided by cue A. Thus, when integrating, the animal would choose a location much closer to the location predicted by cue A than would be predicted by a Pure Averaging strategy (see Figure 1.6c).

While Bayesian integration has been shown to be used by adult humans for integrating multiple sources of perceptual information both within (Jacobs, 1999; Jacobs & Fine, 1999; Oruç, Maloney, & Landy, 2003) and across modalities (Deneve & Pouget, 2004; Alais & Burr, 2004; Ernst & Banks, 2002), as well for localizing a goal (Battaglia, Jacobs, & Aslin, 2003), to date very little research has directly investigated whether non-human animals can integrate multiple sources of spatial information in a similar manner for goal localization. Specifically, while some early studies of integration reported results that are suggestive of Bayesian integration (Cheng, 1988, 1989, 1990), these studies were not designed to test for it. This is because Bayesian integration has only recently become a popular theory used to explain multiple cue integration in animals, argueably rising to popularity after publication of Cheng et al. (2007). To my knowledge, only two published papers exist showing evidence that non-human animals can integrate multiple sources of spatial information in a Bayesian fashion. The first paper reanalyzed the data from several previously published experiments (Cheng et al., 2007). Cheng et al. (2007) found that in a study of spatial localization in pigeons by Spetch and Mondloch (1993), pigeons' responses to cue conflict were highly suggestive of a search strategy based on Bayesian inference. The second paper comes from work by Collett (2012) with desert ants. Specifically, Collett (2012) found that when displaced, foraging desert ants integrated information derived from a learned heading direction with information from path integration to choose a direction of travel. Interestingly, ants' chosen direction was consistent with the direction that would be predicted using Bayesian inference. Thus, it seems that animals can use a Bayesian integration strategy to integrate multiple conflicting sources of spatial information, at least in some situations.

1.4 Goal of Current Work

The goal of this work is to further our understanding as to how animals use multiple cues for navigation and goal localization, particularly in situations where cues provide conflicting information. This work will use two model species, specifically pigeons (*Columba livia*) studied in the laboratory, and desert ants (*Melopherous bagoti*) studied in the wild. At first glance, these two species seem incompatible for comparison. However, upon closer examination, they make an excellent comparative sample for understanding multiple cue use in spatial localization. This is because pigeons and ants rely on many similar spatial cues to localize a goal. For example, both pigeons and desert ants use proximal (pigeons: Cheng, Spetch, Kelly, & Bingman, 2006; Kelly, Spetch, & Heth, 1998; ants: Narendra, Si, Sulikowski, & Cheng, 2007; Narendra, 2007) and distal (pigeons: Strasser & Bingman, 1996; Spetch & Edwards, 1988; Legge et al., 2009; ants: Graham & Cheng, 2009, 2009a) visual cues to localize a goal. Furthermore, both pigeons and ants can also use celestial cues to orient themselves (pigeons: Muheim, Moore, & Phillips, 2006; Phillips & Waldvogel, 1988; ants: Schwarz, Albert, Wystrach, & Cheng, 2010; Legge, Spetch, & Cheng, 2010), as well as use many forms of proprioceptive cues for distance estimation and navigation (e.g., Ronacher & Wehner, 1995).

Thus, even though pigeons and ants are physiologically very different, they rely on similar sources of spatial information to accomplish similar tasks (e.g., navigation, orientation, and goal localization). Coupled with the fact that ants and pigeons exploit different ecological niches and methods of navigation (e.g., terrestrial vs. airborne), and have very different neurological structures, similarities in how these animals use and combine spatial information can be particularly illuminating. For example, if both ants and pigeons were found to integrate conflicting distal and proximal visual spatial cues in a similar manner, it would indicate that such an ability: (1) evolved either very early in a common ancestor or via convergent evolution, (2) does not require a complex central nervous system, and (3) does not require a particular ecological niche for exploitation.

My work described in this thesis investigates multiple cue use in both pigeons and ants in five chapters. In Chapters 2 and 3 I describe experiments that test specific properties of multiple cue use in both pigeons and ants, while Chapters 4 and 5 describe experiments that test how pigeons and ants cope with spatial cue conflict. Specifically, in both Chapters 4 and 5, I test whether animals use hierarchal, independent or integrative strategies to cope with different types of cue conflict. Readers should note that chapters are arranged in terms of how complex the methods are for investigating multiple cue use in animals. Specifically, chapters progress in terms of how complex a strategy animals are reported to use for coping with multiple sources of conflicting information, from the relatively simple (hierarchal strategy use, Chapter 2), to very complex (Bayesian weighted cue use, Chapter 5). How the results from each of these four sets of experiments fit together and enhance our understanding of multiple cue use in animals is discussed in Chapter 6.

1.5 References

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Chapter 2

Pigeons' (*Columba livia*) hierarchical organization of local and global cues in touch screen tasks

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2.1 Abstract

Redundant encoding of local and global spatial cues is a common occurrence in many species. However, preferential use of each type of cue seems to vary across species and tasks. In the current study, pigeons (*Columba livia*) were trained in three experiments on a touch screen task which included redundant local positional cues and global spatial cues. Specifically, pigeons were required to choose the middle out of three choice squares, such that the position within the array provided local information and the location on the screen provided global information. In Experiment 1, pigeons were trained and tested on vertically aligned arrays. In Experiment 2, pigeons were trained and tested on horizontally aligned arrays, and in Experiment 3, pigeons were trained and tested with vertical, horizontal and diagonally aligned arrays. The results indicate that preference for cue type depends upon the type of spatial information being encoded. Specifically, on vertical and diagonally aligned arrays, pigeons preferred global cues, whereas on horizontally aligned arrays, pigeons preferred local cues.

2.2 Introduction

Spatial information is important for all animals that navigate through their environment, and can be critical for many activities including procuring food, returning to mates, and locating suitable breeding sites (Gallistel, 1990). However, the type of spatial information used by animals for orientation and navigation can vary widely among species, the type of task to be performed, and the environment in which the animal resides. The various types of spatial information animals use to orient and navigate can be broadly categorized as providing either local or global cues. The terms local and global are arbitrary and context-specific. In general, however, local cues are close to the goal and can include non-spatial visual features at or near the goal (e.g., a color or pattern), spatial cues provided by objects near the goal (e.g., local landmark or beacon) or positional cues (e.g., position in an array of objects). Global cues are more distal and can include stable environmental cues such as a mountain ridgeline or the edge of a ravine (Hurly & Healy, 1996), an absolute location within an arena (Spetch & Edwards, 1988), or the geometry of an enclosure (Tommasi & Vallortigara, 2004). Many species have been shown to encode different kinds of spatial information redundantly, including many avian species (e.g., black capped chickadees, Brodbeck, 1994; pigeons, Kelly et al., 1998; dark-eyed juncos, Brodbeck & Shettleworth, 1995; hummingbirds, Hurly & Healy, 1996; Clark's nutcrackers, Gibson & Kamil, 2001; marsh and blue tits, Clayton & Krebs, 1994), and several species of mammals (e.g., rats, Cheng, 1986; squirrels, Nesterova, 2007; dogs, Fiset et al., 2000).

Redundant encoding of local and global cues is thought to be an adaptive strategy for at least two reasons. First, encoding multiple cues allows animals to use both types of cues in tandem to more accurately pinpoint a location than is possible using only a single cue (e.g., Kamil & Cheng, 2001). Second, redundant information may provide a back-up source of information in the event that one cue is lost or changes suddenly (e.g., a sudden snowfall; a flash flood). Encoding both local and global information makes it more likely that at least one source will remain intact (i.e., a snowfall will obscure local cues on the ground, but not global cues such as the ridgeline of a mountain). For example food-storing birds living in northern climates can still recover food-caches that they stored in the fall even after the land is covered in snow (Sherry, 1992; Vander Wall, 1982; Bossema, 1979).

Although redundancy in encoding of local and global cues has been demonstrated in many species, the hierarchical organization of these cues appears to vary across species. For example, in a study with pigeons by Spetch and Edwards (1988), the goal was redundantly defined by the location in the room (global cue) and the position of the goal in an array of containers (local cue). Both cues were encoded but when a conflict existed between local and global cue information, the local cue information was preferred. However, in similar kinds of tests, chickadees (Brodbeck, 1994), Clark's nutcrackers (Gould-Beierle & Kamil, 1996), hummingbirds (Hurly & Healy, 1996) and Columbian ground squirrels (Vlasak, 2006a, 2006b) seemed to prefer global cues over local cues when the cues were placed in conflict. Furthermore, Brodbeck and Shettleworth (1995) found that dark-eyed juncos (a non-storing bird) showed no consistent preference between local and global cues, indicating species differences in preferred cue use. The hierarchical organization of preferential cue use can also vary by individual within species (adult humans, Steck & Mallot, 2000) and may change with age (squirrels, Nesterova, 2007).

In many recent studies, redundant cues for orientation have been provided by the geometry of an enclosure and features near the goal. With only a few exceptions (e.g., Gray et al., 2005), organisms readily encode geometric information, but species and developmental differences have been found in the extent to which local features are also used (see Cheng & Newcombe, 2005 for a review). Interestingly, the use of featural information also appears to depend on the size of the enclosure for young children (Learmonth et al., 2002), chicks (Vallortigara et al., 2005), and fish (Sovrano et al., 2005): in each of these species, features were more likely to be encoded or preferred in larger enclosures than in smaller enclosures. These results indicate that stimulus factors can play an important role in the hierarchy of cue use.

The present study was designed to investigate stimulus factors in pigeon's use of redundant local position cues and global location cues. In the study by Spetch and Edwards (1988), pigeons showed a strong preference for local positional cues over global room location cues. However, the more typical result in other species appears to be a preference for global location cues over local position cues. In the present study, we developed a touch-screen analogue of Spetch and Edwards' open-field experiment to determine if pigeons' hierarchical organization of cue use would generalize to a different type of search task with a vertically oriented search space (i.e., a touch screen). We also varied the orientation of the positional information (vertically, horizontally or diagonally aligned arrays) to determine whether orientation of the array alters the hierarchy of cue use. In our experiments, pigeons were trained with different arrays of three yellow squares on a touch-screen. In training, a peck to the middle square was reinforced. In this case, the positional information of the correct square within the array (i.e., the middle) was considered to be the local cue information because it was provided by nearby visual cues (i.e., the other choice locations in the array). The specific position of the goal square on the screen was considered to be the global cue information. This global information could be provided by any of a number of cues, including proprioceptive cues, distance from the edges of the screen, location relative to food hoppers, or geometric properties of the screen or operant chamber. Pigeons were given a variety of tests in which the position of the array on the screen was altered or local and global cues were placed in conflict, to determine whether the pigeons independently encoded both local and global information and which of the two types of information dominated.

Three experiments were conducted. In Experiment 1, pigeons were trained with only vertically aligned arrays. In Experiment 2, pigeons were trained with only horizontally aligned arrays. In Experiment 3, pigeons were trained with horizontal, vertical, and diagonally aligned arrays. These studies were designed to determine whether pigeon's hierarchical organization of cue use in an operant task would remain consistent with those reported by Spetch and Edwards (1988) in the open field (i.e., show a preference for local information), and whether pigeons' preferences would change depending on the orientation of the array.

2.3 Experiment 1: Vertical Array

2.3.1 Method

Subjects

The subjects were four adult pigeons (*Columba livia*) with varied previous experience in tasks conducted on computer screens. None had any previous training with tasks requiring a choice between discrete spatial locations. 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 0600). Grit and water were freely available in the home cages.

Stimuli and Apparatus

The choice stimuli were identical yellow squares, approximately 3 cm × 3 cm. The locations of the squares were selected using a 9 column × 7 row grid (not visible to subjects). In training, three choice squares were aligned vertically in the center of the computer screen (horizontal grid location five from left). The correct square was at vertical grid location four from the top of the screen (see Figure 2.1). In testing, the number and location of the squares varied across trials. The experiment was conducted in custom-built operant chambers, equipped with a 15-inch color LCD screen and an infrared touch frame that recorded the location of the pigeons pecks. The touch frame was fitted to an opening of approximately 29 cm × 22 cm at the back wall of the chamber and the monitor was attached behind the frame. The chamber 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 1–2 s of feeding duration, depending on the weight of the bird. Computers located in an adjacent room controlled the experimental contingencies and recorded the responses.

Training

The pigeons received one session per day, 5 or 6 days per week. A few of the birds required pretraining to establish reliable pecking at a yellow square. During pretraining sessions, a single yellow square was presented in a randomly selected location on the computer screen for 8 s or until the bird pecked at it, after which food was presented. Pretraining sessions were given until the bird pecked at the square on over 80% of the trials. During training, each trial began with the presentation of the three vertically aligned yellow squares against a grey background. The first peck in any of the three squares terminated all three stimuli, leaving a blank grey screen. A peck to the center stimulus was followed by a food reward, whereas a peck to the top or bottom square terminated the trial without food. The trial also ended without food if the bird failed to peck any of the stimuli within 2 min of stimulus onset. A 5 s intertrial interval with the grey screen preceded the start of the next trial. Each session contained 64 trials. Once pigeons reached an accuracy criterion of a minimum of 80% correct choices over 2 consecutive days, the percentage of reinforcement for correct choices was decreased over sessions to 75% and then to 50%. Non-reinforced correct choices resulted in termination of the trial without food. This was designed to encourage persistent choice behavior in the subsequent testing phase. The pigeon moved to testing when they reached an accuracy criterion of a minimum of 80% for five consecutive sessions on 50% reinforcement.

Testing

Ten testing sessions were presented, each containing 36 training trials with reinforcement for correct responses, nine non-reinforced training trials, and 21 non-reinforced probe trials. The order of training and test trials was randomized within each block of 22 trials. There were four types of probe tests. In *Conflict Tests*, the three squares were moved down or up by one grid location; this produced a conflict between the local cues (middle position in the array) and the global cues (location on the screen). On *2-Choice Tests*, either the top or the bottom square was removed, thus eliminating the local cues provided by position in the array. On *Horizontal Move Tests*, the three squares were moved horizontally by one grid location either to the left or the right, but the vertical location of the array remained unchanged. Finally, in the *5-Choice Test*, an extra square was added to each side of the array. In this case, the middle square was still in the globally correct screen location. Depending on how the local information was encoded, any of the three center squares might serve as locally correct locations.

Data Analyses

The data in these experiments are frequencies of pecks to each of the presented locations. Following the lead of Brodbeck (1994), we analyzed these frequencies using a replicated G-test of Goodness of Fit (Sokol & Rohlf, 1995), which is distributed as a chi-square but allows one to pool data from several subjects and separate variance due to individual subjects from variance due to choice locations. For each test condition, we report the pooled G-statistic (G_p: which tests whether choice frequencies differ from expected frequencies pooled across all subjects) and the G-statistic for heterogeneity (G_h: which tests for differences among birds). When inter-bird differences were significant, we also report G-statistics for individual birds. All statistics are presented in Appendices A–C. For between condition comparisons (e.g., training to test trials), we calculated the proportion of responses made by each bird to a particular location and then analyzed the results with a paired t-test.

For some test conditions (e.g., *2-Choice* and *Training*), we analyzed responding to all presented locations. However, for other conditions (e.g., *Conflict*) the comparison of interest was between a subset of the locations presented (e.g., globally or locally correct locations). In these cases, we graphically present the frequencies for all presented locations, but we report statistical comparisons between only the relevant subset. Finally, we summed across tests that were functionally equivalent (e.g., *Conflict tests* in which the locations were moved up or down) both for graphical presentation and statistical analyses.

2.3.2 Results

The four pigeons took between 31 and 59 sessions of training (mean = 42) to reach the criterion required to start testing. During test sessions, accuracy in selecting the middle location on training trials was high for all birds (78% to 90%, mean = 84%) and was significantly above chance (33%), $t(3) = 15.6$, $p < .01$.

Figure 2.1 shows choice behavior on each type of test trial. The outlined squares indicate the particular choice locations available on a particular trial type, and the size of the filled square corresponds to the proportion of choices of that location.

In *Conflict Tests*, birds chose the globally correct location most frequently and the locally correct location with the next highest frequency. The location that was neither globally nor locally correct was never chosen by one bird and infrequently chosen by the remaining birds. A comparison of the frequencies to the globally or locally correct locations revealed that most choices were to the globally correct location, $G_p(1) = 19.6$, $p < .001$ but inter-bird differences were also significant, G_h $(3) = 8.7$, $p < .05$. Two of the four birds showed a significant preference for the globally correct location. The remaining two birds showed a non-significant preference for the globally correct location. In *2-Choice Tests*, the birds showed a significant preference for the globally correct location, G_p $(1) = 231.2$, $p < .001$ and there was no significant inter-bird variation. Moving the vertical array to the left or right in *Horizontal Move Tests* had little apparent effect on choice behavior: the birds continued to show highly significant choice of the middle location compared to the two outer locations, G_p $(1) = 319.8$, $p < .001$ and there was no significant variation among birds. Moreover, the proportion of choices in the vertically central location on *Horizontal Move* trials (82%) was not significantly different from that on training trials (84%), $t(3) = 1.56$, $p > .1$. The birds also continued to respond most frequently to the middle location on the *5-Choice Test* in which an extra location was added above and below the array. Comparison

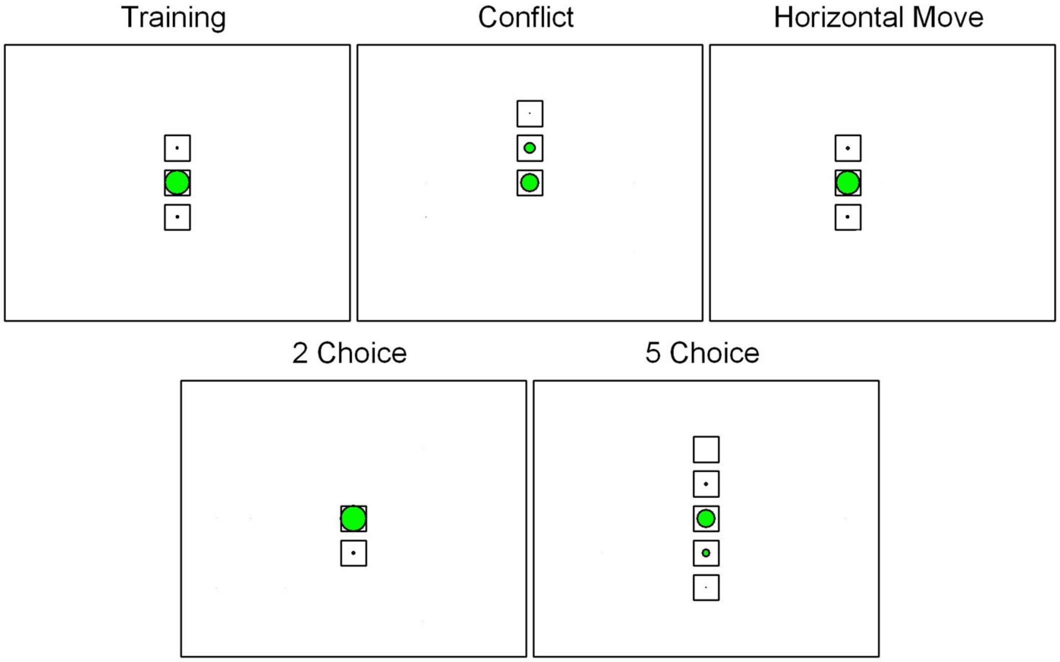

Figure 2.1: Proportion plots for each type of test trial in Experiment 1. The small squares are the individual squares of each array and indicate where the array was located on the screen. The size of the shaded circle inside the squares indicates the proportion of choices birds made to that particular location across test trials.

of choices to the middle location vs. the two inner locations revealed above chance choice of the middle location, $G_p\ (1) =\ 59.02,\ p\ <\ .001$ with no significant inter-bird variation. However, choice of the center location (63%) was lower than on training trials and this decrease approached significance, $t(3) =\ 2.98,\ p\ <\ .06$. In summary, the birds appeared to be unaffected by a small horizontal shift in location but were slightly affected by the addition of two outside locations on the *5-Choice Test*.

2.3.3 Discussion

The results of Experiment 1 indicate stronger control by the global vertical location on the screen than by the local position in the array. Specifically, pigeons showed strong control by the globally correct vertical location on *2-Choice Tests* when only global information was available and control by the global location dominated when local and global cues were placed in conflict.

This dominance of global over local cues contrasts with the results found by Spetch and Edwards (1988) for pigeons in an open room. It seems possible that global vertical location is highly salient to a pigeon pecking on a computer screen because distinct proprioceptive cues would be correlated with pecking at different heights. If so, then global location may be less dominant in the horizontal dimension. Experiment 2 was similar to Experiment 1 except that the training array was aligned horizontally rather than vertically, and some additional tests were included.

2.4 Experiment 2: Horizontal Array

2.4.1 Method

Subjects

The subjects were seven adult pigeons (*C. livia*) with varied previous experience in tasks conducted on computer screens. None had any previous training with tasks requiring a choice among discrete spatial locations. The birds were maintained and housed as described in Experiment 1.

Stimuli and Apparatus

The stimuli and experimental chambers were the same as described in Experiment 1. In training, three choice squares were aligned horizontally on the computer screen (see Figure 2.2). The correct location was five grid locations from the left and three grid locations from the top of the screen. In testing, the number and location of the squares varied across trials.

Training

The procedure was identical to Experiment 1 except that during training the three yellow squares were aligned horizontally. A peck to the center square was followed by a food reward, whereas a peck to the left or right square terminated the trial without food. All other aspects of the procedure remained unchanged from Experiment 1.

Testing

Ten testing sessions were presented, each containing 36 training trials with reinforcement for correct responses, 12 non-reinforced training trials, and 30 non-reinforced probe trials. The order of training and test trials was randomized within each block of 26 trials. There were six general types of probe tests. In *Conflict Tests*, the three squares were moved left or right by one location; this produced a conflict between the local (middle position in the array) and global cues (location on the screen). In *2-Choice Tests*, either the left or the right square was removed, thus eliminating the local cues provided by position in the array. In *Vertical Move Tests*, the three squares were moved down by three locations, but the horizontal location of the array remained unchanged. In *Horizontal Move Tests*, the three squares were moved left or right by three locations, but the vertical location of the array remained unchanged. In *5-Choice Tests*, an extra square was added to each side of the array. In this case, the middle square was still in the globally correct screen location. Finally, in *5-Choice Horizontal Move Tests*, five squares were presented but the horizontal location of the array was shifted left or right. In these tests, the middle square of the array was shifted by two locations left or right of the middle square in training so that the square on the edge of the array was in the globally correct screen location.

2.4.2 Results

The seven pigeons took between 16 and 93 sessions of training (mean = 41) to reach the criterion required to move to testing. During testing, accuracy in selecting the middle location on training trials was high for all birds (69%–94%, mean = 78%) and was significantly above chance (33%), $t(6) = 12.4$, $p < .001$.

Test results are shown in Figure 2.2. In *Conflict Tests*, birds chose the locally correct location most frequently and the globally correct location with the next highest frequency. The location that was neither globally nor locally correct was never chosen by one bird and infrequently chosen by the remaining birds. In trials in which the birds chose a globally or locally correct location, most choices were to the locally correct location, $G_p\ (1) = 65.5$, $p < .001$ but inter-bird differences were also significant, $G_h\ (6) = 20.7$, $p < .01$. Although all seven birds chose the locally correct location most frequently, the degree of preference varied and preference for the locally correct location was not significant for two of the birds.

In *2-Choice Tests*, in which local cues were removed, there was a significant overall preference for the globally correct location, $G_p\ (1) = 29.15$, $p < .001$. Inter-bird variation was not significant.

In the *5-Choice Tests*, the birds never (three birds) or infrequently (four birds) chose the added locations. Comparison of the middle location to the two inner locations revealed a significant preference for the middle location, $G_p\ (1) = 24.0$, $p < .001$ with no significant inter-bird variation. Nevertheless, the addition of the two outside locations affected pigeons' choice of the three center locations. Considering only the center three locations, the birds chose the middle location 50% of the time which was significantly lower than choice of the center location on training trials (78%), $t(6) = 7.3$, $p < .001$.

Moving all squares three locations down on the screen on the *Vertical Move Tests* had a substantial effect on the pigeons' behavior. Six of the seven birds failed to peck one of the squares on some of the trials; across all birds an average of 34% of the trials ended without a choice. On the trials in which a peck occurred, the middle square was not chosen significantly more than the two outer locations, $G_p\ (1) = 0.4$, $p > .05$ and inter-bird variation was also not significant, $G_h\ (6) = 9.9$, $p > .05$. Only one bird showed a significant preference for the middle location. Thus, the tendency to choose the horizontally middle location did not transfer to an array lower on the screen.

In the *Horizontal Move Test*, four pigeons never chose the square furthest from the training locations and three pigeons chose it only once. Therefore, we compared choice of the locally correct middle square to choice of the outer square that was closest to the training locations. The birds showed a significant preference for the globally closer outer location over the middle location, $G_p\ (1) = 107.8$, $p < .001$. Although inter-bird differences were also significant,

G_h (6) = 21.08, $p < .01$ all birds chose the globally correct location more than the middle location and this preference was significant for all but one bird.

Finally, in the *5-Choice Horizontal Move Test*, pigeons rarely (two birds) or never (five birds) chose the two locations farthest from the training area. Choice of the location that was in the middle of the array was also very low (less than 7% of the trials on average with no bird choosing the middle square on more than 12% of the trials). We therefore compared the globally correct outer location to the closest inner location. The birds showed a significant preference for the inner location, G_p (1) = 20.1, $p < .001$. There was no significant inter-bird variability, G_h (6) = 5.01, $p > .05$.

2.4.3 Discussion

In summary, the results of the *Conflict* and *2-Choice* tests are similar to those found by Spetch and Edwards (1988) for pigeons in an open room, and they contrast with those found in Experiment 1 with a vertical array. Specifically, pigeons showed hierarchical redundant control by local and global cues: the local position in the horizontal array dominated in *Conflict Tests*, but global location was also encoded. However, the remaining tests indicated that control by local position was constrained by global location cues. When the array was moved far from the correct global location, either in the vertical or horizontal dimension, pigeons did not continue to select the locally correct square. This latter result contrasts with the findings of Spetch and Edwards in the open field. In their study, pigeons continued to choose the locally correct location even when the array was moved far from the global training location in the room.

In Experiment 3, we trained pigeons with vertical, horizontal and diagonal alignments of the array to provide a within-subject comparison of cue use at different array orientations. Experiment 3 was also designed to assess whether global cues would still exert control if they provided imprecise information in training. Specifically, each array orientation occurred in three different absolute locations on the screen so that, across all trials, the correct global

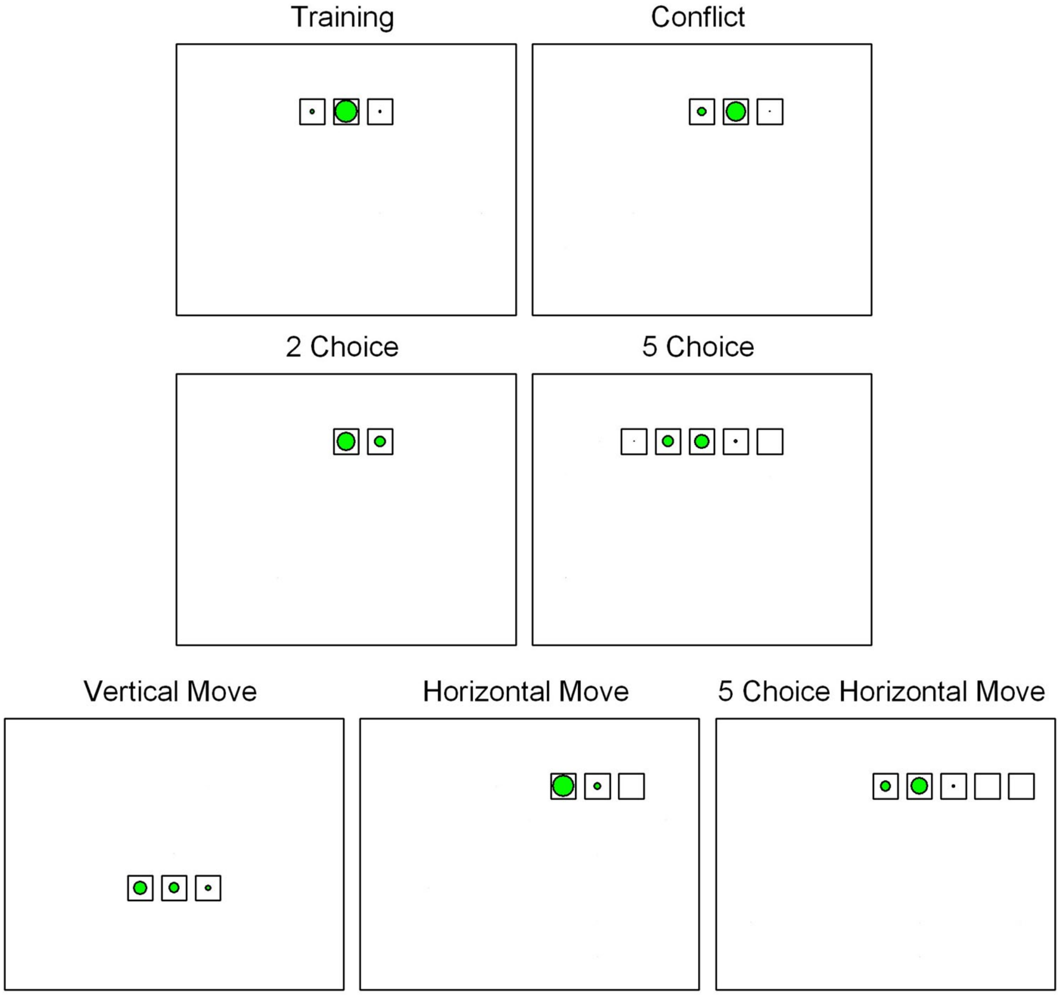

Figure 2.2: Proportion plots for each type of test trial in Experiment 2. The small squares are the individual squares of each array and indicate where the array was located on the screen. The size of the shaded circle inside the squares indicates the proportion of choices birds made to that particular location across test trials.

location was a set of nine possible locations rather than single fixed location on the screen (see Figure 2.3 for more detail).

2.5 Experiment 3: Vertical, Horizontal and Diagonal Arrays

2.5.1 Method

Subjects

The subjects were seven adult pigeons (*C. livia*) with varied previous experience in tasks conducted on computer screens. None had previously been trained to make a discrete spatial choice. The birds were housed and maintained as described in Experiment 1.

Stimuli and Apparatus

Three birds were tested in the same experimental chambers described in Experiment 1. The chamber for the four remaining birds was equipped with a 19 inch monitor and had a 34 × 24 cm opening for the touch frame. Trials began with a white circular (diameter = approximately 3 cm) start stimulus that appeared in a random screen location. The choice stimuli were smaller yellow squares (approximately 2.3 × 2.3 cm) than those used in the first two experiments. In training three squares were aligned either horizontally, vertically, or diagonally in a central area of a computer screen with a 3 mm space between each square. In testing, the number and location of the squares varied as described in the testing procedure. The locations of the squares were selected using a 7 × 7 square grid (not visible to subjects) that had a 4.88 cm border on the left and right sides of the screen and a 1.49 cm border on the top and bottom of the screen. This border prevented squares from appearing outside the visible screen area. The border was not visible to subjects.

Training

The pigeons received one session per day, 5 or 6 days per week. All birds first received pretraining to establish reliable pecking at a white circle which appeared randomly on the computer screen. After birds reached a criterion of pecking the white circle 80% of the time within 180 s of it being displayed for 2 consecutive days, subjects were moved to training. In training, the white circle appeared on the screen until the pigeon pecked it, at which time it disappeared and three choice stimuli (i.e., the yellow squares described above) appeared near the middle of the screen in either a vertical, horizontal, or diagonal orientation. For each orientation, the array of choice stimuli occurred equally often in three absolute screen locations. In all cases, the locally correct (middle) square was positioned within a central area of the screen. Across the three orientations, the locally correct square appeared in nine central locations of the 7 × 7 grid (see Figure 2.3 for more detail). After pretraining, subjects received three phases of training, which differed in percentage of reinforcement. The initial training phase provided 100% reinforcement for correct pecks, whereas the second and third training phases provided 75% and 50% reinforcement, respectively. Subjects had to choose the center square in all orientations significantly more often than chance across a five day period in order to advance to the next training phase, and across a 10 day period to advance from the final phase of training to testing. Chi-square tests were conducted to determine if these criteria were met.

Testing

Testing consisted of 10 sessions of 72 trials. Each session had 36 training trials, 12 control trials (i.e., non-reinforced training trials; see Figure 2.4), and 24 test trials, presented in a random order within blocks of 36 trials. For control tests, two of the three training arrays from each orientation were used. The test trials were novel displays of choice stimuli. For each orientation (i.e., horizontal, vertical and diagonal) there was a *2-Choice test*, a *4-Choice test* and a *5-Choice test*. In the horizontal orientation, there were also two distant array tests (*Far Horizontal A* and *Far Horizontal B*) in which the arrays of three squares were moved to the distant edges of the screen so that they were as far as possible from the globally correct area of the screen. Finally, there was a diagonal rotation test in which the horizontal axis of a three square diagonal

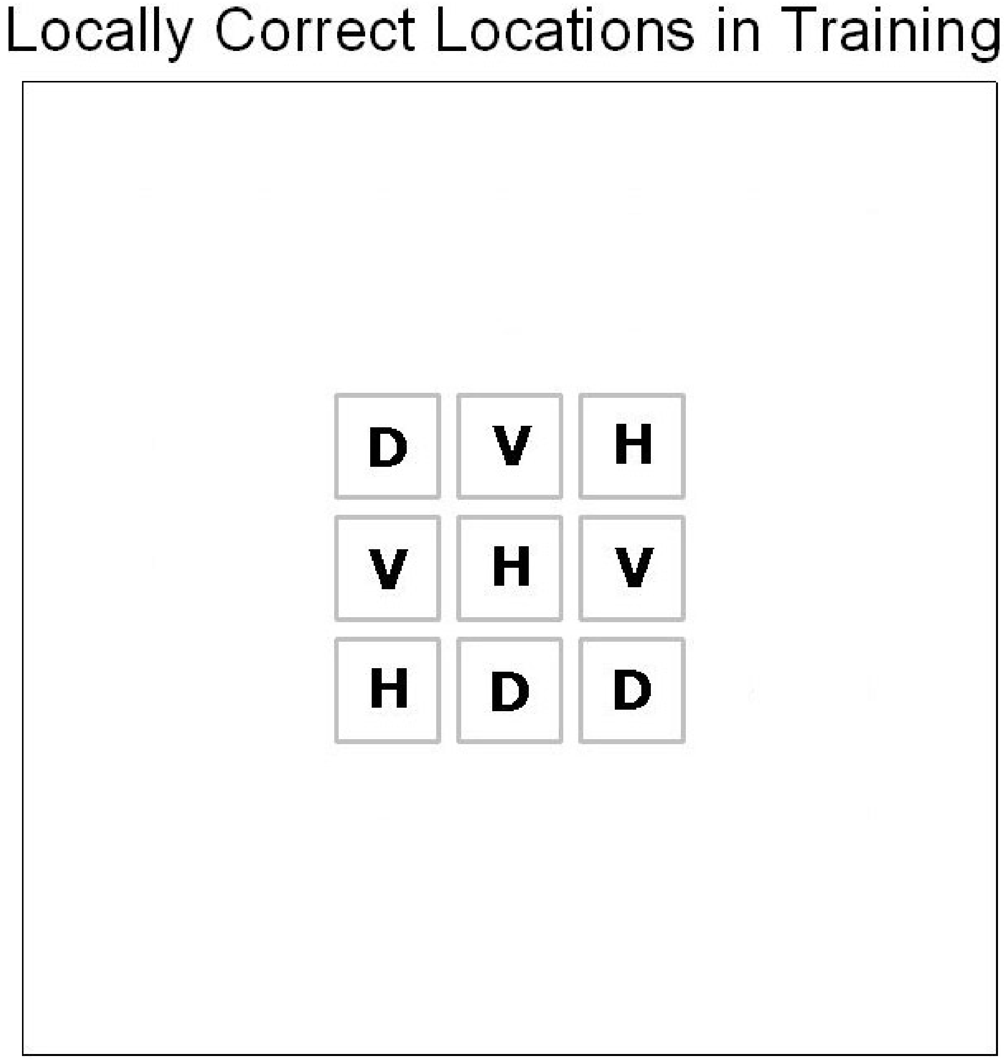

Figure 2.3: This figure indicates where on the screen the center (reinforced) square was for each type of training array in Experiment 3. These locations made up the globally correct area of the screen in test trials. The letter inside each square indicates which type of training array had a central square in that particular location. A “*D*” corresponds to a diagonally oriented training array, a “*V*” to a vertically oriented training array, and a “*H*” corresponds to a horizontally oriented training array.

choice array was transposed so that it was in opposition to the orientation of the diagonal arrays used in training. All birds received all types of tests but the exact position of the array on the screen was as shown in Figure 2.5 for four birds only. For the remaining three birds, the screen positions were transposed for tests to ensure that results were not due to specific screen position effects.

2.5.2 Results

The seven pigeons took between 57 and 102 session of training (mean = 82.42) to reach the criterion required to move to testing. Tests were divided into three categories: horizontally oriented arrays, vertically oriented arrays, and diagonally oriented arrays. Figures 2.4 and 2.5 show choice behavior on each type of test trial. The outlined squares indicate the particular choice locations available on a particular trial type, and the size of the filled circle inside the square corresponds to the proportion of choices to that location. The proportion data is collapsed across all birds for each particular test type displayed.

Horizontally Oriented Arrays

Subjects received two different control tests. In *Control Test A*, birds chose the locally correct square (i.e., the middle square) significantly more often than the two outside squares. The middle square and one of the outside squares were within the globally correct area of the screen. A comparison of frequencies between the middle square and the two outside squares revealed that birds significantly selected the locally correct location more often than the other two locations, $G_p\ (1) = 103.27$, $p < .001$, but there were significant differences among birds, $G_h\ (6) = 14.02$, $p < .01$. All but one of the birds showed a significant preference for the locally correct square; the remaining bird did not show a preference for either square.

In *Control Test B*, birds chose the locally correct square significantly more often than the two outside squares. All three squares were within the globally correct area of the screen. A comparison of frequencies between the middle square and the two outside squares revealed that birds significantly selected the locally correct location more often than the other two locations, $G_p\ (1)$

$= 43.18$, $p < .001$, but there were significant differences among birds, G_h (6) $= 18.54$, $p < .05$. While the majority of birds significantly preferred the locally correct square, two of the birds did not display a preference for any square.

In *2-Choice Tests*, there was no locally correct location but one of the two squares was in the globally correct area of the screen. A comparison of frequencies between the two locations revealed that there was no significant difference between the selection of the globally correct square compared to the other square G_p (1) $= 1.38$, $p > .05$, but there were significant differences among birds, G_h (6) $= 28.32$, $p < .001$. Five of the birds did not show a preference for either square; the remaining two birds displayed a preference for the square that was not in the globally correct location of the screen.

In *4-Choice Tests*, there was once again, no locally correct location, and none of the four squares were within the globally correct area of the screen experienced during training. However, we thought it likely that, although there was no true locally correct location, birds may treat both of the inner two squares as locally correct. A comparison of frequencies between the inner two locations compared to the outside two locations revealed that birds significantly preferred the inner squares to the outer squares, G_p (1) $= 56.98$, $p < .001$. There were no significant differences among birds, G_h (6) $= 8.28$, $p > .05$.

In *5-Choice Tests*, there was a locally correct location (i.e., the middle square), and three globally correct locations (i.e., the inner three squares). The frequencies of choices to the outer two locations were very low, and thus were excluded from the analysis. A comparison of frequencies of the middle square to the other two inner squares revealed no significant difference, G_p (1) $= .67$, $p > .05$. There were no significant differences among birds, G_h (6) $= 4.34$, $p > .05$.

In the *Far Horizontal A* tests, none of the squares were in the globally correct area of the screen, but the middle square was locally correct. A comparison of the frequencies to the locally correct location compared to the other two locations revealed a significant preference for the locally correct location,

G_p (1) = 19.15, $p > .001$. However, there were significant differences among birds, G_h (6) = 26.01, $p < .001$. Four of the seven birds significantly preferred the middle square, one bird significantly preferred the outer two squares, and two birds did not display a significant preference for any square.

In the *Far Horizontal B* tests, none of the three squares were in a globally correct area of the screen, but the middle square was locally correct. A comparison of the frequencies to the locally correct location compared to the other two locations revealed a significant preference for the locally correct location, G_p (1) = 45.30, $p < .001$. However, there were significant differences among birds, G_h (6) = 31.78, $p < .001$. Five of the seven birds displayed a significant preference for the middle square, while two of the birds did not display a significant preference for any square.

Vertically Oriented Arrays

In *Control Test A*, birds chose the locally correct square (i.e., the middle square) more often than the two outside squares. The middle square and one of the outside squares were inside the globally correct area of the screen. A comparison of frequencies between the middle square and the two outside squares revealed that birds significantly preferred the locally correct location more often than the two outside locations, G_p (1) = 160.22, $p < .001$, but there were also significant differences among birds, G_h (6) = 24.28, $p < .001$. Six of the seven birds preferred the locally correct square, while one bird did not display a significant preference for any square.

In *Control Test B*, birds chose the locally correct square more often than the two outside squares. All squares were within the globally correct area of the screen. A comparison of frequencies between the middle square and the two outside squares revealed that birds significantly selected the locally correct location more often than the other two locations, G_p (1) = 221.66, $p < .001$. There were no significant differences among birds, G_h (6) = 12.04, $p > .05$.

In *2-Choice Tests*, there was no locally correct location but one of the two squares was in the globally correct area of the screen. Overall, birds chose the globally correct square more often than the other, non-globally correct square. A comparison of frequencies between the two locations revealed that birds displayed a significant preference for the globally correct square, G_p (1) = 100.18, $p < .001$, but there were also significant differences among birds, G_h (6) = 20.74, $p < .01$. While six of the seven birds displayed a significant preference for the globally correct square, one bird did not display a significant preference for either square.

In *4-Choice Tests*, there was no locally correct location, and none of the four squares were within the globally correct area of the screen. However, the birds might treat both of the inner two squares as locally correct. A comparison of frequencies between the inner two locations compared to the outside two locations revealed that birds significantly preferred the inner squares to the outer squares, G_p (1) = 223.38, $p < .001$. There were no significant differences among birds, G_h (6) = 8.05, $p > .05$.

In *5-Choice Tests*, there was a clear locally correct location (i.e., the middle square), and three locations within the globally correct area of the screen (the middle square, one inner square and one outer square). The frequencies of choices to both outer locations were very low, and thus were excluded from the analysis. A comparison of frequencies between the middle location and to the two inner squares revealed that birds displayed a significant preference for the middle location, G_p (1) = 18.49, $p < .001$, but there were also significant differences among birds, G_h (6) = 36.13, $p < .001$. Only two of the seven birds displayed a significant preference for the middle location. Four birds did not display a significant preference for any square, while one bird displayed a significant preference for the inner squares. Due to this high level of inter-bird variability, two further comparisons were conducted.

First, we compared choices of the inner square that was outside the global area to choices of the inner square that was inside the global area. Birds significantly preferred the globally correct inner square to the non-globally correct inner square, G_p (1) = 63.90, $p < .001$, but there were significant differences among birds, G_h (6) = 38.13, $p < .001$. Five of the seven birds displayed a significant preference for the globally correct inner square, while two birds did not display a preference for any square.

Second, we compared choices of the globally correct inner square to the middle square, which was locally correct and within the globally correct area of the screen. Birds did not display a significant preference for either square, G_p (1) = .11, $p > .05$, but there were significant differences among birds, G_h (6) = 53.98, $p < .001$. Two out of seven birds displayed a significant preference for the middle square, two birds did not display a preference for either square, and three birds displayed a significant preference for the globally correct inner square.

Diagonally Oriented Arrays

In *Control Test A*, birds chose the locally correct square (i.e., the middle square) significantly more often than the two outer squares. The middle square, and one of the outside squares were inside the globally correct area of the screen. A comparison of frequencies between the middle square and the two outer squares revealed that birds displayed a significant preference for the locally correct location, G_p (1) = 34.92, $p < .001$, but there were significant differences among birds, G_h (6) = 14.66, $p < .05$. While six of the seven birds displayed a significant preference for the locally correct square, one bird did not display a preference for any square.

In *Control Test B*, birds chose the locally correct square significantly more often than the two outer squares. The middle square and one of the outside squares were inside the globally correct area of the screen. A comparison of frequencies between the middle square and the two outer squares revealed that birds displayed a significant preference for the locally correct location, G_p (1) = 141.06, $p < .001$, but there were significant differences among birds, G_h (6) = 14.97, $p < .05$. While six of the seven birds displayed a significant preference for the locally correct square, one bird did not display a preference for any square.

In *2-Choice Tests*, there was no locally correct location and neither square was in the globally correct area of the screen. However, one of the squares was closer to the globally correct area of the screen than the other. A comparison of frequencies between the two locations revealed that birds displayed a significant preference for the square closest to the globally correct area of the screen, G_p (1) = 245.67, $p < .001$, but there were also significant differences among birds, G_h (6) = 54.93, $p < .001$. While six of the seven birds significantly preferred the square closest to the globally correct area of the screen, one bird did not display a preference for either location.

In *4-Choice Tests*, there was once again, no locally correct location but birds may treat both of the inner two squares as locally correct. Two of the four squares (one inner and one outer square) were within the globally correct area of the screen. A comparison of frequencies between the two inner locations and the two outer locations revealed that birds displayed a significant preference for the inner squares, G_p (1) = 13.97, $p < .001$, but there were significant differences between birds, G_h (6) = 35.73, $p < .001$. Only two of the seven birds displayed a significant preference for the inner squares; the remaining five birds showed no significant preference. Only one of the inner squares was within the globally correct area of the screen. A comparison of frequencies between the globally correct inner square and the other inner square that was outside the globally correct area revealed that birds displayed a significant preference for the globally correct inner square, G_p (1) = 136.54, $p < .001$, but there were significant differences among birds, G_h (6) = 15.97, $p < .05$. All birds significantly preferred the globally correct inner square to the other inner square, but the magnitude of their preference varied.

In *5-Choice Tests*, the middle square was both locally and globally correct. None of the other squares were in the globally correct area of the screen. The frequencies of choices to the two outer squares were very low, and thus were excluded from the analysis. Therefore, we analyzed the middle square against the two inner squares. A comparison of frequencies revealed that birds did not display a significant preference for the middle square which was both locally and globally correct, G_p (1) = 3.63, $p > .05$. However, there were significant differences among birds, G_h (6) = 20.34, $p < .01$. Only one of the seven birds displayed a significant preference for the middle square.

In *Diagonal Rotation Tests*, one of the outside squares was in the globally correct area of the screen. The other outside square was neither locally or globally correct. None of the birds ever selected the square that was neither globally or locally correct and thus it was excluded from the analysis. A comparison of frequencies between the locally (i.e., middle) and globally correct (i.e., outside) squares revealed that birds displayed a significant preference for the globally correct square, G_p (1) $=$ 143.38, $p < .001$, but there were significant differences among birds, G_h (6) $=$ 38.19, $p < .001$. Six out of the seven birds displayed a significant preference for the globally correct location, while one bird did not display a preference for either square.

Discussion

Clearly, hierarchical control by local and global cue information is variable and depends on the type of spatial information encoded. Specifically, when the local spatial cues were horizontally aligned, local cue information appeared to dominate and overshadow global cue information. This is best shown by results from the horizontal *2-Choice* and*4-Choice* tests where local cues were absent or ambiguous and the pigeons did not seem to rely on global cues. However, when the local spatial cues were either vertically or diagonally aligned, global cue information seemed to dominate local cue information. This is evidenced by results from the vertical *2-* and *5-Choice* tests, as well as the diagonal *2-Choice*, *4-Choice*, and *Rotation* tests. In sum, the results of Experiment 3 suggest that pigeons' hierarchical ordering of local and global cues for retrieval depends on the orientation of the information being encoded. When stimuli are horizontally aligned, local cues seem to be preferred to global cues. When stimuli are vertically or diagonally aligned, pigeons appear to prefer global cues to local cues, but they can use local cues when global information is not present or is ambiguous.

2.6 General Discussion

Our experiments demonstrate that the hierarchical ordering of spatial information varies according to the type of spatial information being encoded. When arrays were horizontally aligned, pigeons primarily attended to and used local

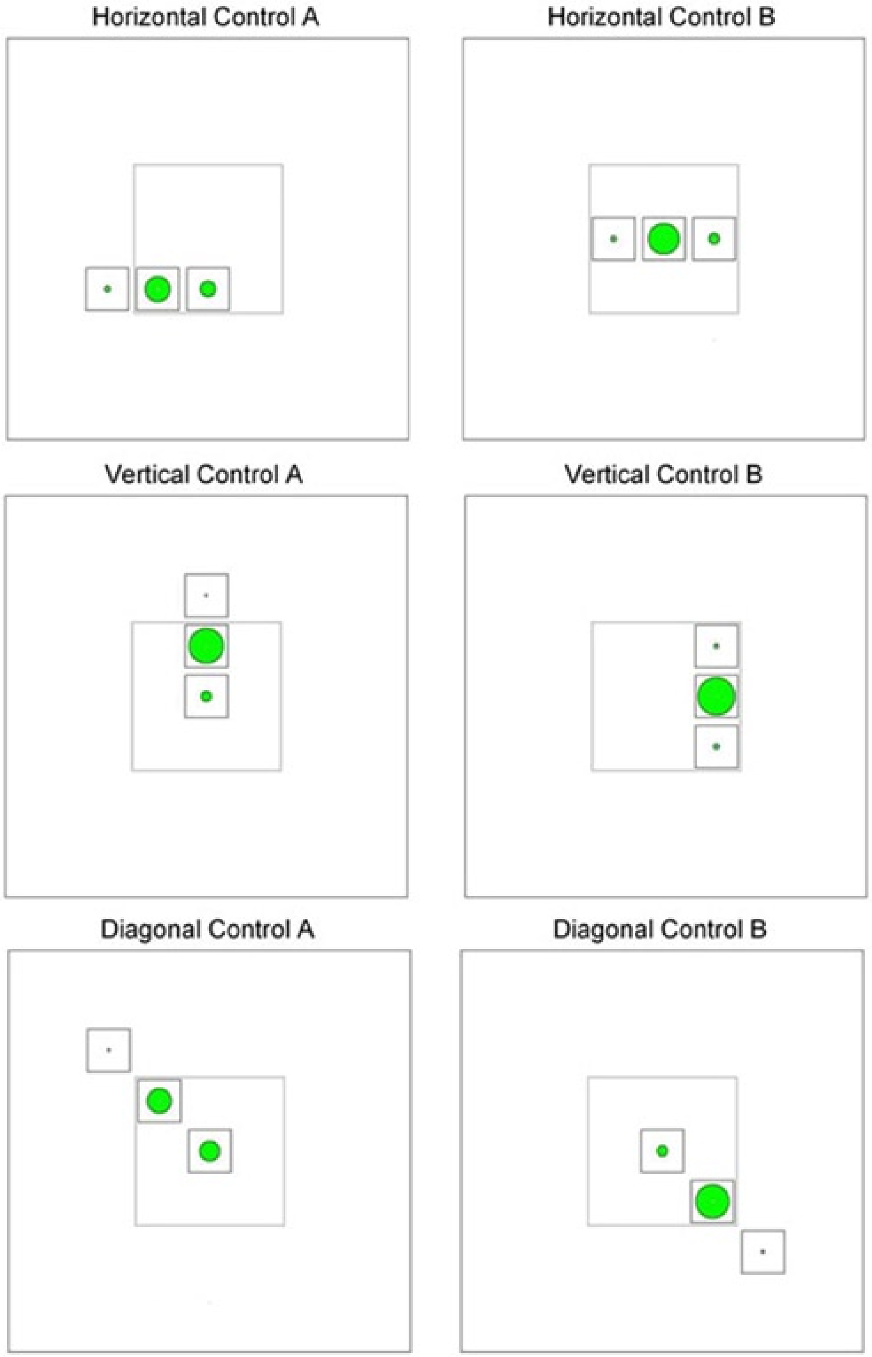

Figure 2.4: Proportion plots for each type of control test trial in Experiment 3. The large, central square in all figures indicates the globally correct area of the screen. The small squares are the individual squares of each array and indicate where the array was located on the screen. The size of the shaded circle inside the smaller squares indicates the proportion of choices birds made to that particular location across test trials.

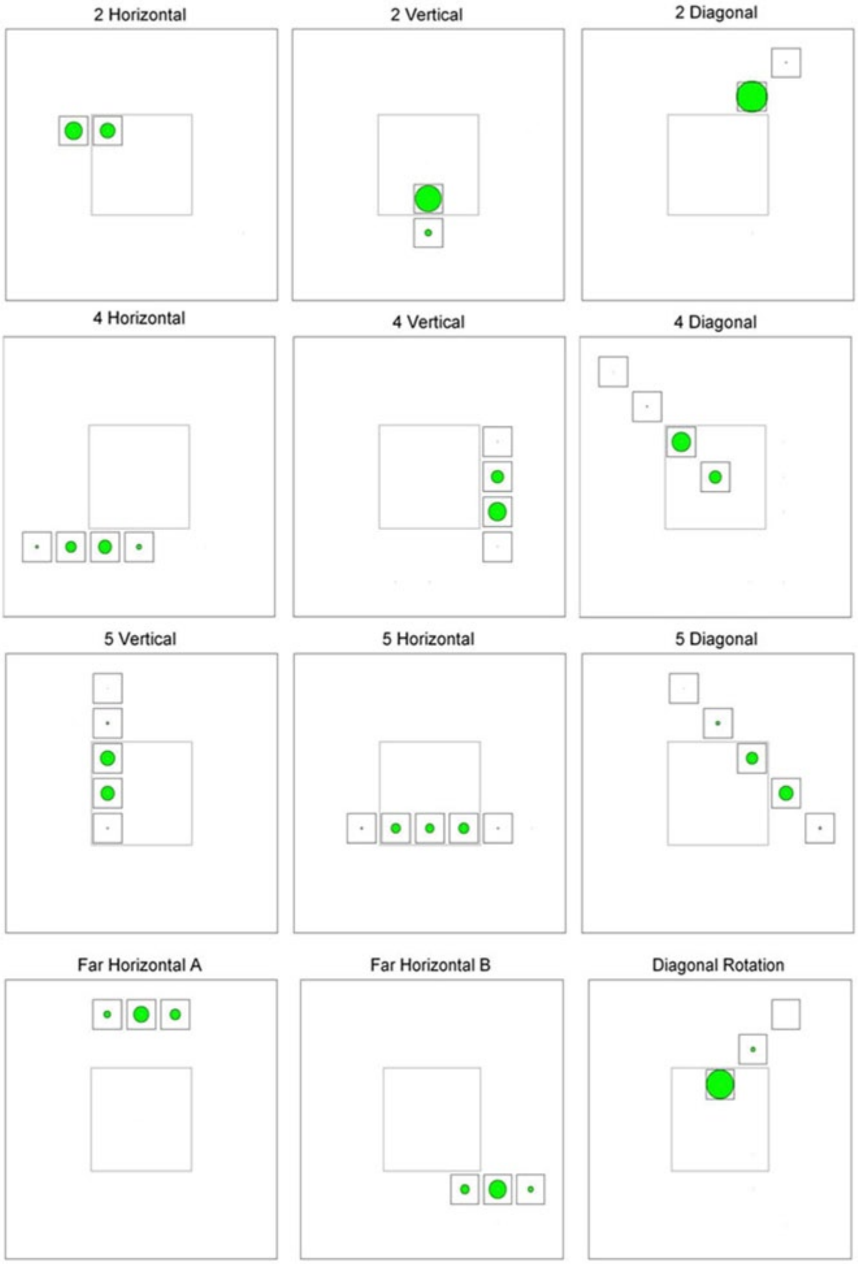

Figure 2.5: Proportion plots for each type of test trial in Experiment 3. The large, central square in all figures indicates the globally correct area of the screen. The smaller squares indicate the individual squares of each array and indicate where the array was located on the screen for the first four birds. Arrays for the remaining three birds were transposed for all tests. However, because there was no significant difference between birds who received the arrays depicted above and those who received transposed arrays, data was collapsed. The size of the shaded circle inside the smaller squares indicates the proportion of choices birds made to that particular location across test trials.

cues. In contrast to this, when arrays were vertically or diagonally aligned, pigeons primarily attended to and used global cues. These findings indicate that the hierarchical organization of spatial information is flexible and that the cues pigeons use depend in part upon environmental factors.

Our finding that pigeons rely on global cues much more when arrays are vertically aligned is interesting and could reflect the operation of a gravity-defined privileged axis. Results suggesting that gravity-defined axes may be privileged have been reported in various species (e.g., bees, Cartwright & Collett, 1982; ants, Rossel & Wehner, 1986; humans, Kelly & Spetch, 2004a; pigeons, Kelly & Spetch, 2004b). Vertically aligned arrays that were presented against a stable environmental background such as the computer screen may have encouraged orientation-specific encoding of global cue information. To determine if this was the reason for the enhanced control by global cues in vertically aligned arrays, it would be interesting to test pigeons in an operant box in which a touch screen is horizontally positioned on the floor (e.g., Wright, Cook, Rivera, Sands, & Delius, 1988), thus alleviating the potential effects of gravity.

Alternatively, the stronger control by global cues in the vertical dimension could have been influenced by the orientation of the rectangular frame provided by the monitor. Specifically, pigeons may have used distance from an edge as a global cue. If so, they may have found it easier to judge the absolute goal location in the vertical dimension because distance to the nearest edge is smaller than in the horizontal dimension. Future tests that vary the orientation of the monitor and/or the absolute location of the goal on the screen (e.g., center of the screen or nearer to an edge) may help to reveal the type of global cues pigeons use.

A second notable finding of our experiments was that even with the horizontal arrays in which local cues were preferred in *Conflict Tests*, the control by local cues was constrained by global cues. Specifically, when the globally correct area of the screen was a single fixed location (i.e., Experiments 1 and 2), pigeons did not continue to prefer the locally correct square on tests in which the array was moved far from the globally correct area of the screen.

This contrasts with the findings of Spetch and Edwards (1988) in which pigeons continued to choose the locally correct location even when the array was moved far from the global training location in the open field. It may be that global cues are more salient in touch screen tasks than in open field tasks, perhaps due to inherent differences between the tasks such as the size of the search space and the type of movement required to reach the goal. When the globally correct area of the screen was a range of locations (Experiment 3), control by local cues appeared to be less constrained by global location in the horizontal dimension, but strong control by global cues still appeared in the vertical and diagonal dimensions.

Finally, we observed considerable individual variability among birds, even when the results were significant overall on many of the tests. Although this was not expected, it is consistent with other experiments investigating the hierarchical organization of local and global cues in spatial tasks (e.g., adult humans Steck & Mallot, 2000). This potential for high levels of individual variability, coupled with evidence that the hierarchical organization of spatial information is pliable and depends upon environmental factors is evidence that researchers should carefully consider the types of tasks used when comparing spatial strategies across species.

There are several areas of future research that would be useful to conduct. One such area would be to further examine how lateralization of brain functioning influences the way in which spatial information is hierarchically organized. Several recent studies have begun to investigate the neurological bases of spatial navigation, especially in respect to encoding of local and global information (e.g., Tommasi & Vallortigara, 2004; Vallortigara, Pagni, & Sovrano, 2004). The avian visual system is strongly lateralized, thus most of what is seen by the left eye is processed by the contralateral hemisphere (i.e., right hemisphere) and vice versa (Cheng et al., 2006). Consequently, hemispheric control can be studied by occluding one eye during training and/or testing. Research in birds has indicated that the right hemisphere relies mainly on global cues and the left hemisphere relies on both global and local cues for navigation (Prior, Lingenauber, Nitschke, & Güntürkün, 2002; Vallortigara et al., 2004).

When birds are trained binocularly with both local and global cues, tests in which either the left or right eye is occluded can affect which cue is used most dominantly. Tommasi and Vallortigara (2004), for example, trained chicks to find food near a landmark in the center of a square arena. During monocular tests, the landmark was shifted to one corner of the arena. Chicks tested with their left eye (right hemisphere), tended to use the global information and searched predominantly in the center of the arena. Conversely, chicks tested with their right eye (left hemisphere) relied on the local information provided by the landmark, searching mainly in the corner of the arena. However, there is some evidence that positional information is processed similarly to larger scale global information (Tommasi, Andrew, & Vallortigara, 2000). Specifically, chicks were trained such that both colour and positional cues indicated the goal location. When the cues were placed in conflict, chicks tended to prefer the colour cue, but left-eyed chicks were more likely than right-eyed or binocular chicks to choose the positional location. Thus, further investigation into lateralization of local positional cues vs. global spatial cues is warranted. This line of research would be especially interesting in light of the differences we found between horizontal and vertical arrays. Specifically, are arrays of different orientations processed differently within the avian brain?

The malleability of preferential cue use is another interesting area for future research. A recent study by Brown et al. (2007) showed that rearing environment can alter preferential use of geometric and featureal information in fish. In tests in which geometry and features were placed in conflict, fish that had been raised in a circular tank showed significantly less use of geometric information than fish that had been raised in a rectangular tank. It would be interesting to examine whether rearing conditions also affect preferences for local position and global location cues. For example, if an animal was raised in an environment in which global cues were constantly changing, would that animal be more predisposed to rely on local cues in new situations?

In summary, the research presented in this paper adds to the literature suggesting that spatial information is hierarchically organized. Our findings also suggest that the hierarchical ordering of spatial information differs depending on the orientation of the spatial array. With horizontal arrays, pigeons strongly preferred local cues but they encoded global cues as well. With vertical or diagonal arrays, global cues dominated. The malleability and neural basis of the effect of orientation are interesting questions for future research.

2.7 Acknowledgements

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2.8 Appendix Tables

Experiment 1: Vertical Orientation

Test	G_h ($df = 3$)	G_p ($df = 1$)	Individual Birds			
			1	2	3	4
Training, *middle* vs. *outer*	59.02	2643.89	503.05^{c}	829.61^{c}	845.06^{c}	525.19^{c}
Conflict, *global* vs. *local*	8.69	19.58	20.12^{c}	$0.80^{ns, c}$	1.05^{c}	6.29^{c}
2 Choices, *global* vs. *other*	2.18^{ns}	231.2	54.63^{c}	73.50^{c}	54.63^{c}	50.62^{c}
Horizontal Move, *middle* vs. *outer*	5.58^{ns}	319.81	58.08^{c}	86.75^{c}	107.03^{c}	73.53^{c}
5 Choices, *middle* vs. *inner*	3.39^{ns}	59.02	25.59^{c}	25.59^{c}	5.97^{c}	16.69^{c}

Table 2.1: This table reports all G-statistics from replicated G-tests for Goodness of Fit. Each replicated G-test for Goodness of Fit is reported for the most informative test we conducted for each array type. The specific comparison the replicated G-test for Goodness of Fit that we are reporting is specified in italicized text in the first column. In this table, G_h represents the G-statistic for heterogeneity among birds and G_p represents the pooled G-statistic for a particular test. G-statistics for individual birds are also reported. A superscript *ns* by a value indicates that it was not significantly different from chance ($p < .05$). When reporting G-statistics for individual birds, a superscript *c* indicates that performance was congruent with our hypothesis for that test, while a superscript *r* indicates it was not. A superscript e indicates that values were equal for all cells, thus showing no preference.

Experiment 2: Horizontal Orientation

Test	G_h ($df = 6$)	G_p ($df = 1$)	Individual Birds						
			1	2	3	4	5	6	7
Training, *middle* vs. *outer*	179.22	2803.26	281.09^{c}	396.98^{c}	823.59^{c}	394.10^{c}	262.49^{c}	250.48^{c}	573.74^{c}
Conflict, *global* vs. *local*	20.67	65.46	3.99^{c}	$0.02^{ns, c}$	23.13^{c}	22.15^{c}	16.30^{c}	$3.41^{ns, c}$	17.14^{c}
2 Choices, *global* vs. *other*	10.47^{ns}	29.15	$2.42^{ns, c}$	23.13^{c}	4.32^{c}	4.32^{c}	$1.07^{ns, c}$	$3.30^{ns, c}$	$1.07^{ns, c}$
5 Choices, *middle* vs. *inner*	1.75^{ns}	24.03	$1.10^{ns, c}$	$3.53^{ns, c}$	4.83^{c}	$3.53^{ns, c}$	$2.28^{ns, c}$	7.75^{c}	$2.76^{ns, c}$
Vertical Move, *middle* vs. *outer*	9.89^{ns}	0.41^{ns}	$0.43^{ns, c}$	4.16^{c}	$0^{ns, c}$	$1.62^{ns, r}$	$1.30^{ns, c}$	$2.27^{ns, r}$	$0.53^{ns, r}$
Horizontal Move, *global* vs. *middle*	21.08	107.79	$2.89^{ns, c}$	48.76^{c}	11.65^{c}	24.10^{c}	7.64^{c}	22.19^{c}	11.65^{c}
5 Choice Move, *inner* vs. *global*	5.01^{ns}	20.13	$0.64^{ns, c}$	$0.86^{ns, c}$	7.92^{c}	3.99^{c}	6.97^{c}	$0.46^{ns, c}$	4.30^{c}

Table 2.2: This table reports all G-statistics from replicated G-tests for Goodness of Fit. Each replicated G-test for Goodness of Fit is reported for the most informative test we conducted for each array type. The specific comparison the replicated G-test for Goodness of Fit that we are reporting is specified in italicized text in the first column. In this table, G_h represents the G-statistic for heterogeneity among birds and G_p represents the pooled G-statistic for a particular test. G-statistics for individual birds are also reported. A superscript *ns* by a value indicates that it was not significantly different from chance ($p < .05$). When reporting G-statistics for individual birds, a superscript *c* indicates that performance was congruent with our hypothesis for that test, while a superscript *r* indicates it was not. A superscript *e* indicates that values were equal for all cells, thus showing no preference.

Experiment 3: Horizontal, Vertical and Diagonal Orientations

	Test	$G_h(df = 6)$	$G_p(df = 1)$	Individual Birds						
				1	2	3	4	5	6	7
Horiz. Tests	Control A, *middle* vs. *outer*	14.02	103.27	33.48^{c}	8.62^{c}	34.78^{c}	17.42^{c}	7.58^{c}	$0^{\text{ns, e}}$	15.42^{c}
	Control B, *middle* vs. *outer*	18.54	43.18	5.02^{c}	$2.83^{\text{ns, c}}$	4.58^{c}	$0.18^{\text{ns, c}}$	28.31^{c}	14.42^{c}	5.39^{c}
	2 Choices, *global* vs. *other*	20.32	1.38^{ns}	$0.02^{\text{ns, c}}$	5.75^{c}	$1.48^{\text{ns, r}}$	$1.10^{\text{ns, r}}$	$0.31^{\text{ns, r}}$	20.72^{c}	$0.33^{\text{ns, c}}$
	4 Choices, *inner* vs. *outer*	8.28^{ns}	56.98	19.03^{c}	$1.01^{\text{ns, c}}$	9.22^{c}	9.64^{c}	11.56^{c}	$1.10^{\text{ns, c}}$	13.72^{c}
	5 Choices, *middle* vs. *inner*	4.34^{ns}	0.67^{ns}	$0.14^{\text{ns, c}}$	$0.21^{\text{ns, c}}$	$1.39^{\text{ns, r}}$	$1.19^{\text{ns, r}}$	$0.30^{\text{ns, c}}$	$0.09^{\text{ns, r}}$	$1.69^{\text{ns, r}}$
	Far Horiz. A, *middle* vs. *inner*	26.01	19.15	$0.83^{\text{ns, c}}$	11.11^{c}	6.98^{c}	6.27^{c}	$3.06^{\text{ns, c}}$	7.22^{r}	9.70^{c}
	Far Horiz. B, *middle* vs. *inner*	31.78	45.3	4.79^{c}	$2.29^{\text{ns, c}}$	$0.07^{\text{ns, r}}$	8.41^{c}	19.65^{c}	24.74^{c}	17.13^{c}
Vert. Tests	Control A, *middle* vs. *outer*	24.28	160.22	43.24^{c}	11.09^{c}	61.50^{c}	23.74^{c}	5.81^{c}	38.22^{c}	$0.91^{\text{ns, c}}$
	Control B, *middle* vs. *outer*	12.04^{ns}	221.66	27.76^{c}	31.13^{c}	67.59^{c}	38.22^{c}	19.06^{c}	33.01^{c}	16.93^{c}
	2 Choices, *global* vs. *other*	20.74	100.18	7.14^{c}	19.50^{c}	38.92^{c}	20.72^{c}	23.17^{c}	$1.84^{\text{ns, c}}$	9.64^{c}
	4 Choices, *inner* vs. *outer*	8.50^{ns}	223.38	47.71^{c}	20.72^{c}	64.50^{c}	18.29^{c}	30.19^{c}	38.82^{c}	11.64^{c}
	5 Choices, *middle* vs. *inner*	36.13	18.49	27.76^{c}	$1.23^{\text{ns, c}}$	19.13^{c}	$1.04^{\text{ns, r}}$	4.79^{r}	$0.38^{\text{ns, r}}$	$0.30^{\text{ns, c}}$
Diag. Tests	Control A, *middle* vs. *outer*	14.66	34.92	$2.79^{\text{ns, c}}$	$2.83^{\text{ns, c}}$	36.32^{c}	$2.29^{\text{ns, c}}$	$2.05^{\text{ns, c}}$	$3.30^{\text{ns, c}}$	$0^{\text{ns, e}}$
	Control B, *middle* vs. *outer*	14.97	141.06	23.77^{c}	19.06^{c}	49.37^{c}	17.42^{c}	$0.91^{\text{ns, c}}$	33.01^{c}	12.50^{c}
	2 Choices, *closer to global* vs. *other*	54.92	245.67	85.95^{c}	37.43^{c}	88.72^{c}	33.27^{c}	23.17^{c}	31.88^{c}	$0.17^{\text{ns, c}}$
	4 Choices, *inner* vs. *outer*	33.73	13.97	$0^{\text{ns, e}}$	$2.50^{\text{ns, r}}$	11.20^{c}	$0.18^{\text{ns, r}}$	$3.65^{\text{ns, c}}$	30.19^{c}	$1.99^{\text{ns, c}}$
	5 Choices, *middle* vs. *inner*	20.34	3.63^{ns}	7.57^{r}	$1.39^{\text{ns, c}}$	$3.00^{\text{ns, c}}$	3.73^{c}	$3.68^{\text{ns, c}}$	4.60^{c}	$0^{\text{ns, e}}$
	Diag. Rotation, *local* vs. *global*	38.19	143.38	18.84^{c}	26.26^{c}	67.09^{c}	12.97^{c}	14.78^{c}	41.59^{c}	$0.04^{\text{ns, c}}$

Table 2.3: This table reports all G-statistics from replicated G-tests for Goodness of Fit. Each replicated G-test for Goodness of Fit is reported for the most informative test we conducted for each array type. The specific comparison the replicated G-test for Goodness of Fit that we are reporting is specified in italicized text in the first column. In this table, G_h represents the G-statistic for heterogeneity among birds and G_p represents the pooled G-statistic for a particular test. G-statistics for individual birds are also reported. A superscript *ns* by a value indicates that it was not significantly different from chance ($p < .05$). When reporting G-statistics for individual birds, a superscript c indicates that performance was congruent with our hypothesis for that test, while a superscript r indicates it was not. A superscript e indicates that values were equal for all cells, thus showing no preference.

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Chapter 3

Not using the obvious: Desert ants, *Melophorus bagoti*, learn local vectors but not beacons in an arena

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3.1 Abstract

Many ant species travel large distances to find food, sometimes covering distances that are up to one million times their body length. Even when these foraging trips follow convoluted paths, the ants usually find their way back to their nest with precision (Wehner, Michel, & Antonsen, 1996). Ants have been shown to use both compass cues in the sky (pattern of polarised light) and landmarks on Earth to return to their nest. We present two experiments conducted on a solitary foraging ant: *Melophorus bagoti* in their natural habitat in the central Australian desert. Ants were trained and tested *in situ*. We tested foragers' ability to exit a circular arena which provided an undifferentiated panorama. Artificial visual landmarks were located near a small exit. On tests in which path integration information was not available, foragers did not use artificial landmarks as beacons. Instead, they oriented in the learned exit direction, whether or not it pointed to the nest. We suggest that *M. bagoti* foragers learned a context-specific local vector when cued by the context of the circular arena. Our findings present the first evidence that *M. bagoti* foragers learn context-specific compass directions to chart their initial path home.

3.2 Introduction

Many ant species travel large distances to find food, sometimes traveling distances up to one million times their body length (Wehner et al., 1996). Even when these trips are lengthy and follow convoluted paths, the ants usually find their way back to their nest with precision (Wehner et al., 1996). While the mechanisms by which ants navigate vary widely across genus and habitat, many ants have been shown to use visual cues to some degree (e.g., Franks et al., 2007; Graham & Collett, 2002; McLeman, Pratt, & Franks, 2002; Vilela, Jaffě, & Howse, 1987). For example, North African desert ants (*Cataglyphis fortis*) have been shown to rely heavily on compass cues that stem predominantly from the pattern of polarised light (Wehner & Müller, 2006; Wehner & Srinivasan, 2003). Additionally, *Cataglyphis* ants have also been shown to use context-specific local vectors in certain situations (Cheng, 2006; Collett, Collett, Bisch, & Wehner, 1998). For example, Collett et al. (1998)'s *Cataglyphis* ants learned to head south when coming out of an experimentally provided channel, and this context-specific local vector appeared to be controlled by compass cues. Thus, in this case, it is thought that the unique visual panorama of the experimentally provided channel cued the ants to head south at the first available opportunity upon exiting from the channel.

In addition to compass cues and local vectors, many ant species have also been shown to use landmarks for navigation. Landmarks are generally used as beacons, ards which the ants aim while traveling along a fixed route. These landmarks then function as an intermediate goal along their route, thus allowing them to break their route into more manageable segments (Graham, Fauria, & Collett, 2003; Nicholson, Judd, Cartwright, & Collett, 1999). Furthermore, some ant species have also been shown to memorise arrays of landmarks surrounding their nest or reliable feeding sites (Graham, Durier, & Collett, 2004; Narendra et al., 2007; Wehner & Räber, 1979), thus increasing their navigational precision and reducing the amount of time they spend searching for their goal.

One species that has been shown to use landmarks for navigation along a fixed route (Kohler & Wehner, 2005; Narendra, 2007) and for locating their nest and reliable food sources (Narendra et al., 2007) is the Central Australian desert ant, *Melophous bagoti*, which resides in the feature rich, semi-arid deserts of Central Australia. When foraging, *M. bagoti*'s use of visual cues for defining routes and pinpointing target locations is similar to *Cataglyphis* ants (Cheng et al., 2009; Wehner & Räber, 1979), wood ants (*Formica rufa*: Graham et al., 2003; Graham & Collett, 2006; Harris, Ibarra, Graham, & Collett, 2005), and rain forest ants (*Gigantiops destructor*: Macquart, Garnier, Combe, & Beugnon, 2006; Wystrach & Beugnon, 2009). Additionally, similar to wood ants (Fukushi, 2001; Fukushi & Wehner, 2004), *M. bagoti* has been shown to use panoramic visual cues (Graham & Cheng, 2009a, 2009; Narendra, 2007). Specifically, Graham and Cheng (2009a, 2009) found that *M. bagoti* foragers used the contrast between terrestrial objects and skyline when navigating, and that the lower 27° of elevation in the panorama was attended to the most.

Our research was designed to extend knowledge of the cues used by *M. bagoti* as they initially leave a feeding site to head back to the nest. We know that *M. bagoti* foragers sometimes follow fixed, idiosyncratic routes between a food source and their nest (Kohler & Wehner, 2005) using both path integration (Narendra, 2007b) and visual landmarks (Narendra, 2007). We also know that they use visual landmarks placed at the nest (Narendra, 2007), as well as visual panorama cues at the feeding site (Graham & Cheng, 2009a). We do not know, however, whether they would use a specific landmark at a food source as a beacon to set the initial course home, and if so, how use of this cue might interact with other cues. We also do not know whether *M. bagoti*, like *Cataglyphis* ants, learn context-specific compass-based local vectors to return from a feeding site. Thus our experiments provide the first test whether *M. bagoti* will use beacons or a learned context-specific compass direction to start the journey home from a feeding site.

In order to address these questions we provided ants with a feeder placed in the centre of a cue-controlled arena in their natural habitat. The arena allowed us to control the landmark information available to the ants and it provided only a single exit, which we marked with a visual landmark to serve as a beacon. The top of the arena was open, thereby allowing the ants to use compass cues to form a local vector. After ants had learned to enter and exit the arena readily, we then rotated the landmark to determine whether the landmark was used and how it interacted with other cues.

Our general strategy in these experiments was to train ants *in situ* to find food within our enclosed arena. Finding the feeder should not be a problem because numerous natural cues could be used on the outward route to find the entrance to the arena. Once ants had obtained a piece of food from the feeder, they had to locate a small exit in the arena in order to return home. However, from inside the arena, natural terrestrial landmark cues were blocked from view by the arena walls. This allowed us to control and manipulate the cues available to the ants from within the arena that would help them locate the exit.

In our experiments, we provided ants with visual cues above or beside the exit, cues that we thought might serve as beacons. Additionally, we left the top of the arena open, which provided the ants with access to celestial compass cues. The ants therefore could learn to use the landmarks as beacons, and/or they could learn a context-specific local vector based on celestial compass cues. After training, we conducted tests to determine whether they used one or both of these cues. On tests, before transporting ants to a test arena, we allowed them to complete their homeward journey from the training arena and captured them when they started to search for their nest. Previous research has shown that *M. bagoti* no longer retain a homeward vector once they start searching for the nest (e.g., Graham & Cheng, 2009; Narendra, 2007). Thus, this procedure allowed us to nullify any effects of path integration on orientation in testing.

We conducted two experiments, using ants from separate nests. The first experiment provided a solitary landmark located above the exit of an artificial arena. In this experiment, the arena exit was aligned with the nest such that the compass direction to the exit was the same as the homeward compass direction. The second experiment used a set of three-dimensional landmarks on each side of the arena exit. Moreover, the exit was rotated away from the nest-feeder direction so that there was a large disparity between the compass direction to the exit and the homeward compass direction. Tests in which we rotated the landmark in an identical arena allowed us to investigate whether *M. bagoti* foragers learned to use our experimentally provided landmark and/or whether they learned to use a context-specific local vector based on celestial compass cues to navigate out of the arena. Additionally, if *M. bagoti* learned both a context-specific local vector and the beacon, our rotation tests would allow us to determine how they would respond when these cues are placed in conflict. Specifically, we tested whether the ants would integrate these two sources of information.

3.3 Experiment 1

3.3.1 Method

Subjects

Experiment 1 was undertaken with 120 solitary foraging desert ants (*Melophorus bagoti*), from a single nest within their natural semi-arid habitat at a field site approximately 10 km south of Alice Springs, Northern Territory, Australia, in January-March 2009.

Materials and Apparatus

A circular training arena (diameter = 1.5 m, height = 50 cm) made out of 1 mm thick sheet metal (inside colour: dark blue; outside colour: light grey) was placed in the field so that the centre of the arena was 5.2 m East of the main nest entrance. A white plastic feeder (~15 cm (L) × ~15 cm (W) × 9.5 cm (H)) was buried in the ground up to its lip in the centre of the arena. Sticks were placed in the feeder so that subjects could easily climb in and out. The arena contained a small opening for subjects to enter and exit (W = ~10 cm, H = ~4 cm). The entrance/exit was a small depression in the ground which led under the arena wall. The location of the entrance/exit in the arena was aligned with the nest as shown in Figure 3.1a.

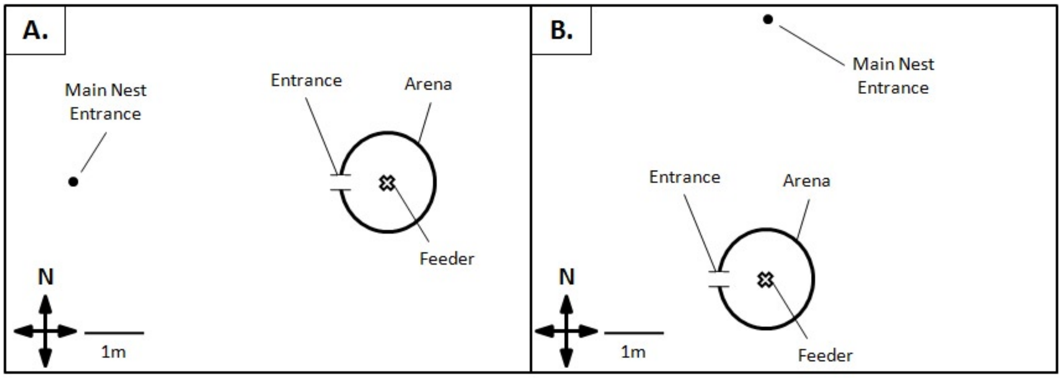

Figure 3.1: [**A.**] Drawing showing the main nest entrance relative to the arena in Experiment 1. [**B.**] Drawing showing the main nest entrance relative to the arena in Experiment 2. Drawings are to scale.

A landmark was attached to the interior of the arena indicating the exit location. The landmark was a large yellow diamond constructed of foam-paper (30 cm (L) × 30 cm (W)), positioned directly above the centre of the exit (see Figure 3.2a).

For testing, a second identical arena was placed approximately 7.7 m due East of the nest, measured from the centre of the arena to the main nest entrance. The testing arena did not contain an exit or feeder, but contained a landmark that was identical to that used in the training arena. Additionally, a large wooden goniometer (60 cm (L) × 60 cm (W) × 1 cm (D)) was always present in the centre of test arena. The goniometer contained a small yellow plastic lid (diameter = 3 cm, height = 1 cm) in its centre to provide a starting position for subjects when they were released into the arena. The goniometer was divided into 24 equal sections of 15 ° each. These sections were numbered from 1-24 to simplify the recording of subject headings. Circles were marked at distances of 15 cm and 30 cm from the centre of the goniometer, allowing us to record a heading at each of these distances. In addition, the 24 directional segments were marked on the arena walls, allowing us to take one final heading when subjects touched the arena wall. The 0 ° point of the goniometer always pointed in the direction of the nest entrance.

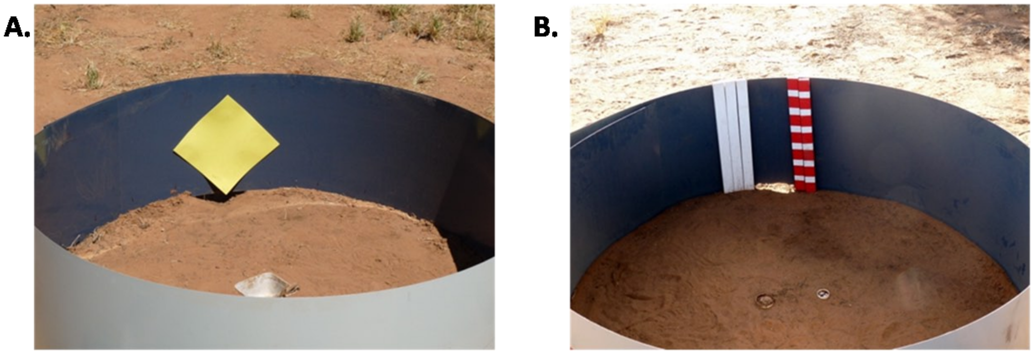

Figure 3.2: [**A.**] Photograph of the arena and landmark used in Experiment 1.[**B.**] Photograph of the arena and landmarks used in Experiment 2.

Procedure

An ample supply of cookie crumbs and/or meal worm pieces were placed inside the feeder and, during training, foraging ants were free to arrive and depart from the feeder. Occasionally we placed a trail of cookie crumbs leading from the nest to the feeder to encourage new foragers to search for the feeder. On their first observed visit, we captured ants as they left the feeder and marked them with a small dab of acrylic paint on the top of their abdomen. We held the ants while the paint dried and then released them back into the arena to find their way back to their nest. After being painted, ants were left alone to forage and train themselves for at least 1 day before testing. We used different colours of paint for ants on each day, to identify on which day the ant first arrived at the feeder. All ants had a minimum of 1 day of training and at least one visit to the arena on the test day prior to testing, but our observations of the ants' foraging activity indicated that most painted foragers made multiple trips between the feeder and the nest prior to testing. All testing was conducted in the afternoon, between 13 : 00 and 17 : 00 hour local time.

For testing, an ant was allowed to enter the training arena and take a piece of food from the feeder. Once the ant exited the feeder we followed it as it returned to the nest. To prevent the ant from entering the nest, the entrance was temporarily sealed with a glass jar. We observed the ant until it began to take circular paths around the nest area, which indicated that the ant had entered a search mode (Wehner & Srinivasan, 1981). Previous research has shown that *M. bagoti* no longer retain a homeward vector once they start their search mode, and hence they are considered to be zero-vector ants (Graham & Cheng, 2009; Narendra, 2007). We then captured the ant near the nest entrance by trapping it within a yellow plastic hoop and scooping it into a small plastic vial. Once caught, we transported the ants in the vial to the testing arena. During transport the experimenter kept one hand around the vial and another on top to block light and celestial cues.

Once at the testing arena, the experimenter checked to ensure that the ant still held the piece of food. If the ant had lost its food, the experimenter provided it with another piece and watched until it grabbed and held it with its mandibles. The ant was then released from the transport vial into the small lid located at the centre of the goniometer in the centre of the arena. The experimenter stood outside the arena and released the ant by tipping the vial to the side. The experimenter's position relative to the arena was varied across trials. Once the ant was released into the testing arena, we recorded its heading vector when it stepped over the 15- and 30 cm lines on the goniometer, as well as when it first touched the wall of the arena. Once ants had completed a test, they were re-marked with a special colour of paint to denote that they had been tested and to prevent them from being tested more than once.

Four landmark-position tests were conducted, with the landmark placed in the arena at 0, 90, 180 or 270 degrees of rotation relative to the direction of the nest. Both the nest direction and the exit location in the training arena were at 0°.

Data Analysis

Because the data we collected were directional bearings, we used circular statistics and associated tests (see Batschelet, 1981; Jammalamadaka & SenGupta, 2001; Mardia, 1972; Upton & Fingleton, 1985; Zar, 2009). We conducted V-tests to determine whether ants were significantly oriented towards the landmark or towards the trained exit direction. The V-test determines whether observed angles (i.e., heading directions of each ant) are clustered around an expected angle (Batschelet, 1981). In our case, the expected angle is either the location of the landmark or the compass direction at which the exit was located in training. V-tests were corrected for the grouping of data into the 15° segments recorded with our goniometer. We also pooled the data in two ways in order to determine whether there was a significant overall orientation towards the landmark or the trained exit direction. To pool the data for landmark orientation, the data were rotated so that the landmark direction always pointed to 0°. When data were pooled to test for orientation towards the trained exit direction, no transformation was applied.

3.3.2 Results

Figure 3.3 shows the results of tests at each of the four landmark rotations. The ants showed clear orientation at the wall when the landmark location was at 0° (i.e., consistent with both the home and trained exit directions). On the other hand, orientation was variable when the landmark was rotated: in some cases (e.g., 270°), ants appeared to be oriented toward the landmark, while in others (e.g., 180°) they appeared to be oriented toward the trained exit direction. Figure 3.4 shows the data pooled across all tests, ignoring landmark locations (top panel) and pooled across all tests transformed so that the landmark direction always pointed to 0° (bottom panel). This figure shows that over all tests, ants appeared to be oriented more strongly towards the trained exit direction than towards the landmark, at least by the time they reached the wall.

V-tests were conducted to determine whether ants were oriented towards the landmark or toward the trained exit direction at distances of 15 cm, 30 cm and 75 cm (at the wall) for each test condition and for the pooled data. None of these tests were significant after 15 cm or 30 cm from the centre of the arena ($p > .05$). At the wall, orientation towards the landmark was significant when the landmark was at 0° ($p < .001$) and at 270° ($p < .05$), but not at the other rotations ($p > .05$). Orientation towards the exit direction was significant at 0° ($p < .001$) and 180° ($p < .01$), but not at the other rotations ($p > .05$). When the data were pooled, orientation towards the landmark was not significant ($p > .05$), but orientation towards the trained exit direction was highly significant ($p < .001$).

To determine whether the ants were integrating a vector between the landmark direction and the trained exit direction when trying to exit the arena, we pooled our data for 90° and 270° by reflecting the data collected when the landmark was at 270° along the vertical axis. Ants were assumed to be integrating a vector based on the landmark and trained exit directions if V-tests were significant at both orientations (e.g., 0° and 90°). At 15- and 30 cm, V-tests revealed that ants were not significantly oriented towards the trained exit direction (0°; 15 cm: $v = -0.119$, $p > .05$; 30 cm: $v = -0.035$, $p > .05$) or the landmark (90°; 15 cm: $v = 0.002$, $p > .05$; 30 cm: $v = 0.088$, $p > .05$). However, all the wall V-tests revealed that the ants were significantly oriented towards both the trained exit direction (0°; $v = 0.155$, $p < .05$) and the landmark (90°; $v = 0.158$, $p < .05$). We then conducted a final V-test at the arithmetic average between the two points (45°) to determine whether the ants were integrating a vector between both the landmark and trained exit directions. This V-test was statistically significant (45°; $v = 0.221$, $p < .05$) and suggests that the ants were integrating a vector between the landmark and trained exit direction (see Figure 3.5, top panel).

Although the ants did not show significant orientation toward either the landmark or the exit direction at 15 cm or 30 cm distances, an examination of the data suggests that their orientation was bidirectional, with a tendency to head in the exit direction and in its polar opposite. Given that directional ambiguity is consistent with sky compass use, we conducted further statistical analyses to test whether this bidirectional tendency was significant. For these tests, we followed procedures advocated by Batschelet(1981, pg. 21-30 and 51). First, we doubled the angles in order to transform the bimodal sample into a unimodal sample (Batschelet, 1981, pg. 51). We then conducted a V-test with the expected direction of 0°. Because we doubled the angles, these V-tests were corrected for the grouping of data into the 30° rather than 15° segments. These analyses confirmed that the ants showed significant bidirectional orientation at both 15 cm ($v = 0.254$, $p < .001$) and 30 cm

($v = 0.332, p < .001$).

3.3.3 Discussion

In this experiment, there was only weak evidence for orientation towards the landmark. However, the pooled results revealed a strong tendency for orientation towards the trained exit direction at the wall. The initial orientation of the ants at 15 cm and 30 cm from the centre of the arena was bidirectional and oriented toward the trained exit direction as well as to the polar opposite direction.

The lack of strong orientation towards the landmark is interesting because the landmark was selected to provide a high contrast against the dark wall and was located directly above the exit in training. Based on what is known about vision in *M. bagoti*, we expected that this landmark would provide a salient cue (unpublished data). Moreover, this lack of orientation towards the landmark was surprising because past research has shown that ants (including *M. bagoti*) use artificial landmarks placed at the nest (Narendra et al., 2007) or along a homebound route (Narendra, 2007) as beacons or "signposts" (Cheng, 2006). There are several differences between our experimental design and prior studies showing landmark use. For example, our arena blocked all natural panoramic cues. Moreover, our landmark was effectively two dimensional, whereas previous studies used three-dimensional objects as landmarks.

While the ants did not show a strong tendency to orient towards the landmark, and instead seemed to orient more towards the trained exit direction, we pooled our data for 90° and 270° (by reflecting the data collected when the landmark was at 270° along the vertical axis) to determine whether the landmark would show any effect of influencing the directional headings of the ants by causing them to integrate a vector between the trained exit direction and the direction indicated by the landmark. Our analysis revealed evidence that the ants were integrating a vector by the time they reached the arena wall, but did not do so at 15 or 30 cm. While this is the first evidence that *M. bagoti* foragers integrate compass and landmark information, the findings were not exceptionally strong. The topic of integration of compass cues will

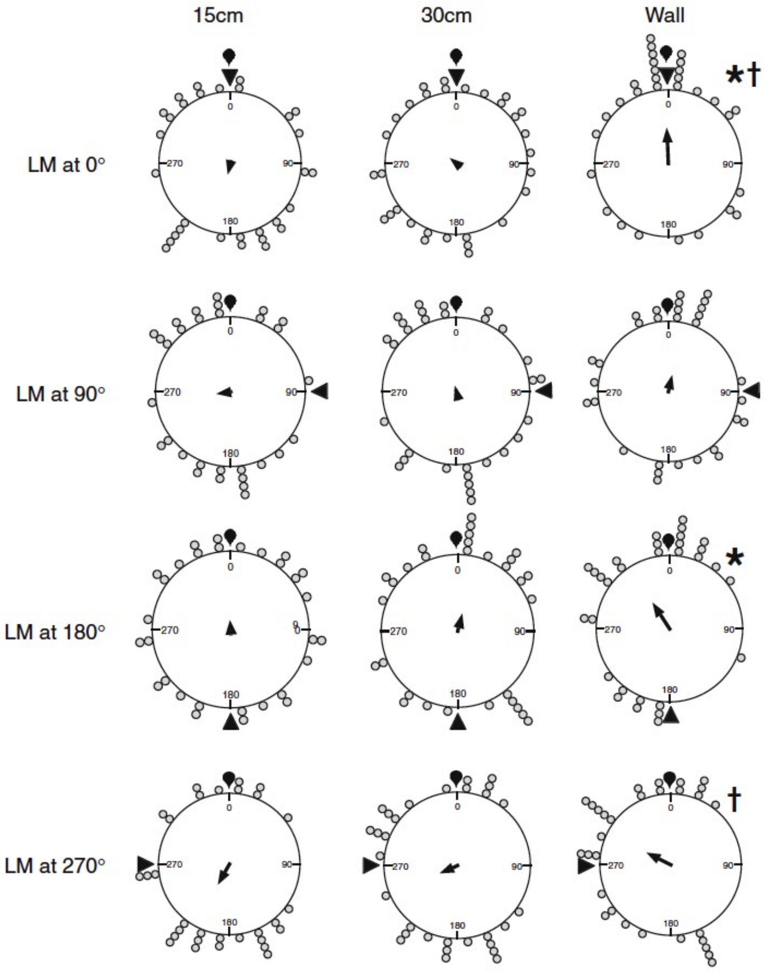

Figure 3.3: Directional bearings of ants at 15 cm, 30 cm and the wall (75 cm) during testing in Experiment 1. The *top graphs* show the test condition in which the landmark was consistent with the trained exit direction and the remaining graphs show the tests in which the landmark was rotated away from the trained exit direction. Each *grey circle* indicates one subject. The *black arrow* extending from the centre of the *circle* indicates the mean vector for the given distribution (r). The four values on the outside of the *solid circle* (0 °, 90 °, 180 °, and 270 °) indicate the angle of deviation from the nest direction. The *dark triangle* indicates where the landmark was located while the *dark teardrop* indicates the trained exit direction. An *asterisk* in the *upper left* corner of the graph indicates that ants were significantly oriented towards the trained exit direction (0 °, $p < 0.05$), while a *dagger* indicates that ants were significantly oriented towards the landmark ($p < 0.05$). The nest and trained exit direction was at 0 ° in all tests. Each graph contains the data from 30 subjects. P-values reported in this figure caption stem from V-tests reported in the main text.

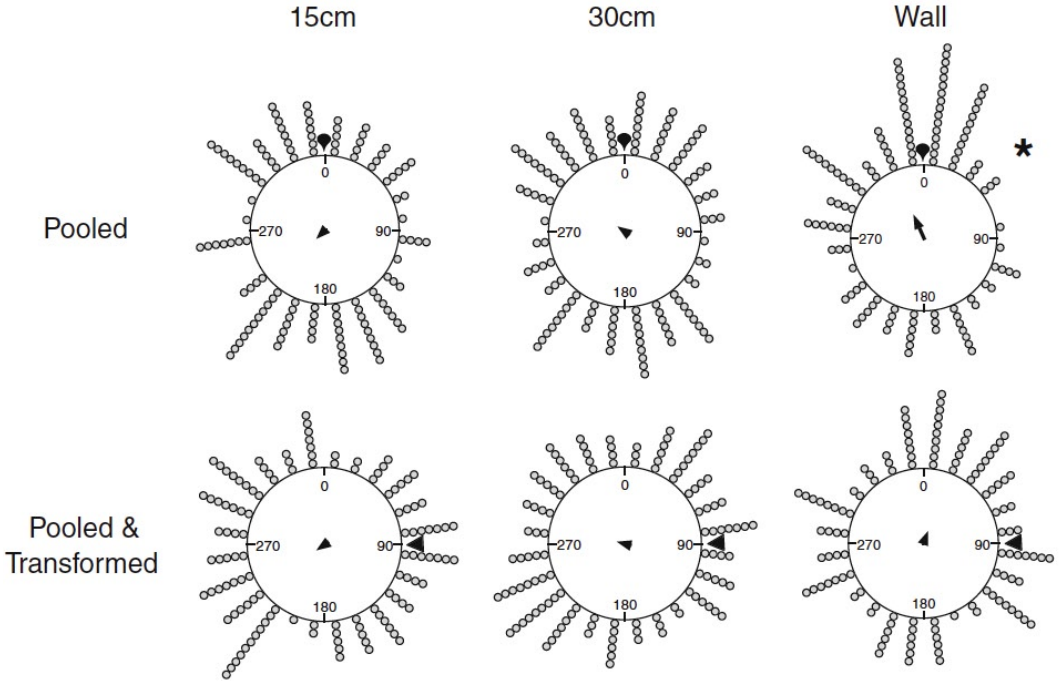

Figure 3.4: Directional bearings of ants at 15 cm, 30 cm and the wall (75 cm) pooled across the four types of tests in Experiment 1. For the *top graphs* the data are pooled without transformation. The *bottom graphs* show bearings in terms of landmark location; for these graphs, the data from landmark rotation tests were transformed by rotating them to place the landmark at 90 °. *Symbols* and other graphical conventions are the same as those described in the caption of Figure 3.3. An *asterisk* in the *upper left* corner of the graph indicates that ants were significantly oriented towards the trained exit direction (0 °; *top panel* only; $p < 0.05$). The nest direction is located at 0 ° in the *top panel*. Nest and exit direction cannot be identified in the *bottom panel* due to the transformation that was applied. Each graph contains the data from 120 subjects. *P*-values reported in this figure caption stem from *V*-tests reported in the main text.

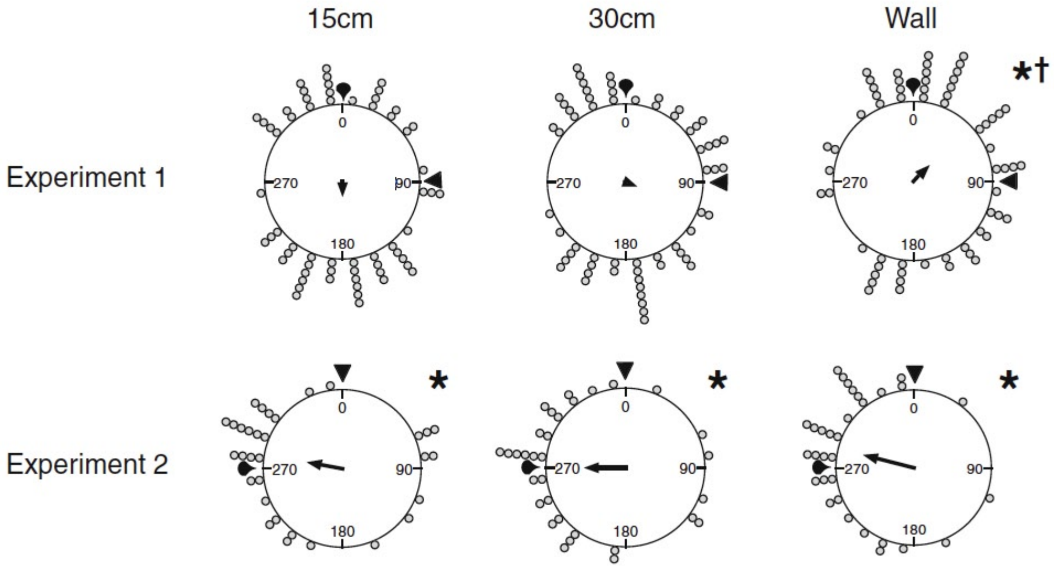

Figure 3.5: Directional bearings of ants at 15 cm, 30 cm and the wall (75 cm) pooled across the two landmark locations in Experiment 1 (*top panel*) and Experiment 2 (*bottom panel*). In Experiment 1, data were pooled from 90 ° and 270 °. This was done by reflecting the data from 270 ° condition across the vertical axis. Thus, all data are pooled at 90 °. In Experiment 2, data were pooled from 0 ° and 180 °. This was done by reflecting the data from 180 ° across the horizontal axis. Thus, all data are pooled at 0 °. *Symbols* and other graphical conventions are the same as those described in the caption of Figure 3.3. An *asterisk* in the *upper left* corner of the graph indicates that ants were significantly oriented towards the trained exit direction (0 °, *top panel*; 270 °, *bottom panel*; $p < 0.05$), while a *dagger* indicates that ants were significantly oriented towards the landmark (90 °, *top panel*, $p < 0.05$). The nest direction is located at 0 ° in the *top panel*. The nest direction cannot be determined in the *bottom panel* due to the transformation that was applied. Each graph in the *top panel* contains data from 60 subjects. Each graph in the *bottom panel* contains data from 32 subjects. P-values reported in this figure caption stem from V-tests reported in the main text.

require future experimentation to understand in what situations, and to what extent the ants integrate multiple sources of visual information, research that we are currently carrying out.

The significant orientation at the exit direction was interesting because it suggests that ants are using some form of compass for orientation (e.g., magnetic, celestial, spectral, etc.). Although the ants were not significant orientated toward the exit direction at 15 cm and 30 cm from the centre of the arena, they showed a significant bidirectional orientation toward the exit direction and its polar opposite. This is consistent with use of a compass that has some directional ambiguity (e.g., a sky or magnetic compass) (Wehner, 1994). For example, one side of the wall was brighter than the opposite side. Furthermore, some such source of information must have been used at the wall because the bimodal pattern was replaced by a unimodal pattern of orientation at the wall. Our results therefore point to the possibility that the ants may have learned a context-specific local vector, similar to that described by Collett et al. (1998) to orient towards the arena exit. However, in this experiment, the learned exit direction is also the homeward direction and therefore we cannot rule out the possibility that ants used a global vector provided by residual traces of path integration. Although many previous studies have shown that the capture procedures we used completely eliminates path integration information (e.g., Graham & Cheng, 2009; Narendra, 2007), we conducted a second experiment to ensure that path integration could not account for the orientation towards the exit.

3.4 Experiment 2

Experiment 2 was conducted using a new nest of ants and was designed to replicate and clarify the results of Experiment 1. In an attempt to increase landmark salience, we replaced the flat two-dimensional landmark from Experiment 1 with a set of three-dimensional landmarks. To clarify whether the ants had learned a local vector that directed them to the arena exit, as opposed to orienting towards their nest direction, we dissociated the direction of the arena exit from the direction of the nest.

3.4.1 Method

Subjects

This experiment was conducted using 64 *M. bagoti* foragers from a different nest in the same field site as Experiment 1.

Materials and Apparatus

New training and test arenas were constructed. The apparatus was identical to that used in Experiment 1 with the following exceptions. First, the centre of the training arena was located 4.2 m South of the nest. Second, the entrance/exit was a small rectangular hole cut into the base of the arena wall (17 cm (L) × 2.5 cm (H)) and was rotated by 90 ° counter-clockwise from the nest direction. Thus, in contrast to Experiment 1, the home direction and training arena exit direction were dissociated in Experiment 2 (see Figure 3.1b). Third, the feeder was a small white plastic lid (diameter = ~6.3 cm, height = ~1 cm); as in Experiment 1, it was located in the centre of the arena. Fourth, there were two distinct landmarks, one positioned on each side of the exit. These landmarks were constructed from rectangular pieces of wood and they differed from one another in size, colour and pattern. The landmark to the left of the exit was white with no pattern, while the landmark on the right contained thick red stripes made from red duct tape, interspersed with white paint. The landmark on the left was also larger (13.5 cm (W) × 2 cm (D) × 50 cm (H)) than the landmark on the right (9 cm (W) × 2 cm (D) × 50 cm (H)) (see Figure 3.2b). Finally, the testing arena was located approximately 15.1 m due South of the nest entrance.

Procedure

The training procedure was identical to Experiment 1. The testing procedure was similar to Experiment 1 except that ants were tested in the morning, between 09 : 00 and 12 : 00 hour local time. In addition, we changed the manner in which the ant was released into the test arena. In this experiment, string was attached to the base of the transport jar and the experimenter stepped into the arena and placed the jar upside down onto the lid in the centre of the arena. The experimenter then stepped outside the arena and used the string to lift the jar straight up. As in Experiment 1, the position of the experimenter relative to the arena was varied across trials.

Data Analysis

The data were analysed in the same manner as in Experiment 1

3.4.2 Results

Figure 3.6 shows the results of tests at each of the four landmark rotations. The ants showed clear orientation after 15 cm, 30 cm, and at the wall when the landmark location was at 270 ° (i.e., consistent with the trained exit direction). When the landmark was rotated, the ants remained well oriented in every case towards the exit direction. They showed some orientation towards the landmark at the wall only when it was at 180 °, but were clearly not oriented towards the landmark on other tests. Figure 3.7 shows the data pooled across all tests, ignoring landmark locations (top panels) and pooled across all tests transformed so that the landmark direction always pointed to 90 ° (bottom panels). This figure shows that across all tests, ants were strongly oriented towards the trained exit direction, but not toward the landmark.

V-tests were conducted to determine whether ants were oriented towards the landmark or towards the trained exit direction for each test condition and for the pooled data. Towards the landmark, ants showed significant orientation at distances of 15, 30, and 75 cm (at the wall) when the landmark was consistent with the trained exit direction ($p \leq .05$). They were also significantly oriented at the wall when the landmark was at 180 ° ($p < .05$). None of the other tests were significant for orientation towards the landmark ($p > .05$). Orientation towards the exit direction was significant at 15 cm, 30 cm and at the wall for all tests ($p \leq .05$). When the data were pooled, orientation toward the landmark was not significant at 15 cm, 30 cm or the wall ($p > .05$), but orientation toward the trained exit direction was highly significant at all three distances ($p < .001$).

To determine whether the ants were integrating a vector between the landmark direction and the trained exit direction when trying to exit the arena, we pooled our data for 0 ° and 180 ° (both separated from the trained exit direction by 90 °) by reflecting the data collected when the landmark was at 180 ° along the horizontal axis. Ants were assumed to be integrating a vector based on both the landmark and trained exit directions if V-tests were significant at both orientations (e.g., 0 ° and 270 °). At 15, 30 cm, and the wall, V-tests revealed that ants were significantly oriented towards the trained exit direction (270 °; 15 cm: $v = 0.389$, $p < .001$; 30 cm: $v = 0.456$, $p < .0001$; Wall: $v = 0.59$, $p < .0001$) but not the landmark (0 °; 15 cm: $v = 0.072$, $p > .05$; 30 cm: $v = 0.003$, $p > .05$; Wall: $v = 0.15$, $p > .05$) (see Figure 3.5, bottom panel). Thus, there was no evidence indicating that ants were integrating a vector based on landmark and local vector information.

3.4.3 Discussion

Consistent with results from Experiment 1, the ants showed very strong orientation towards the trained exit direction. Moreover, in this experiment, the ants oriented toward the exit even at 15 cm and 30 cm from the release point. However, as in Experiment 1, the ants showed little evidence of using the landmarks as beacons to find the exit. Thus, the change to three-dimensional landmarks did not appear to increase the tendency for ants to use the landmarks for orientation.

In this experiment, the significant orientation towards the exit direction was not confounded with homeward orientation because the trained exit direction was rotated by 90 ° away from the direction to the nest (see Figure 3.1). Therefore, the results suggest that the ants learned a context-specific local vector.

While the ants did not show a strong tendency to orient towards the landmark, and instead seemed to orient more towards the trained exit direction, we pooled our data for 0 ° and 180 ° (by reflecting the data collected when the landmark was at 180 ° along the horizontal axis) to determine whether the

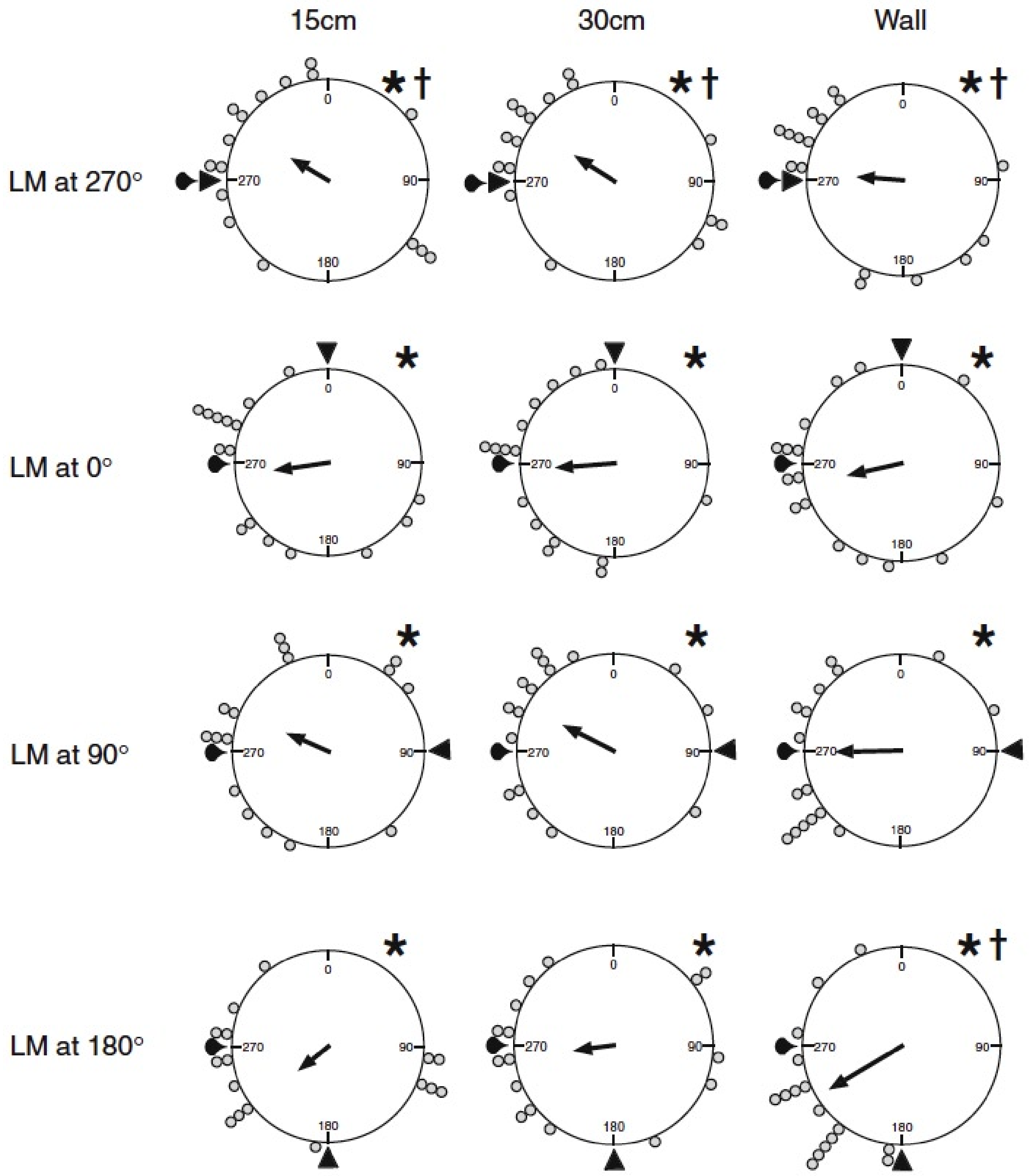

Figure 3.6: Directional bearings of ants at 15 cm, 30 cm and the wall (75 cm) during testing in Experiment 2. The *top graphs* show the test condition in which the landmark was consistent with the trained exit direction (270 °), and the remaining graphs show the tests in which the landmark was rotated away from the trained exit direction. *Symbols* and other graphical conventions are the same as those described in the caption of Figure 3.3. An *asterisk* in the *upper left* corner of the graph indicates that ants were significantly oriented towards the trained exit direction (270 °, $p < 0.05$), while a *dagger* indicates that ants were significantly oriented towards the landmark ($p < 0.05$). The nest was always located at 0 ° in all tests. Each graph contains data from 16 subjects. P-values reported in this figure caption stem from V-tests reported in the main text.

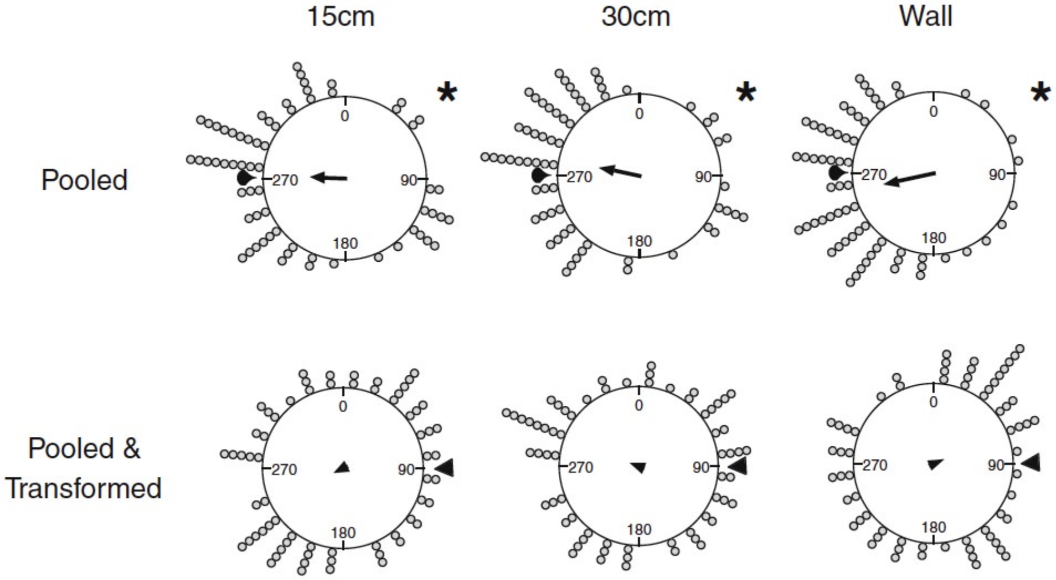

Figure 3.7: Directional bearings of ants at 15 cm, 30 cm and the wall (75 cm) pooled across the four types of tests in Experiment 2. For the *top graphs*, the data are pooled without transformation. The *bottom graphs* show bearings in terms of landmark location; for these graphs, the data from landmark rotation tests were transformed by rotating them to place the landmark at 90 °. *Symbols* and other graphical conventions are the same as those described in the caption of Figure 3.3. An *asterisk* in the *upper left* corner of the graph indicates that ants were significantly oriented towards the trained exit direction (270 °; *top panel* only; $p < 0.05$). The nest direction is located at 0 ° in the *top panel*. Nest and exit direction cannot be identified in the *bottom panel* due to the transformation that was applied. Each graph contains the data from 64 subjects. *P*-values reported in this figure caption stem from *V*-tests reported in the main text.

landmark would show any effect of influencing the directional headings of the ants by causing them to integrate a vector between the trained exit direction and the direction indicated by the landmark. Our analysis revealed that the ants did not show any evidence of integrating a vector at 15 cm, 30 cm, or at the wall. These findings contradict those found in Experiment 1, thus it is still an open question whether ants integrate vectors based on multiple sources of spatial information.

3.5 General Discussion

Our results showed little evidence for landmark use but strong evidence for use of a context-specific local vector specifying a compass direction of travel. Specifically, the ants oriented towards the learned exit direction whether it was consistent with the homeward direction (Experiment 1) or inconsistent with the homeward direction (Experiment 2). This evidence for learning a local vector in *M. bagoti* is consistent with findings in *Cataglyphis* ants (Collett et al., 1998). Collett et al. (1998)'s *Cataglyphis* ants learned, for example, to head south when coming out of an experimentally provided channel and this context-specific local vector appeared to by controlled by compass cues. We suggest that our ants similarly learned a local vector towards the exit direction based on compass information. Presumably, this local vector was activated when the ants were in the context of the arena and motivated to carry food home. The directional instruction appeared to come from compass information gathered by past homebound trips, not from the path integration system calculating progress on the current journey. Path integration was ruled out because we only tested zero-vector ants which no longer have path integration information available (Graham & Cheng, 2009). Moreover, in Experiment 2, the learned local vector was inconsistent with the homeward direction specified by path integration. Experiment 2 also ruled out the use of any remembered global vector between the feeder and the nest, that is, the vector at the feeder before the ant returned (almost) home and was captured for a test. This is because the feeder-nest direction was different from the compass direction to the exit of the arena. And it was the latter direction that controlled the ants behaviour. To our knowledge, this is the first evidence that *M. bagoti* foragers can learn a context-specific local vector.

It is not clear which features of the arena were important for defining the context, but we can rule some cues out. Terrestrial cues that appeared above the arena walls were unlikely to play a role. Few cues by way of tall trees were visible above the walls from the centre of the arena. Our test arenas were in any case displaced from the training site, so that any such cues above the walls differed from those found in training. Furthermore, Graham and Cheng (2009) found that panoramic cues above 27 ° elevation were neither necessary nor sufficient for zero-vector ants navigating home using panoramic cues. The position of the landmark was also not important as a contextual cue because the ants oriented equally well towards the arena exit no matter where the landmark was. But the arena was a key contextual cue. Once the ants in Experiment 2 had exited the arena, our observations of the ants' behaviour indicated that they no longer headed in the centre-exit direction, but turned to head generally in the nest direction (data not formally presented).

Surprisingly, our ants showed little evidence of using the experimentally provided landmark information to help them find the exit of the arena. Previous research on *M. bagoti* navigation has indicated that foragers could use landmark information along a route to help them return to their nest (Kohler & Wehner, 2005; Narendra, 2007). To human vision, our landmarks seemed to be the strongest terrestrial cue in the arena because they provided high contrast against the dark walls of the arena. Moreover, they were sufficiently large that they should have been noticeable even with the lower visual acuity of ant vision. Nevertheless, even with the three-dimensional landmarks used in Experiment 2, the ants did not follow the landmarks when they were rotated away from the exit direction. Interestingly, in one case in Experiment 1, after pooling the data from 90 ° and 270 °, we found evidence for landmark use in the form of it being used as one component of an integration with local vector information. Specifically, at the wall, ants were shown to take an intermediate direction between the landmark and the trained exit direction. While this finding is intriguing, it will need further study to determine under what circumstances *M. bagoti* foragers integrate multiple sources of spatial information. Support for integration was only found at the wall in Experiment 1, and not at 15 cm or 30 cm, and the finding was not replicated in Experiment 2.

Why did our ants not show strong evidence of landmark use in our experiments? It is possible that while our landmarks were salient to human eyes, they may not have been salient orienting cues to the ants. One possibility, suggested by a reviewer, is that because the two landmarks we used were lighter than the background against which they were placed, the ants may have ignored them. It is possible that ants only use landmarks for orientation and/or navigation when they contrast darkly against the environmental background, as they normally do in nature (e.g., trees against the sky). However, to our knowledge, there is no research investigating this in solitary foraging desert ants and further testing would be required to determine whether this is indeed the case. Related to this, it is possible that ants only pay attention to landmarks if they are put in contrast with the panoramic skyline. Graham and Cheng (2009) recently showed that the skyline contour provided by the tops of terrestrial objects formed a crucial panoramic cue for homebound navigation in *M. bagoti*. The landmarks that we used, being against the walls, did not provide unique skyline information and, as a result, might not have been salient enough to be used for navigation. This was shown to be the case in digger wasps by Tinbergen (1972). Landmarks were most salient to the wasps when they stood up on open ground, cutting into the skyline. Two-dimensional flat landmarks were less salient.

An untested hypothesis worth investigating is that natural objects along a route are salient to the extent that they carve out a chunk of the skyline to the navigating ant. Insect vision has limited resolution, and their view-based navigation systems might capitalize on the highest-contrast edges. These are found in the contrast between the tops of terrestrial objects and the sky; the skyline contour. The skyline contains a big jump in overall light level, with the sky becoming brighter in general than ground objects. But using overall light level to segregate ground from sky requires an adjustment threshold that varies with light level. More promising theoretically is green-ultraviolet (UV) contrast (Möller, 2002), with ground objects reflecting more wavelengths that would excite the "green receptors" of insects (Bernard & Wehner, 1980; Menzel & Blakers, 1976), and the sky providing relatively higher levels of UV wavelengths that would excite the "UV receptors" of insects. Whether insects can and do use such a green-UV opponent-processes channel has yet to be determined.

In conclusion, this paper shows two novel findings concerning navigation and orientation in the solitary foraging desert ant, *M. bagoti*. First, our experiments showed that *M. bagoti* foragers did not use the experimentally provided beacon landmarks to orient when the global panorama was undifferentiated. In work in progress, we are testing the possibility that landmarks that alter the arenas artificial skyline will have more influence on the ants' navigation. Second, our experiments showed that ants can learn a context-specific local vector based on some form of compass. This local vector specifies a compass direction to head to the exit, and is triggered by the context in which *M. bagoti* learns spatial information (being at the centre of the arena with a bit of food to take home). We hypothesise that the compass used to specify the local vector is based on polarised light, as it is in other insects (Wehner, 1994), but this remains to be tested. Our findings and the experimental control provided by arenas open up many possibilities for future research regarding how *M. bagoti* uses different forms of spatial information for navigation.

3.6 Acknowledgements

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Chapter 4

Multiple Cue Integration in Navigating Ants

This work has yet to be submitted. The working title and author list for this work is as follows: Legge, E.L.G., Wystrach, A., Spetch, M.L., & Cheng, K.: How compromise gets you home: Multiple cue integration in navigating ants.

4.1 Abstract

Animals use many different sources of information to navigate. Using multiple cues is advantageous in most situations because they increase the overall accuracy and robustness of obtained information. Even though the functional reasons for using multiple cues are well understood, the mechanisms underlying cue integration are unclear. Here, we investigated the behavioural mechanisms responsible for cue integration in a small-brained invertebrate, namely the Australian desert ant *Melophorus bagoti*. We did this by artificially setting different directional cues used by these ants in conflict. Specifically, we set into conflict the direction dictated by: (i) a celestial local vector and view-based navigation along familiar route (Experiment 1) and (ii) ants' path integrator and view-based navigation when displaced off their familiar route (Experiment 2). Integration was found in almost all conflict situations, suggesting that ants may systematically combine the dictates of their different navigational systems and that final integration occurs at the motor output level of processing. Furthermore, we show that ants can weight information in a flexible way. Ants seem to measure the reliability of the visual navigation system by using the current visual familiarity as a proxy for approximating Bayesian variances. We believe that such simple solutions for integrating cues could be widespread across animals.

4.2 Introduction

Animals rely on many different sources of information such as auditory (Gröhn et al., 2005; Rossier et al., 2000; Poulet & Hedwig, 2005), olfactory (Wallace et al., 2002; Steck et al., 2009), visual (reviews: Cheng, 2012; Spetch & Kelly, 2006) and proprioceptive cues (Cheng & Newcombe, 2005; Etienne, Maurer, & Sèguinot, 1996; Kearns, Warren, Duchon, & J, 2002; Ronacher & Wehner, 1995; Cheng, Srinivasan, & Zhang, 1999) for navigation. The reason why animals use such a variety of cues is quite clear. Focusing on a single cue is a fragile strategy because a cue can move or disappear due to environmental changes; or become lost or confounded due to biological errors. Integrating information from multiple cues provides a way to cope with these problems, and thus increases robustness (e.g., in case one of the cues is lost, Spetch & Mondloch, 1993) and accuracy (Kamil & Cheng, 2001; Kamil et al., 2001) of the overall information obtained. While the functional reasons why animals integrate multiple cues are clear, the underlying mechanisms responsible for such integration are still uncertain. Investigating how an animal integrates multiple cues can be achieved by artificially setting the cues in conflict and observing the animal's response (Cheng et al., 2007). Most research on this topic has focused on vertebrate animals (e.g., Spetch & Kelly, 2006; Legge et al., 2009) but we believe that understanding how information is integrated in a small-brained invertebrate can provide insight into the basic mechanisms of cue integration. Navigating ants make an excellent model species for such a task because they rely simultaneously on multiple navigational strategies (Collett, 2012) that can easily be set into conflict.

In the present paper, we investigate how the Australian desert ant, *Melophorus bagoti*, responded when the directional information provided by its different navigational systems were artificially set into conflict. Specifically, we show that *M. bagoti* foragers can integrate between: (i) the dictates of view-based navigation and a celestial local vector (a learned direction based on celestial cues such as the pattern of polarized light) when navigating along a familiar route (Experiment 1) and (ii) between path integration and view-based navigation when displaced off the familiar route (Experiment 2). Furthermore, our results suggest that ants may integrate cues by weighting them according to their current reliability, a notion consistent with Bayesian Inference (Cheng et al., 2007; Friedman, Ludvig, Legge, & Vuong, 2012).

4.3 Experiment 1: View-based navigation vs. Celestial local vector

Experiment 1 was designed to determine whether *M. bagoti* foragers could combine information from view-based navigation (Graham & Cheng, 2009, 2009a) with a celestial local vector (Legge et al., 2010; Collett et al., 1998), two navigational strategies that can be used along a familiar route (Wystrach, Beugnon, & Cheng, 2012; Wystrach, Schwarz, Schultheiss, Beugnon, & Cheng, 2011). Specifically, ants were trained to find food in the center of an arena that provided directional information via an unambiguous artificial skyline formed by a circular wall of irregularly varying height. Ants entered and exited the arena via a small opening located away from the direction of the nest (if the nest was located at a compass direction of 0°, the exit would be located at 270°). Thus, to exit the arena, ants had to ignore information from their path integrator, and learn the location of the exit using view-based navigation and a celestial local vector. After training, ants were captured just before they entered their nest (Zero-vector ants); these ants had no directional information from path integration because the homing vector was close to 0 (cf. Collett et al., 1998; Wehner & Srinivasan, 2003). After capture, Zero-vector ants were released in the center of a replica arena that could be rotated to place the direction dictated by view-based navigation (following the rotation of the arena) in conflict with the direction dictated by the celestial local vector (along the training direction).

4.3.1 Methods

Subjects

Subjects were 181 solitary foraging desert ants (*Melophorus bagoti*) from a single nest within their natural semi-arid habitat at a field site approximately 10km south of Alice Springs, Northern Territory, Australia, between January and March 2010.

Materials and Apparatus

Plastic-coated particleboard walls (10cm (h) × 1cm (w)) were placed around the nest and extended to the entrance of a circular training arena. The corridor created by the particleboard was ∼1m wide, preventing ants from foraging naturally, and forcing them to enter the arena in search of food. The ground within the walled area was cleared of all vegetation and debris for the duration of the experiment. All walls were recessed into the ground by digging a 10cm deep trench. To deter ants from traveling along the walls in the trench, it was filled with dried grass and tussock.

A circular training arena (diameter = 1.5m, maximum height = 50cm) made out of 1mm Lexan® polycarbonate resin thermoplastic (color: flat green) was placed in the field so that the center of the arena was 9.09m North (compass bearing from the nest: 350°) of the main nest entrance. A white plastic feeder (∼15cm (l) × ∼15cm (w) × ∼9.5cm (h)) was buried in the ground up to its lip in the center of the arena. The floor of the arena contained a goniometer constructed out of the same 1mm Lexan® polycarbonate resin thermoplastic used for the arena walls. The goniometer plastic was transparent, but was lightly dusted with sand to ensure the surface the ants were walking on was not foreign. The goniometer was divided into 24 equal sectors of 15° each. Circles were marked at a distance of 30cm from the center of the goniometer, allowing us to record a heading at this distance. The 0° point of the goniometer always pointed in the direction of the nest entrance. Sticks were placed in the feeder so that subjects could easily climb in and out. The arena entrance/exit was a small depression in the ground that led under the arena wall. The location of the arena entrance/exit was located at a compass bearing of 270° relative to the nest entrance (see Figure 4.1a). The top of the arena wall was modified to provide a distinct visual panorama for the ants (see Figure 4.1b-c).

For testing, a second, identical arena was placed behind the training arena. The center of the test arena was 13.41m and 340° from the nest entrance. This test arena did not contain an exit or a central feeder. Instead, the floor of the arena contained a goniometer similar to the one in the training arena, with the exception that it did not contain a central hole for a feeder. As in the training arena, the 0° point of the goniometer always pointed in the direction of the nest entrance.

Procedure

Training Cookie crumbs and/or mealworm pieces were available to ants *ad libitum* in the arena feeder during training. On their first observed visit to the feeder, ants were captured and marked with a small dab of acrylic paint on the top of their abdomen. After being painted, ants were left to forage and train themselves for at least one day before being tested.

Testing Ants were allowed to enter the training arena and take a piece of food from the feeder and return to their nest. However, just before entering the nest, ants were captured and placed in the center of the testing arena. The testing arena was rotated by 0°, 90°, 180°, or 270° relative to the training arena. Directional headings of ants were recorded at 30cm from the release point using a buried goniometer. Each ant was tested only once.

Data Analysis All data analyses were conducted with Oriana® (Kovach Computing Services, Anglesey, Wales, UK). Ants were always tested in the afternoon, between 13:00–18:00h local time.

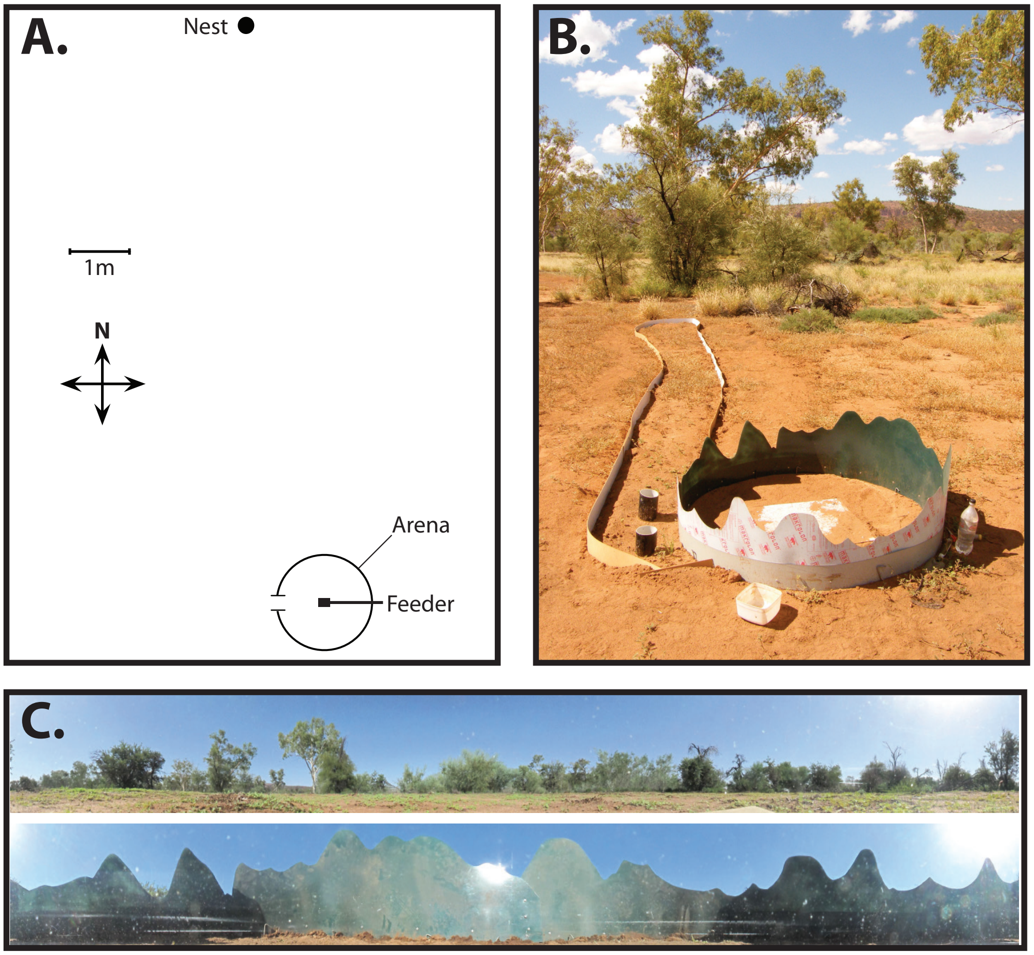

Figure 4.1: [**A.**] A diagram depicting ants' nest relative to the training arena used in Experiment 1. [**B.**] An image of the training arena used in Experiment 1. The channel outside of the arena extends from the nest to the arena wall to prevent ants from foraging naturally. [**C.**] 360° panoramic images taken from the center of the arena (bottom image). The top image is a 360° panoramic image taken at the same location without the arena present. Note that the arena completely obscures the natural skyline.

4.3.2 Control group: No arena rotation

When the test arena was in the same orientation as the training arena, Zero-vector ants were significantly oriented [$r = .74$, $n = 43$, $p < .05$, Figure 4.2a]. Interestingly, ants did not choose a direction that would bring them directly to the arena exit (270°). Instead, they showed a systematic bias toward a point of the arena wall centered at 297.99°. Because of this systematic bias, 297.99° was used as the reference direction for both ants' celestial local vector and their view-based navigation systems for the analysis of conflict tests.

4.3.3 Arena Rotated 180°

When the arena was rotated by 180°, ants' celestial local vector and view-based navigation systems indicated diametrically opposite directions (297.99° and 117.99°, respectively). In this condition, ants were not significantly oriented [$r = .14$, $n = 45$, $p > .05$, Figure 4.2c], and the distribution appeared to be random with no sign of bimodality [Rayleigh test for bimodality: $r = .08$, $n = 45$, $p > .05$]. This result suggests that ants did not rely on a single preferred cue when both cues provided very discrepant information. It is possible, however, that the ants integrated the two opposing directions, with different ants using different weights for the two cues, thus producing a random distribution for the group as a whole.

4.3.4 Arena Rotated 90° and 270°

When the arena was rotated by 90°, ants were significantly oriented [$r = .71$, $n = 48$, $p < .001$]. Ants' mean heading direction [$321.42° \pm 13.26°, M\pm$ the 95% confidence interval] also differed significantly from the direction that would be predicted if ants were relying solely on their celestial local vector or view-based navigational systems [297.99° vs. 27.99°, respectively; One-sample Wilcoxon Signed Rank Test (celestial local vector): $Z = 3.24$, $n = 48$, $p < .01$; One-sample Wilcoxon Signed Rank Test (view-based navigation): $Z = -5.64$, $n = 48$, $p < .001$]. Thus, ants integrated a direction between the two sources of information (see Figure 4.2b).

When the arena was rotated by 270°, ants were once again significantly oriented [$r = .55$, $n = 45$, $p < .001$]. Furthermore, similar to when the arena was rotated by 90°, ants' mean heading direction [236.81° ± 19.6°] indicated they did not rely exclusively on a celestial local vector [One-sample Wilcoxon Signed Rank Test: $Z = -3.92$, $n = 45$, $p < .001$]. Although ants' mean direction also differed from that predicted by exclusive reliance on a view-based navigational strategy, this difference failed to reach statistical significance [One-sample Wilcoxon Signed Rank Test: $Z = 1.6$, $n = 45$, $p > .05$, see Figure 4.2d].

Thus, although heading direction did not differ significantly from that predicted by the exclusive use of view-based navigation at 270°, clear evidence of integration of a celestial local vector and view-based navigation was seen when the arena was rotated by 90°.

4.4 Experiment 2: Path integration vs. View-based navigation

Experiment 2 was designed to determine how *M. bagoti* foragers combine path integration (PI) and visual terrestrial information while navigating in their natural habitat. In this experiment, ants were trained to a stationary feeder and tested for homing at three test locations under two conditions. Specifically, homing ants were captured at their departure from a feeder located 10m away from the nest (Full-vector ants, Fv); these ants had a vector from their path integration system pointing in the absolute feeder-to-nest direction. Other ants were captured very close to their nest for testing (Zero-vector ants, Zv). The three test locations differed in how distant they were from the ants' nest, and thus how closely the visual surround matched the view ants had learned around their nest entrance. Release Point (RP) 1 was located 4m from the nest and provided ants with a very familiar visual surround, RP2 was located 32m from the nest and provided ants with a semi-familiar visual surround, and RP3 was located 64m from the nest and provided ants with a novel, unfamiliar visual surround.

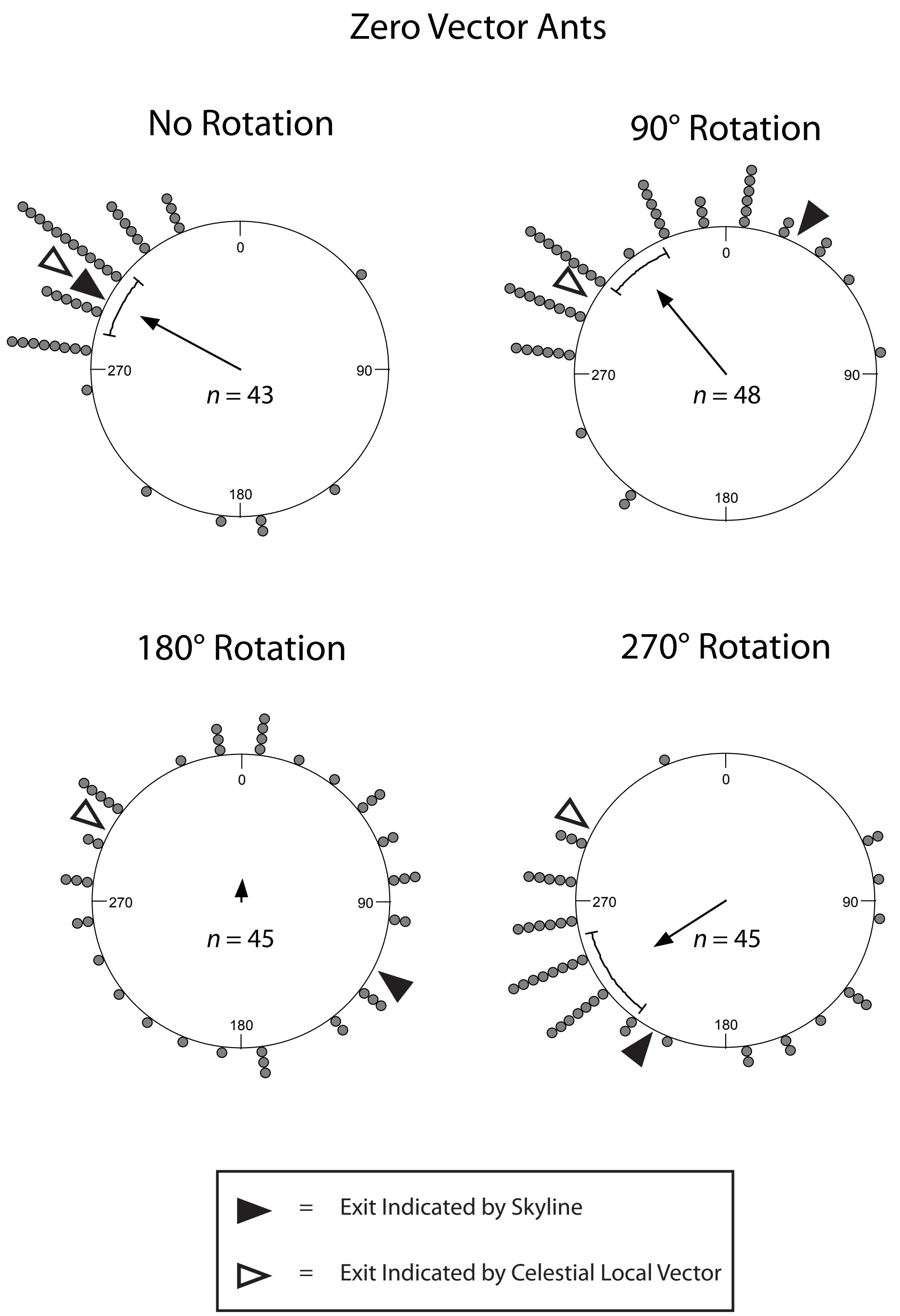

Figure 4.2: Zero-vector ant directional bearings for each test in Experiment 1. Grey circles indicate ants' directional bearings after crossing a marked goniometer line 30cm from a central release location. Open triangular markers indicate the exit direction according to a learned route (celestial local vector). Closed triangular markers indicate the exit direction according to ants' view-based navigational system. Headers above each circular plot indicate the degree the testing arena was rotated relative to the orientation of the training arena. When ants were significantly oriented, the 95% confidence interval of the mean is displayed as a curved marker on the inside of the circular plot.

4.4.1 Methods

Subjects

Subjects were 132 *M. bagoti* foragers at the same field site described in Experiment 1. All testing was conducted between January and March 2010.

Materials and Apparatus

Training Plastic-coated particleboard walls (10cm (h) × 1cm (w)) were placed around the nest in a 1.5m (diameter) circle to prevent the ants from foraging naturally. Attached to one portion of this circle was a 10m (l) × 1.5m (w) corridor constructed of the same material. The ground within the walled area was cleared of all vegetation and debris for the duration of the experiment. On training days, the portion of the wall surrounding the nest and blocking access to the corridor was removed (see dotted line, Figure 4.3a). On these days, cookie crumbs or mealworm pieces were placed at the end of the corridor (∼11m away from the nest; nest was located at a compass bearing of 0° from the feeder). All walls were recessed into the ground by digging a 10cm deep trench. Thus, the walls were flush with the ground and did not obstruct the ants' view of the surrounding terrain and skyline. On days when the portion of the wall that surrounded the nest and connected to the corridor was removed, the ground where the wall had been was filled and flattened to allow ants easy access to the food cache at the end of the corridor. To deter ants from traveling along the walls in the trench, it was filled with dried grass and tussock (see grey area, Figure 4.3a).

Testing Three wooden goniometers, each containing 24 sectors (15°/sector) with a measurement point at 60cm from the centroid, were placed at three release points in the field. Release Point 1 (RP1) was 4m away from the nest and located at a compass bearing of 135° from the nest. RP2 was located 32m away from the nest at a compass bearing of 292.5°. RP3 was located 64m away from the nest at a compass bearing of 255°. All collected data were transformed so that 0° indicated the same direction for all tests. Figure 4.3b presents 360° panoramic images taken at the nest and the three release points.

Procedure

Training Either cookie crumbs or mealworm pieces were available *ad libitum* at the end of the corridor. Foragers were free to run back and forth between the nest and the feeder on training days when the barrier surrounding the nest was removed (barrier location indicated by a dotted line on Figure 4.3a).

Testing Ants were let free to forage to and from the feeder for at least one full day. Given the natural ontogeny of the foraging paths in *M. bagoti* (Muser, Sommer, Wolf, & Wehner, 2005), we assume that an ant venturing 11m away from its nest has already performed several learning walks and is not naïve to the visual environment surrounding the nest. A single food-carrying forager was captured in a tube either very close to the nest, so that it has no information from its path integrator (referred to as "Zero-vector ant"); or when it had just left the feeder, so that its path integration vector points in the feeder-to-nest absolute direction (referred to as a "Full-vector" ant). After capture, the ant was released at two of the three release points. Order and choice of release points were counterbalanced across ants.

Data analysis

During each test, the ant's heading direction was measured at 60cm from the release point and it was recaptured as soon as it left the goniometer board. All data were transformed so that 0° indicated the same direction for all tests. All data analyses were conducted with MATLAB® (MathWorks, Natick, MA, USA) and/or Oriana® (Kovach Computing Services, Anglesey, Wales, UK).

4.4.2 Test for Path Integration Alone

Due to the distance of RP3 from the nest (64m), the visual surround was unfamiliar to the ants. Fv ants were significantly oriented at this location [$r = .88$, $n = 72$, $p < .0001$, Figure 4.4f] but Zv ants were not [$r = .05$, $n = 68$, $p > .05$, Figure 4.4c]. This shows that, at RP3, ants could only use

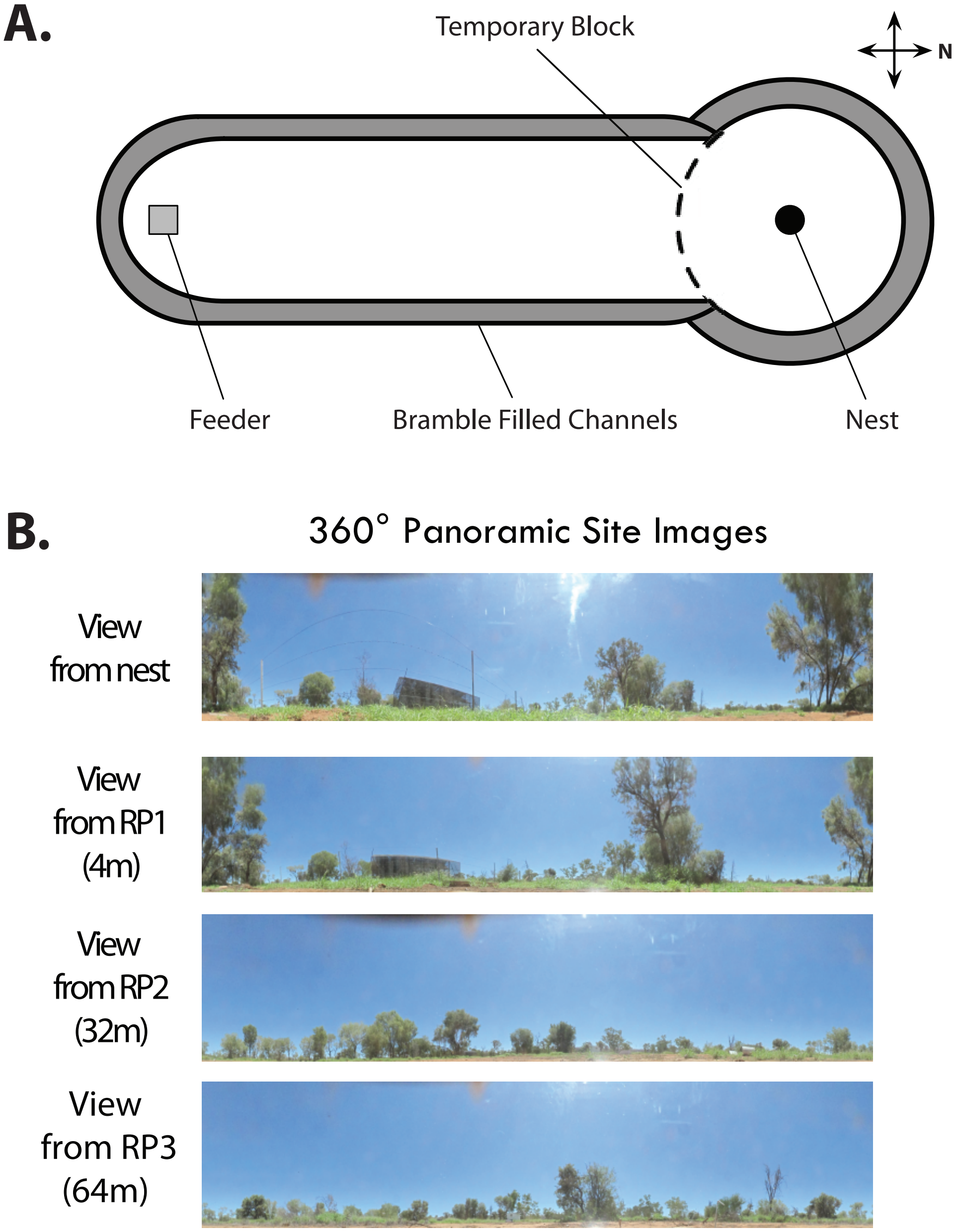

Figure 4.3: [**A.**] Diagram of the training channel used in Experiment 2. Channels were filled with brambles to discourage foragers from leaving the main training path. [**B.**] 360° panoramic images taken at the nest entrance, and at the center of each of the three release points used in Experiment 2. Note that the images are ordered from top to bottom according to their Euclidian distance from the nest entrance. Euclidian distance from the nest entrance is indicated in parentheses for each image.

PI information for orientation, as the visual surround did not provide familiar visual information for orientation.

4.4.3 Test for View-based Navigation Alone

Zv ants were tested at RP1 (4m from nest) and RP2 (32m from nest) to determine whether ants could use the visual surround for orientation when PI information was not available. Specifically, we found that at both RPs, Zv ants were significantly oriented [RP1: $r = .79$, $n = 108$, $p < .0001$; RP2: $r = .47$, $n = 75$, $p < .0001$], indicating that ants could use the visual surround for orientation at these two locations.

4.4.4 Integration of PI and View-based Navigation

Tests on Fv ants at RP1 and RP2 placed the dictates of ants' path integrator (feeder-to-nest direction) in conflict with the terrestrial surround (release-point-to-nest direction). While Fv ants were significantly oriented at both release points [RP1: $r = .66$, $n = 111$, $p < .0001$; RP2: $r = .81$, $n = 81$, $p < .0001$], they did not fully rely on either path integration [Watson-Williams test; Fv-RP1 vs. Fv-RP3: $F(1{,}181) = 112.45$, $p < .0001$; Fv-RP2 vs. Fv-RP3: $F(1{,}151) = 13.81$, $p < .001$], or view matching [Watson-Williams test; Fv-RP1 vs. Zv-RP1: $F(1{,}217) = 134.68$, $p < .0001$; Fv-RP2 vs. Zv-RP2: $F(1{,}154) = 119.72$, $p < .0001$]. Thus, ants did not hierarchically choose one cue to rely upon exclusively in this situation. Instead, they chose an intermediate direction between the dictates of both sources of information (Figure 4.4d-e), thus demonstrating integration.

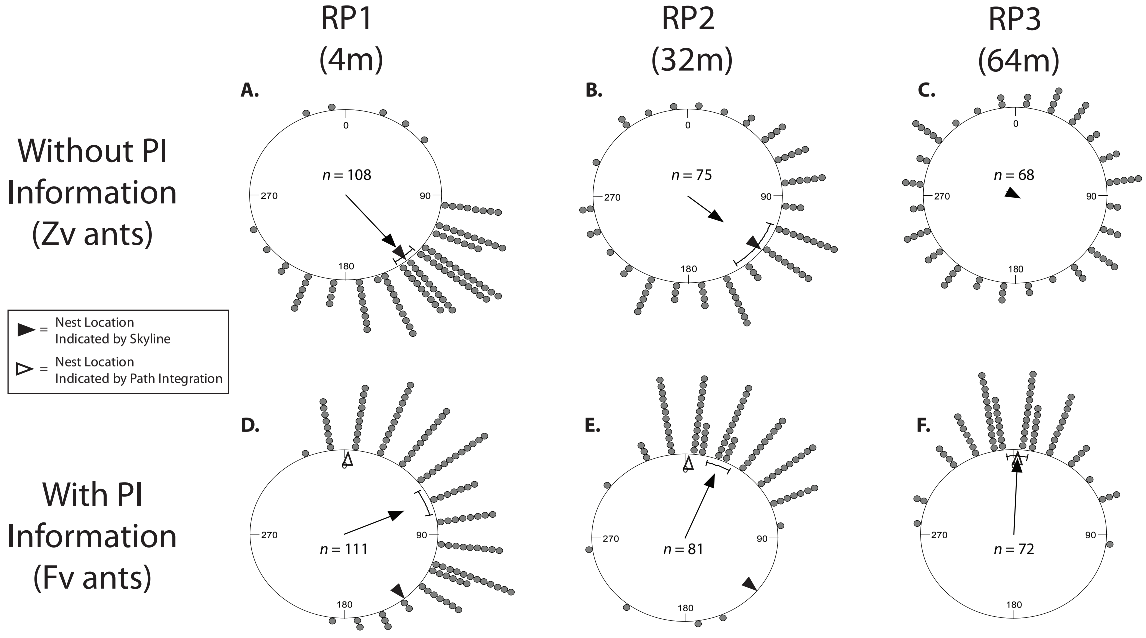

Figure 4.4: Ant directional bearings for each test in Experiment 2. Grey circles indicate an ant's directional bearings after crossing a marked goniometer line 60cm from a central release location. Open triangular markers indicate the nest direction according to ants' path integration system. Closed triangular markers indicate the nest direction according to ants' view-based navigation system. Headers above each circular plot indicate the degree the testing arena was rotated relative to the orientation of the training arena. Note that there are no open triangular markers in panels A-C, as all ants tested here were zero-vector, and did not have access to path integration information. Panel F does not contain a closed triangular marker, as ants could not use view-based navigational cues to orient themselves at this release point when they did not have access to path integration information (see panel C). When ants were significantly oriented, the 95% confidence interval of the mean is displayed as a curved marker on the inside of the circular plot.

Test	Weight: View	Weight: PI
Fv: RP1 (4m)	0.36	0.63
Fv: RP2 (32m)	0.18	0.82

Table 4.1: Weights for each cue in conflict tests in Experiment 2.

4.4.5 Informational Weighting

Interestingly, conflict tests at RP1 and RP2 led to different integrated directions (Watson-Williams test; Fv-RP1 vs. Fv-RP2: $F(1,190) = 44.19$, $p < 0.0001$), indicating that PI and the visual panorama were not equally weighted in both situations (Figure 4.4d-e). Results with Zv ants show that the ants were less accurate at using the visual panorama at RP2 than RP1 [circular Wilcoxon test on scatter, Zv-RP2 vs. Zv-RP1: $Z = 4.43$, $n = 183$, $p < .0001$, Figure 4.4d-e]. This is likely due to the fact the scenery perceived at RP2 (32m away from the nest) appeared less familiar to the ants than at RP1 (4m away from the nest). In the conflict situation (Fv ants), the lower familiarity of the visual panorama at RP2 led to a weaker influence of view-based navigation, and thus a stronger influence of the information provided by PI.

Taken together, this suggests that ants do not only combine the direction dictated by Path Integration and the visual panorama, but weight these cues according to their reliability. The reliability of the visual panorama seems to be based on how familiar it currently appears to the ants, with lower familiarity leading to a weaker weight, and thus a lower influence on the final direction taken (see Table 4.1).

4.5 Discussion

Studying small-brained animals, such as ants, in tests where cues are placed in conflict can provide researchers with a remarkable opportunity to understand the basic mechanisms underlying cue integration. Recent work has shown that ants navigating along a familiar route can integrate the dictates of path integration and view-based navigation on route (Collett, 2012). We investigated additional conflict situations in *M. bagoti* to: 1) test whether ants would also integrate between other navigational systems and 2) shed light on the mechanisms underlying cue integration.

Results of the conflict experiments show that ants integrate the direction dictated by their view-based navigation system and a learned celestial local vector when navigating along a familiar route (Figure 4.2) as well as between path integration and the use of view-based navigation when displaced off their familiar route (Figure 4.4). This suggests that ants may systematically integrate the dictates of their different navigational systems.

4.5.1 How is the information integrated?

Our results reveal that the different navigational systems are not always combined in a rigid way, but can be adaptably weighted. Specifically, Experiment 2 shows that the influence of view-based navigation on the final behavior is modulated according to the familiarity of the view perceived. This makes functional sense, as the direction outputted by the view-based navigation system is based on the comparison between the current and memorized scenes (see Wystrach & Graham, 2012 for a recent review). Therefore, the familiarity of the current scene is a direct indicator of the reliability of the view-based navigation system. That way, ants can obtain information about the system's reliability without the need of computing its overall accuracy over many past experiences. It is possible that such integrations weight cues similar to what would be expected according to Bayesian principles. Specifically, while Bayesian predictions are based on calculations of variances associated with cues (Cheng et al., 2007; Friedman et al., 2012), this does not mean that an animal approximating Bayesian predictions is actually calculating variances in the brain. In the case of our study species, it is more likely that measures that are readily available, such as visual familiarity, serve as proxies for approximating Bayesian variances[1].

4.5.2 Where does the integration occur?

Our experiments show that ants can integrate information from navigational systems that rely on very different sensory inputs. For example, path integration in ants is based on proprioceptive cues (Wittlinger et al., 2006) as well as a celestial compass based in good part on the pattern of polarized skylight detected by the Dorsal Rim Area of their compound eyes (Wehner & Srinivasan, 2003; Labhart & Meyer, 1999; Aepli, Labhart, & Meyer, 1985). In contrast, view-based navigation is based on the appearance of the terrestrial scene based on a wide panoramic visual input (Wystrach, Beugnon, & Cheng, 2011; Schultheiss, Wystrach, Legge, & Cheng, 2012). Additionally, ants integrated information stored in different types of memory. Information from view-based navigation and local vectors are stored in a long-term fashion (Legge et al., 2010; Collett et al., 1998) while information from the Path Integrator is obtained and kept only during the current journey (e.g., Wehner & Srinivasan, 2003).

While primates have been shown to integrate information from different sensory systems into a dedicated area via sensory remapping (Deneve & Pouget, 2004; Macaluso & Driver, 2001; Jay & Sparks, 1987), this is likely not the case in ants. For instance, observation of ants show that path integration and view-based matching work independently (Kohler & Wehner, 2005; Wehner & Müller, 2006; Cruse & Wehner, 2011; Andel & Wehner, 2004), and are likely processed in separate areas as well. Specifically, path integration input is thought to be projected into the central complex (Wehner & Srinivasan, 2003; Labhart & Meyer, 2002; Homberg, 2004), whereas learnt view-based navigation information is thought to be processed in the mushroom bodies (Wehner & Srinivasan, 2003; Heisenberg, 1998). Thus, both behavioral and

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[1] While a true test of Bayesian integration is not compatible with our data, as it requires knowledge of how an individual responds to cue variance based on repeated trials (Cheng et al., 2007; Friedman et al., 2012), we can perform estimated calculations based on the assumption that due to a large sample size, inter-individual variance measures will approximate within-individual variance measures. See Supplementary Information (Section 4.7) for more details and tests of Bayesian integration using the data presented in Experiment 2.

neurological data seem to show that both systems work independently, with no higher center to integrate the information into a higher representation. Thus, the integration shown here is likely to occur just before motor output as a common neural summation into the motor commands as described in the model in Cruse and Wehner (2011). In such integrations, weight could be coded as the strength of the connection between each system and the motor output, or directly as a spike rate reflecting the excitatory level of each system. For example, the spike-rate for view-based matching information could simply depend on the current familiarity of the perceived panorama.

Finally, cue integration in vertebrates seems to occur only when the conflicting information is not too discrepant (Cheng et al., 2007; Körding et al., 2007). In ants we think that integration between cues is mandatory, as there does not appear to be an overarching module or system that can override it. This explains the random directional distribution in the case of the 180° rotation conflict test (Experiment 1). Because ants may average the two dictates with variable weights across individuals, and do not choose one cue over the other, a random distribution of directions is obtained (see Figure 4.2c). Integrating highly discrepant information would be deleterious when reconstructing a unified representation of the world, but would be expected if integration simply happens mandatorily at the motor output.

4.6 Conclusion

We have shown not only that ants can integrate information between the different systems of their navigational toolkit, but they can do so by weighting information according to its reliability. In vertebrates, similar weighted integration seems to be based on Bayesian principles where the reliability of each cue is obtained by calculating its variance over past experience (Cheng et al., 2007; Deneve & Pouget, 2004; Alais & Burr, 2004; Ernst & Banks, 2002). Additionally, at least in primates, these integrations seem to involve a dedicated area of the brain where the information from different modalities can be remapped in a common language for integration (Deneve & Pouget, 2004;

Macaluso & Driver, 2001; Jay & Sparks, 1987).

Here we showed how an apparently similar weighted integration can be achieved without calculating past reliability or involving dedicated "remapping" brain areas. As highlighted previously (Zeil, 2012), the parsimonious explanation arising from the study of insect navigation can help us to understand elementary mechanisms that might be shared across animals (Shettleworth, 2010). In the present case, the ability to integrate information from different navigational systems hints at a system that includes a proxy measure of error with every measure of position or direction. Such error measures are commonly incorporated into navigational systems constructed in Artificial Intelligence (Thrun, 2000). Coupled with previous research (e.g., Cheng et al., 2007), our findings suggest that such a system could be widespread across animals.

4.7 Supplementary Information

According to Bayesian inference, the optimal weighting of two sources of information is a ratio of the inverse of the variances associated with each cue (Cheng et al., 2007; Friedman et al., 2012). As such, to calculate a predicted location based on Bayesian principles, the variability associated with each directional source must be obtained from single-cue conditions. In our experiment, the variance associated with ants' path integrator was obtained from Fv ants at RP3, while the variances associated with the visual surround were obtained from Zv ants at RP1 and RP2.

While a full discussion on how to calculate a predicted location or direction using a Bayesian model have been discussed in detail elsewhere (cf. Cheng et al., 2007; Friedman et al., 2012), we briefly outline the procedure we used below. First, to calculate the expected heading direction based on the Bayesian hypothesis, we obtained a theoretical estimated weight for each source of information based on the cue's variance:

$$\text{Weight}_{PI} = \frac{\sigma^2_{view}}{\sigma^2_{view} + \sigma^2_{PI}} \tag{4.1}$$

$$\text{Weight}_{view} = \frac{\sigma^2_{PI}}{\sigma^2_{PI} + \sigma^2_{view}} \tag{4.2}$$

where σ^2_{view} is the average circular variance of Zv ants' headings at a given release point (i.e., circular variance based on use of view-based information alone) and σ^2_{PI} is the circular variance of full-vector ants' headings at RP3 (i.e., circular variance based on use of path integration alone). Weights were calculated individually for RP1 and RP2, as the circular variance associated with the view-based navigation system differed between the two. Using Eq. 4.3, we used the weights obtained from Eqs. 4.1 and 4.2 to calculate ants' predicted mean heading direction based on the Bayesian model for each release point. In Eq. 4.3, μ is the mean heading direction of ants when only the information denoted with the subscript is available (e.g., μ_{PI} is the mean heading direction of Fv ants at RP3).

$$\begin{aligned}&\text{Bayesian Predicted Heading Direction} = \\ &\qquad ((\mu_{PI} \cdot \text{Weight}_{PI}) \bmod 360°) + ((\mu_{view} \cdot \text{Weight}_{view}) \bmod 360°)\end{aligned} \tag{4.3}$$

Model analysis revealed that ants sometimes integrated information in a manner consistent with a Bayesian inference. Specifically, at RP1 (4m from nest), ants' mean heading direction was $66.44° \pm 9.51°$ (±: the 95% confidence interval). The predicted direction based on the Bayesian model (52.27°) fell slightly outside of this range. However, at RP2 (32m from the nest), ants' mean heading direction was $22.5° \pm 7.93°$, and the predicted direction based on the Bayesian model (25.27°) clearly fell within this range. Thus, while our data cannot truly test whether ants integrated information in a Bayesian manner due to the fact that we do not have measures of individual responses to each cue across multiple trials, if we assume that, due to a large sample size, inter-individual variance measures will approximate within-individual variance measures, our data provides some evidence that ants integrate information in a Bayesian-like manner. Thus, our research provides a useful starting point for researchers wishing to test whether ants integrate multiple sources of information according to Bayesian principles.

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Chapter 5

Multiple cue use and integration in pigeons *Columba livia*

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5.1 Abstract

Encoding multiple cues can improve the accuracy and reliability of navigation and goal localization, but may create problems if one cue is displaced and provides information that conflicts with other cues. Here we investigated how pigeons cope with cue conflict by: (a) training them to locate a goal relative to two landmarks, and (b) experimentally varying the amount of cue conflict. Results showed that pigeons tended to integrate both cues when the amount of conflict was small. However, when the amount of conflict was large, pigeons used information from both cues independently. These results suggest the strategy pigeons use to resolve spatial cue conflict is context dependent.

5.2 Introduction

Animals use many cues for navigation and goal localization. These cues can include auditory (Gröhn et al., 2005; Rossier et al., 2000; Poulet & Hedwig, 2005), olfactory (Steck et al., 2009; Wallace et al., 2002; Wolf & Wehner, 2000), and visual cues (Cheng et al., 2009; Spetch & Kelly, 2006), as well as proprioceptive cues such as optic flow and stride length (Cheng, 2005; Etienne et al., 1996; Kearns et al., 2002; Ronacher & Wehner, 1995; Cheng et al., 1999). When trying to locate a specific location such as a hidden food cache, animals typically encode multiple cues that provide redundant information (e.g., Spetch & Mondloch, 1993; Balda & Turek, 1984). Such redundancy is likely adaptive, as using multiple cues for goal localization has been shown to increase search accuracy (Kamil & Cheng, 2001; Kamil et al., 2001; Cartwright & Collett, 1983) and robustness (e.g., a goal can still be located even if one cue is missing; Spetch & Mondloch, 1993).

While usually adaptive, encoding multiple redundant cues can be problematic if a cue becomes displaced, e.g., by the wind. In these situations, the displaced cue will now provide information that conflicts with the information provided by other nearby cues (known as cue conflict). This informational conflict can lead animals to search in an incorrect location or become lost, thus wasting time, energy, and possibly increasing the risk of predation. One would expect that behavioural strategies for coping with cue conflict would have evolved to ameliorate these negative consequences. Therefore, it is not surprising that recent studies have revealed strategies for coping with spatial cue conflict across a wide range of taxonomic classes including insects (e.g., Collett, 2012), mammals, (e.g., Chalfoun & Martin, 2010), and birds (e.g., Legge et al., 2009).

One method for coping with cue conflict that animals have been shown to use in discrete choice tasks is to encode cues hierarchically (e.g., Spetch & Edwards, 1988; Legge et al., 2009). When using a purely hierarchical strategy (also known as winner-take-all or take-the-best strategies, Gigerenzer & Brighton, 2009; Gigerenzer & Goldstein, 1999; Morgan et al., 1998; Palmer, 1994; Palmer et al., 1993) to cope with cue conflict, animals only use the cue at the top of the hierarchy for localizing a goal. Whereas such a strategy may be useful in some situations due to its simplicity, relying on a single cue while others are still available is not optimal. Specifically, when using a hierarchical strategy, animals discard potentially relevant information from cues that are not at the top of the hierarchy. Furthermore, such a strategy can lead an animal to search in an incorrect location or to navigate in the wrong direction if the cue at the top of the hierarchy was displaced. Some animals have been shown to account for this problem by adopting a win-stay/lose-shift strategy (also referred to as an independent source strategy) when searching for a goal (Hosoi et al., 1995; Hodges, 1985; Kamil, 1983; Gaffan & Davies, 1981). Thus, as with animals using a pure hierarchical strategy to cope with cue conflict, animals using a win-stay/lose-shift strategy would search relative to a preferred cue. Unlike pure hierarchical strategies, if the most preferred cue did not lead to their goal, the animal would then shift to using another encoded cue to search. Though a win-stay/lose-shift strategy could be more successful than a pure hierarchical strategy in some situations, such a strategy may be non-optimal in others by leading an animal to search over a more dispersed area.

An alternative to relying on hierarchical or independent strategies for coping with cue conflict is for animals to integrate the information provided by multiple cues. By integrating, animals can minimize discrepant information provided by a displaced cue and search close enough to a goal for success. While integrative strategies can be more complex than hierarchical strategies, they do not require animals to discard large amounts of information. As such, when cues provide conflicting information, integrative strategies may allow animals to search more accurately than if they were using a hierarchical or win-stay/lose-shift strategy. While a number of integrative strategies have been proposed for explaining animal search behaviour (e.g., simple averaging; Batty, Spetch, & Parent, 2010; MacDonald, Spetch, Kelly, & Cheng, 2004; Kelly, Kippenbrock, Templeton, & Kamil, 2008; Sturz & Katz, 2009), one of the most recent and robust methods of cue integration to be suggested is based on Bayesian inference (termed Bayesian integration; Cheng et al., 2007). Specifically, Bayesian integration assumes animals encode each cues' relative reliability, as well as the location of the goal relative to each cue. Thus, Bayesian integration allows animals to use information derived from past experience (e.g., cue reliability) to determine how heavily they should weight a particular source of information. In many cases where cues provide conflicting information, Bayesian integration should allow an animal to more closely predict the location of a goal relative to other methods.

Thus, animals have a variety of methods for coping with cue conflict. However, direct comparisons between these methods of resolving cue conflict are needed to determine whether the method animals use to cope with cue conflict is situationally dependent, or whether an animal will always prefer a specific strategy in a particular task. Towards this end, the goal of these experiments is to determine the mechanisms used by pigeons (*Columba livia*) to cope with cue conflict in a spatial localization task. Specifically, we trained pigeons to find a hidden goal relative to two landmarks and then shifted the landmarks to place them in conflict. In these shift tests, we removed the goal and recorded subjects' search attempts. To evaluate data collected on these tests, we developed three models, each based on a specific theory as to how animals localize goals in space. Specifically, the three models we used were based on hierarchical, independent, and integrative theories of spatial localization.

Eight pigeons were first trained in an open-field to locate a hidden goal relative to two landmarks (cues): a large blue cue and a small red cue. After the pigeons were reliably finding the hidden goal relative to both cues, we tested each cue alone and then placed the cues in varying degrees of conflict. Specifically, subjects received four tests where the small red cue was experimentally shifted parallel or orthogonal to the large blue cue by either a small (near-shift conditions) or large (far-shift conditions) distance. The resulting four test types were: Orthogonal-Near (OrthN), Parallel-Near (ParaN), Orthogonal-Far (OrthF), and Parallel-Far (ParaF) tests. Figure 5.1c illustrates the landmark positions during each of these tests.

Our results show that pigeons use more than one strategy for coping with cue conflict, and that the strategies they use are context dependent. Specifically, on trials where there was only a small amount of cue conflict (near-shift tests: OrthN and ParaN), pigeons' pooled-subject search behaviour was best predicted by integrative models. Conversely, on trials where there was a large amount of cue conflict (far-shift tests: OrthF and ParaF), pigeons' pooled-subject search behaviour was best predicted by independent source (win-stay/lose-shift) models that assumed pigeons would search relative to each cue independently. However, it is important to note that, especially on far-shift tests, we detected a high degree of variability among birds regarding which strategy best accounted for their search behaviour. Thus, while our results highlight that pigeons' preferred strategy for resolving spatial cue conflict varies by context, they also indicate that, at least on far-shift tests, individual pigeons vary in terms of which search strategy they use.

5.3 Computational Models

We fit three different models to pigeons' search behaviour on conflict tests: a hierarchical, an independent, and an integrative model. Each model was designed to test a specific hypothesis regarding how animals would cope with cue conflict, and each predicted different goal location(s). Specifically, the hierarchical model (HierBest) predicted pigeons would search relative to only a single preferred cue, the independent model (Indep) predicted pigeons would search relative to each cue individually within a trial in a win-stay/lose-shift fashion, and the integrative model (Integ) predicted animals would search at an intermediate location between goal locations predicted by both cues. Probability density functions for each model are plotted in Figure 5.2, and sample data showing how model fits were mapped onto pigeon search behaviour are shown in Figures 5.3 and 5.4.

Note that, while hierarchical, independent, and integrative theories of how animals locate goals in space have been described and used throughout the extant literature for many years, to our knowledge there has been few

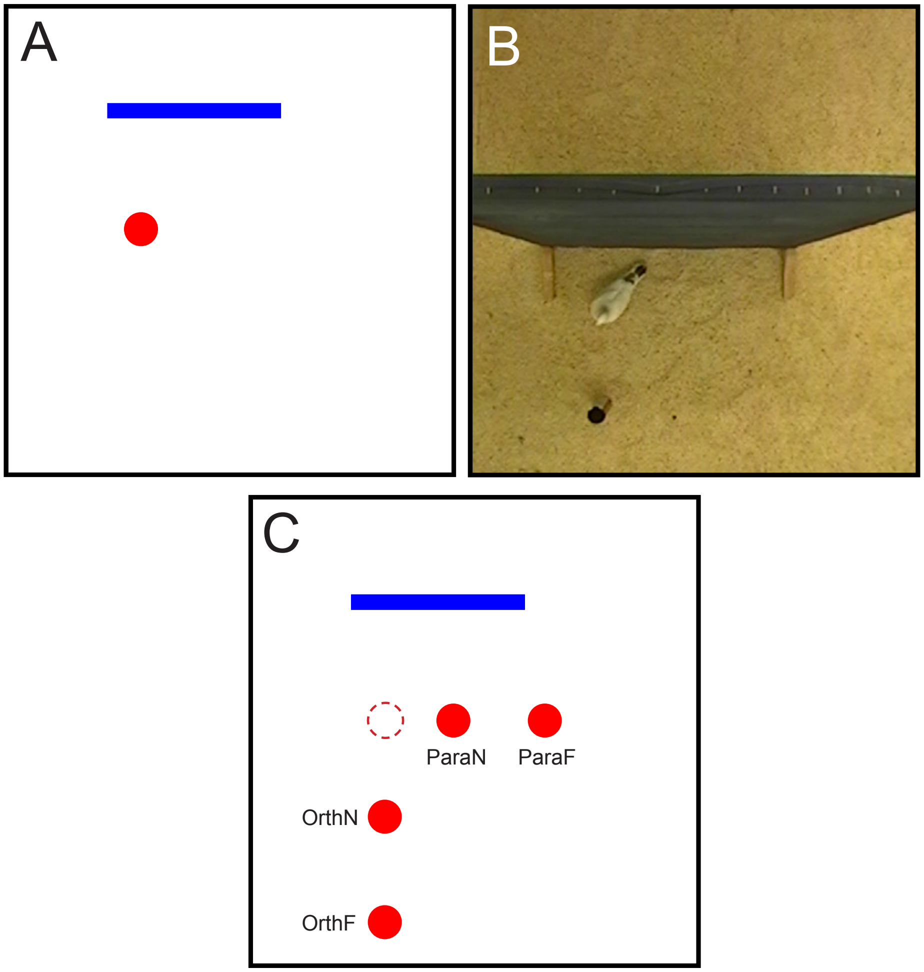

Figure 5.1: Illustrations and photographs depicting landmark locations on training and testing trials. [**A**] A diagram depicting the position of the blue and red cues relative to each other in training. Note that while the distances by which the red and blue cues are separated are to scale relative to the size of the search space (figure panel), the width of the blue cue, and the diameter of the red cue have been expanded for illustrative purposes. [**B**] An overhead image of a pigeon relative to both cues during training. [**C**] A scale diagram depicting the position of the both cues relative to each other on shift tests. The dotted, unfilled circle depicts the location of the red cue during training. For each test, the red cue was shifted by the following distance and direction relative to the blue cue: OrthN: 47.44 cm away along the orthogonal axis, OrthF: 99.49 cm away along the orthogonal axis, ParaN: 35.38 cm away along the parallel axis, ParaF: 82.56 cm away along the parallel axis. On all training and testing trials, the position of the two cues were varied within the room to prevent pigeons from using room features to help localize the goal as described in Section 5.4.3.

previous attempts to mathematically quantify these theories for formal model development and comparison. Because of this, we keep our models as simple as possible, and do not involve parameter search.

5.3.1 Model descriptions

Our first model predicted that subjects would cope with cue conflict by using a hierarchical search strategy. Our hierarchical (HierBest) model assumes that, when cues provide conflicting information, subjects will only rely on a single, preferred cue to locate the goal. First, two hierarchical models are fit to the data, based on each possible hierarchical strategy, one representing if a pigeon preferred the large blue cue (HierBlue), and the other representing if a pigeon preferred the small red cue (HierRed). Of these two models, the best-fitting model is used as HierBest.

Our second model predicts that animals will respond to each cue individually within a trial, adopting a win-stay/lose-shift strategy. Specifically, this independent cue (Indep) model predicts that subjects will search for the goal at the locations predicted by each cue individually, i.e., the goal locations predicted by HierRed and HierBlue. Additionally, the Indep model hypothesizes that animals will weight each cue according to the inverse of its variance (i.e., the cue's reliability[1]), and then allocate the number of search attempts relative to each cue's predicted goal location according to this weighting. That is, if the blue cue had a weight of 0.70, and the red cue a weight of 0.30, the Indep model would predict that the animal would allocate 70% of its searches based exclusively on the large blue cue, and the remaining 30% of its searches to the location based on the small red cue. Thus, this model uses Bayesian inference to determine each cue's weight, as discussed in Cheng et al. (2007) and Friedman et al. (2012).

The third model tested whether animals would integrate (Integ) information from both cues to predict a single, intermediate goal location. Specifically,

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[1] Though this is referred to as precision by some researchers, e.g., Pfuhl et al., 2011, we use the term reliability as it is throughout most of the extant literature (e.g., Fetsch, Pouget, DeAngelis, & Angelaki, 2012; Cheng et al., 2007; Ernst & Banks, 2002; Alais & Burr, 2004; Deneve & Pouget, 2004).

the Integ model assumes that animals will selectively weight each cue according to its subjective reliability to predict the goal location. However, unlike the Indep model, the Integ model predicts that animals will use the weights for determining the single predicted goal location (cf. Cheng et al., 2007; Friedman et al., 2012).

5.3.2 Model Comparisons

For each model, we calculated a Bayesian Information Criterion (BIC) value (Li, Wang, Palmer, & McKeown, 2008; Stephan, Marshall, Penny, Friston, & Find, 2007; Raftery, 1999) (see Section 5.4.3 for calculations). This value represents the relative fit of a model to subjects' search accuracy data. For model comparison, we calculated the pairwise difference in BIC values for each model by subtracting the best-fitting model's BIC from each model's BIC, resulting in a ΔBIC value for each model. Thus, the best-fitting model always had a ΔBIC of 0. By convention, if the difference between two model fits is less than two ($\Delta BIC < 2$), then neither model is significantly better than the other (Burnham & Anderson, 2002, 2004). Note that the HierBest had an additional degree of freedom relative to the Indep and Integ models, and this was corrected for through the BIC calculations.

Data across all subjects, calculated as ΔBICs in Table 5.1. Additionally, model fits to individual subject data are shown in ΔBIC values reported in Table 5.3.

Model	OrthN	ParaN	OrthF	ParaF
HierBest	90.713	11.9	325.07	129.91
Integ	**0**	**0**	157.88	64.757
Indep	44.031	16.264	**0**	**0**

Table 5.1: ΔBIC values for each model and each test on the pooled-subject dataset. Bolded values are significantly different from unbolded values.

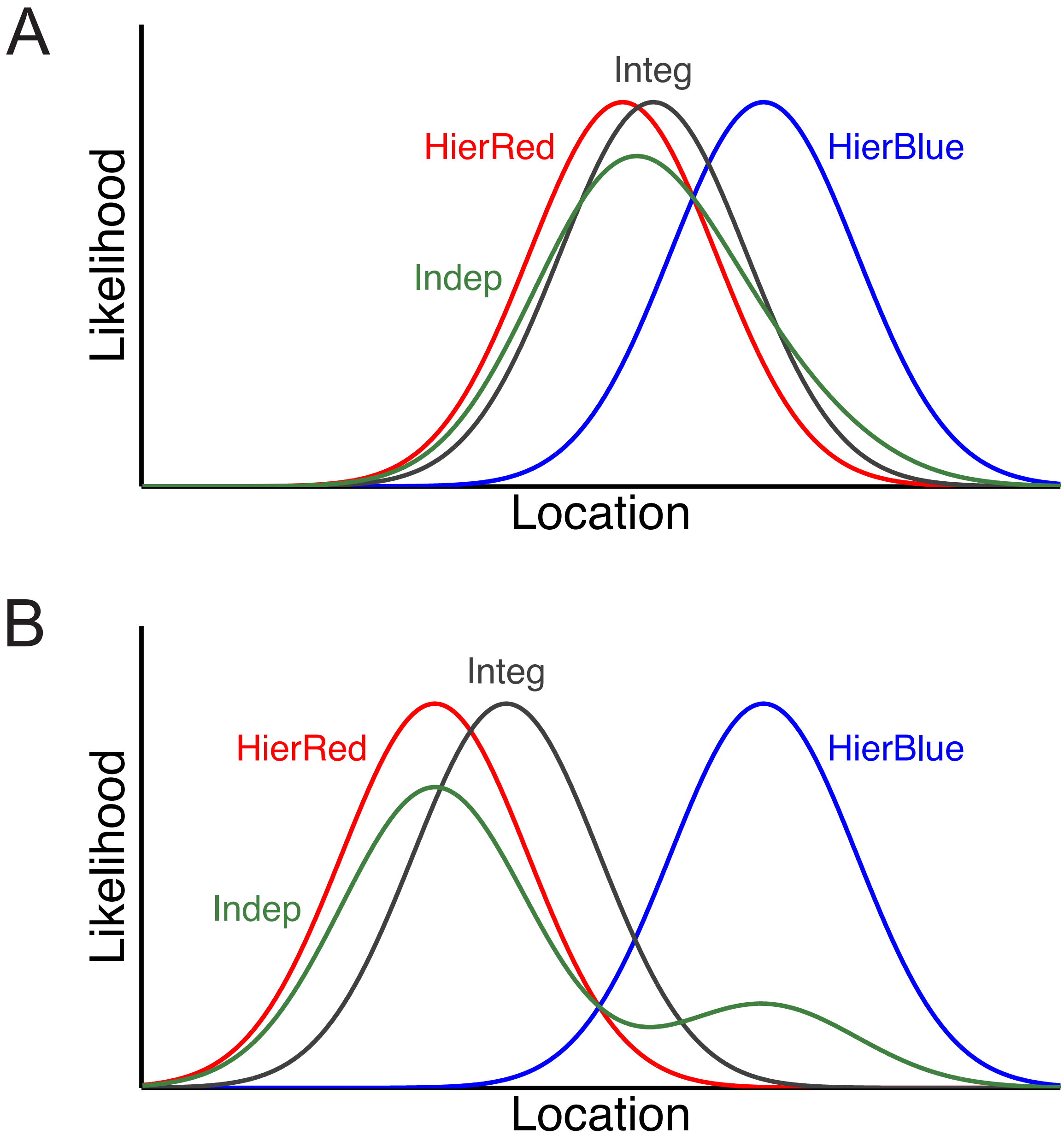

Figure 5.2: Probability density function (PDF) plots for each model. [**A**] OrthN tests. [**B**] OrthF tests. PDFs shown here are based on data from bird 943.

5.4 Method

5.4.1 Subjects

Subjects were eight adult pigeons (*Columba livia*) with varied previous experience in operant box and open-field tasks. All subjects had no previous experience with landmarks similar to those used in this experiment. Subjects were maintained between 85% and 90% of their free-feeding weights by pigeon pellets obtained during experimental sessions and supplemental feedings in their home cages. All subjects were housed in large individual cages under a 12h:12h light-dark cycle (light onset at 06:00). Grit and water were available *ad libitum* in their home cages.

5.4.2 Stimuli and Apparatus

The experiment took place in a 2.05 m (width) × 3.20 m (depth) × 2.89 m (height) testing room. The room contained a large square plywood floor (2 m^2) with a raised edge that was filled with aspen chips (see Figure 5.1b). This floor also contained a hidden grid under the aspen-chips for easy positioning of the landmarks (each grid square measured 0.2 m^2). Two visually distinct landmarks were used to allow pigeons to pinpoint a hidden goal containing food (a 0.03 m diameter bottle cap). One landmark was very large rectangle (0.92 m [width] × 0.04 m [depth] × 1.56 m [height]) and consisted of a dark blue fabric stapled tightly to a wooden frame, which we call the blue cue. The second landmark was a small red cylinder (0.06 m [diameter] × 0.26 m [height]), which we call the red cue. The red cue had a 0.05 m (width) × 0.26 m (height) vertical white stripe painted on it to give it a directional feature.

Pigeons started each trial in an opaque enclosed start box outside the testing room (0.49 m [width] × 0.39 m [depth] × 0.40 m [height]). The start box was built into the door to the room and contained a vertical sliding panel that the experimenter opened to allow the pigeon into the room. After pigeons entered the testing room, the sliding panel was closed until the trial ended. The start box contained a circular food well (15 cm diameter) that was baited while the pigeon was in the testing room. When the trial ended, the door to the start box opened and the pigeon entered to eat the food in the food well. All test trials were video recorded and digitized before being scored.

5.4.3 Procedure

Training

The position of the landmark array and its corresponding goal location varied across trials within the aspen-chip-covered search space. This was done to prevent subjects from using stable environmental cues (e.g., room geometry, distance from walls, etc.) to localize the goal. During training, subjects received 10 trials per day.

Subjects were initially trained to find the goal in relation to the two landmarks while it was completely visible and sat on top of the aspen-chip bedding. After subjects reliably ate the food from the goal container, the goal was gradually buried under the aspen-chip bedding until it was completely covered. Subjects were trained to find the covered goal by sweeping the bedding with their beaks. On all training trials where the goal was completely covered by bedding, subjects were given a maximum of 2 minuets to find the goal. Subjects progressed to the next stage of training when they found the goal on at least 80% of trials across three consecutive days.

In the next phase of training, trials in which the goal contained food were decreased to 6/10 trials per day. During unreinforced trials, the goal container was not present in the testing room. On these trials, subjects were given 2 minutes or a maximum of 30 search attempts, whichever came first, to search for the goal prior to being allowed to return to the baited start box. The ordering of the daily trials was pseudo-randomized with the restriction that the first trial of each day was always reinforced and subjects could not receive more than two consecutive unreinforced trials. To progress to testing, subjects had to complete at least five days of training in which they received 6/10 reinforced trials per day. On reinforced trials, subjects must have successfully located the hidden goal on at least 80% of trials for three consecutive days.

Testing

There were two testing phases: (a) single-cue and (b) shift. In both phases, the position of the landmark array within the search-space varied as described in Section 5.4.3. Additionally, as in the final phase of training, subjects received 10 trials per day, four of which were unreinforced. Of these four unreinforced trials, two were control trials. These control trials were the same as the unreinforced trials described in section Section 5.4.3. The remaining two unreinforced trials each day were unique to each stage of testing (single-cue or shift testing). The position of unreinforced trials was pseudo-randomized as described in Section 5.4.3.

On reinforced trials, subjects had a maximum of 2 minutes to find the goal before they could return to the start box. During unreinforced trials, subjects had a maximum of 2 minutes or 30 search attempts, whichever came first, to search for the goal before they could return to the start box.

Single-cue Two unique test trials were given to subjects each day, where only one of the two cues was presented. Specifically, each day one trial was given to birds with only the blue cue present (Blue-only or BO), and one trial was given to bird with only the red cue present (Red-only or RO). These tests provided an independent measure of the subjects' search accuracy and variance relative to each cue in isolation. Subjects were given at least 10 single cue trials for each landmark and 20 control trials before proceeding to shift testing.

Shift Shift tests were conducted that placed the two cues in conflict. There were four types of test trials: Orthogonal-Near (OrthN), Orthogonal-Far (OrthF), Parallel-Near (ParaN), and Parallel-Far (ParaF). In each of these test trials, the two cues were experimentally separated. The amount and direction of shift for each test trial is illustrated and listed in Figure 5.1. The type of shift test given to a subject each day was pseudo-randomized. Test type assignment was limited so that only one trial of a specific shift test could be given to subjects each day. Subjects were given at least 10 trials of each type of shift test and 40 control trials before completing the experiment.

Scoring

Data was scored by first transferring the position of each cue and each search location (beak sweep) from recordings of each trial to overhead transparencies. During this process, each peck was numbered sequentially. After transfer, each transparency was digitized using in-house software such that each cue and search location received x- and y-coordinates.

Data Analysis

In shift testing, data were smoothed by removing pecks that fell outside 1.5 standard deviations (SD) from the mean peck location on the non-shifted axis for each test (e.g., for an orthogonal shift test, only pecks that fell outside of 1.5 SD on the parallel axis were removed). Data smoothing was implemented for each subject and each shift test. Across all shift tests and birds, data smoothing removed 10.58% of pecks from subsequent analyses.

Predicted goal location Each model predicted a different goal location for each shift test and each subject (see Figures 5.3 and 5.4). For simplicity of exposition, we assume that only the red cue moved during shift tests (see Figure 5.1c).

For the HierBlue model, the predicted goal location ($g_{HierBlue}$) was the mean search location during BO single-cue trials. For the HierRed model ($g_{HierRed}$), the predicted goal location was the mean search location during RO single-cue trials. For each type of shift test, the predicted goal location for the HierRed model was calculated by adding the amount of landmark shift to the predicted goal location on RO single cue trials. Of these two models, only the best-fitting model was used as HierBest.

For the Indep model, the two predicted goal locations corresponded to the two goal locations predicted by the HierBlue and HierRed models.

The predicted goal location for the Integ model (g_{Integ}) was calculated separately for each subject. To determine the weighting of each landmark for a given subject, we calculated the amount of search variability on single cue trials (BO and RO), and then computed the weight of a cue in both the x- and y-dimensions (corresponding to the parallel and orthogonal dimensions, respectively) using the formulae described in Friedman et al. (2012), and as shown in Equation 5.1 and Table 5.2.

$$w_{Bayes_{B_x}} = \frac{\sigma^2_{RO_x}}{\sigma^2_{RO_x} + \sigma^2_{BO_x}} \tag{5.1a}$$

$$w_{Bayes_{B_y}} = \frac{\sigma^2_{RO_y}}{\sigma^2_{RO_y} + \sigma^2_{BO_y}} \tag{5.1b}$$

$$w_{Bayes_{R_x}} = \frac{\sigma^2_{BO_x}}{\sigma^2_{BO_x} + \sigma^2_{RO_x}} \tag{5.1c}$$

$$w_{Bayes_{R_y}} = \frac{\sigma^2_{BO_y}}{\sigma^2_{BO_y} + \sigma^2_{RO_y}} \tag{5.1d}$$

We then calculated the predicted goal location (g_{Integ}). To do this, we multiplied the weights of each landmark by the predicted goal location for the two hierarchical models as shown in Equation 5.2.

$$g_{Integ_x} = w_{Bayes_{B_x}} g_{HierBlue_x} + w_{Bayes_{R_x}} g_{HierRed_x} \tag{5.2a}$$

$$g_{Integ_y} = w_{Bayes_{B_y}} g_{HierBlue_y} + w_{Bayes_{R_y}} g_{HierRed_y} \tag{5.2b}$$

Note that the predicted goal location for the Integ model would predict the same goal location as a Pure Averaging integrative model if w_{Bayes} for both the blue and red cue, and in both the x- and y-dimensions, was found to be 0.5.

Variance of predicted goal location A pooled variance estimate was calculated for each bird. This was done separately for the x- and y-dimensions, as shown in Equation 5.3, where n denotes the number of search attempts made by a subject in the given single-cue test.

$$\sigma^2_{p_x} = \frac{(n_{BO_x} - 1)\sigma^2_{BO_x} + (n_{RO_x} - 1)\sigma^2_{RO_x}}{n_{BO_x} + n_{RO_x} - 2} \tag{5.3a}$$

$$\sigma^2_{p_y} = \frac{(n_{BO_y} - 1)\sigma^2_{BO_y} + (n_{RO_y} - 1)\sigma^2_{RO_y}}{n_{BO_y} + n_{RO_y} - 2} \tag{5.3b}$$

Calculating response likelihoods for hierarchical and Integ models To determine the probability (i.e., likelihood) of a given response for each model ($P(r_{Model})$), we calculated probability density functions (N) based on normal distributions with the mean as the predicted goal location and the variance estimates described in Sections 5.4.3 and 5.4.3. The product of the likelihood for a given response occurring at a given x- and y-coordinate was used as the likelihood of the given response.

$$P_x(r_{Model}) = N(r_x; g_{Model_x}, \sigma^2_{p_x}) \tag{5.4a}$$

$$P_y(r_{Model}) = N(r_y; g_{Model_y}, \sigma^2_{p_y}) \tag{5.4b}$$

Calculating response likelihoods for the Indep model To determine the response likelihoods for the two independent sources models, we first calculated the likelihood of a response at the x- and y-coordinate, separately, given the HierBlue and HierRed models. Then, a weighted average of these two likelihoods were calculated based on the weights determined with Equation 5.1, as shown in Equation 5.5. As in Section 5.4.3, the product of the likelihood for a given response occurring at a given x- and y-coordinate was used as the likelihood of the given response.

$$P_x(r_{Indep}) = w_{Bayes_{B_x}} P_x(r_{HierBlue}) + w_{Bayes_{R_x}} P_x(r_{HierRed}) \tag{5.5a}$$

$$P_y(r_{Indep}) = w_{Bayes_{B_y}} P_y(r_{HierBlue}) + w_{Bayes_{R_y}} P_y(r_{HierRed}) \tag{5.5b}$$

Note that the Indep model would predict an equal proportion of pecks for each predicted goal location if w_{Bayes} for both the blue and red cue, and in both the x- and y-dimensions, was 0.5.

Model likelihoods and comparisons Response likelihoods were multiplied together to determine the likelihood that all responses, from a given subject and in a given test, were based on each of the three models. This value was then transformed into log-space (ln) to determine the log-likelihood (LL) for each model.

$$P(r_{Model}) = P_x(r_{Model})\ P_y(r_{Model}) \tag{5.6}$$

After determining the LLs for a given model for each subject, LLs were summated across the subjects to produce a group LL (gLL), as done by Stephan, Penny, Daunizeau, Moran, and Friston (2009) among others. gLLs for each model were then subtracted from each other (resulting in a Group Bayes Factor [GBF], see Li et al., 2008; Stephan et al., 2007), and then transformed into BIC (Bayesian Information Criterion, following from Raftery, 1999). Differences in BIC between models (ΔBIC) are reported in Table 5.1. By convention, if the difference between two models fits, $\Delta BIC < 2$, then neither model is significantly better than the other (Burnham & Anderson, 2002, 2004).

5.5 Results and Discussion

5.5.1 Single-cue tests

On single-cue tests, cues were presented to pigeons individually to obtain an unbiased measure of pigeons' search variance relative to each cue. This search variance was then used to determine how strongly pigeons weighted each of the two cues, as described in Eq. 5.1. Despite variability across birds in their overall preference for the red or blue cue, all birds weighted the red cue more heavily in the parallel axis than the orthogonal axis. Conversely, all birds weighted the blue cue more in the orthogonal axis than the parallel axis. Cue weights for each bird are shown in Table 5.2.

5.5.2 Near-shift tests

As illustrated in Figure 5.3, on tests where both cues were separated by a small distance (near-shift tests, see Figure 5.1c), the Integ model best predicted subjects' search behaviour, regardless of whether the red cue was shifted parallel or orthogonal to the blue cue (see Table 5.1). Additionally, pigeons' preference for using an integrative strategy was found to be very consistent across subjects, as the Integ model best fit subjects' data on 13 out of 16 near-shift

	Red cue			Blue cue		
Bird	Parallel	Orthogonal	M	Parellel	Orthogonal	M
61	0.35	0.22	0.29	0.65	0.78	0.71
85	0.87	0.36	0.62	0.13	0.64	0.38
473	0.40	0.11	0.26	0.60	0.89	0.74
887	0.76	0.64	0.70	0.24	0.36	0.30
943	0.78	0.51	0.65	0.22	0.49	0.35
948	0.59	0.53	0.56	0.41	0.47	0.44
975	0.44	0.37	0.41	0.56	0.63	0.59
2767	0.70	0.36	0.53	0.30	0.64	0.47
Mean	0.61	0.39	0.50	0.39	0.61	0.50

Table 5.2: Cue weights based on Bayesian inference.

tests (Table 5.3). Taken together, these findings indicate that when cues were only shifted by a small distance and thus provided only a small amount of cue conflict, subjects preferred to integrate the information provided by each cue.

The finding that pigeons integrated information from both cues to search in an intermediate location is congruent with previous research. For example, in studies where animals were trained to locate a hidden goal in the centre of an array of landmarks or an enclosure, animals sometimes continued to search in the centre after it was expanded or contracted symmetrically along the diagonal, e.g., adult humans (Spetch et al., 1997; MacDonald et al., 2004), pigeons (Gray et al., 2004; Sturz & Katz, 2009), chicks (Tommasi & Vallortigara, 2000)[2]. We extend this work by evaluating strategies that potentially underly such an averaging process in pigeons, namely an encoding of each cues' relative reliability. Furthermore, our experiment only expanded the array along a single dimension in each test, allowing us to directly compare shifts in the parallel and orthogonal dimensions. As both manipulations resulted in the same best-fitting model, pigeons' search behaviour was not influenced by the axis of shift when the cues were only separated by a small distance.

5.5.3 Far-shift tests

In tests where the two cues were separated by a large degree (far-shift tests), the Indep model best predicted subjects' search behaviour, regardless of whether the red cue was parallel or orthogonal to the blue cue (see Table 5.1). Thus, on far-shift tests, pigeons preferred searching relative to each cue independently and allocated the number of searches made to each location as a function of each cue's subjective reliability (i.e., the inverse variance).

However, it is important to note that there was a high degree of individual variability on far-shift tests in terms of which model best fit each subjects' data. At an individual level, the Indep model best fit subjects' data in only 7 out of 16 cases, the same number of cases in which the Integ model best fit subjects' data (Table 5.3). Thus, there was individual variability in which strategy subjects preferred to use for coping with the large degree of cue conflict presented in far-shift tests. One possible explanation for this individual variability is that the amount of cue conflict present in far-shift tests was very close to the boundary where subjects would switch from using a strategy that predicts a single, intermediate goal location (Integ), to using a strategy that predicts two unique goal locations, each relative to a single cue (Indep). Such a boundary has been postulated to exist by others (e.g., Pfuhl et al., 2011; Cheng et al., 2007; Körding et al., 2007) because as the amount of cue conflict increases, it will eventually reach a point where the cues appear unrelated. In such cases, an integrative strategy would no longer be viable, as integrating the information provided by unrelated cues would lead an animal to search in an erroneous

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[2] Note that these studies are the exception, rather than the rule, when investigating how animals search relative to multiple cues within an array/enclosure. In many studies, animals tend to rely on the precise vector locations of learned cues to localize goals (Batty et al., 2010; Collett, Cartwright, & Smith, 1996; Spetch et al., 1997; Kelly et al., 2008; Collett, Cartwright, & Smith, 1986; MacDonald et al., 2004; Winter & Stich, 2005), similar to what would be predicted by our Indep model. While it is an open question why these studies show animals using different strategies to solve similar tasks, it is likely a combination of species differences, differences in training/testing procedures and apparatuses, and the distance by which cues were shifted (Jones et al., 2002; Collett, Cartwright, & Smith, 2003; Kamil & Jones, 1997, 2000).

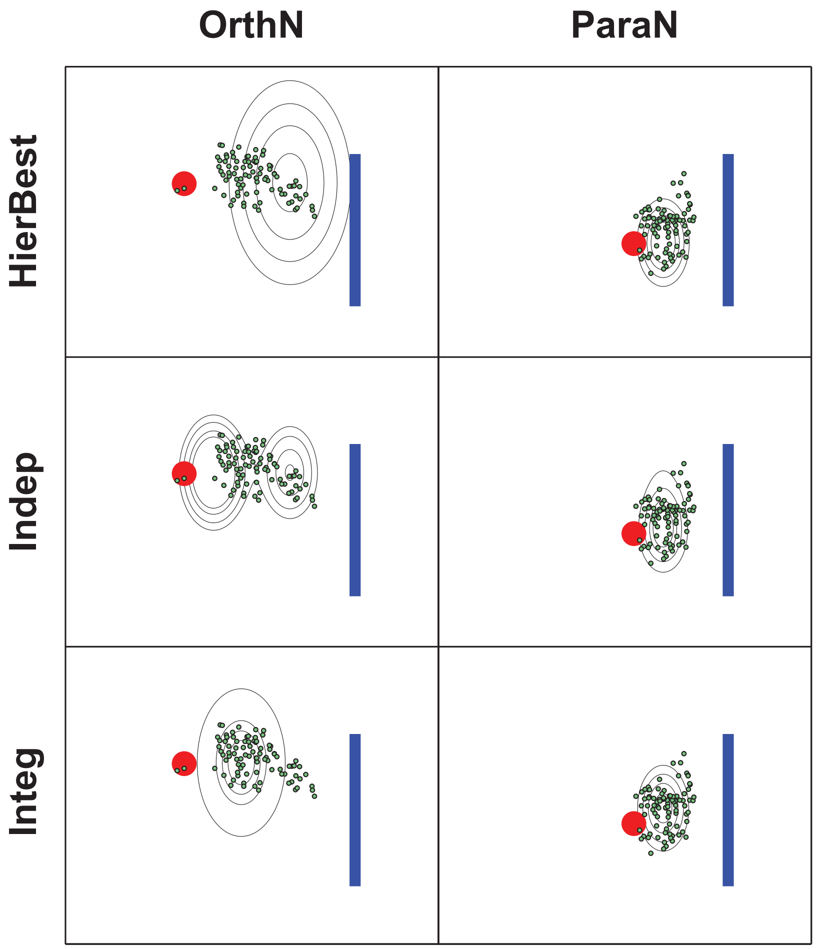

Figure 5.3: Graphical representation of model fits for pigeon responses on Near-shift tests. Responses (small green dots) on near-shift tests plotted relative to the two cues. Note that the width of the blue cue, and the diameter of the red cue were enlarged for illustrative purposes. Contour plots in the background denote model likelihoods. Each ring of the contour plot captures 20% of a pigeons' responses, up to a maximum of 80%. Plotted data is from bird 887. Response data are replicated in each column to highlight model predictions.

location. Instead animals should switch to an independent source strategy where it will search relative to each cue individually, as long as the cost to travel between the cues is not prohibitive[3] (Pfuhl et al., 2011). Additional tests that provide a much larger degree of separation between the two cues than we use in our far-shift tests would be required to validate this hypothesis.

Overall, results from our pooled-subject datasets are consistent with theoretical interpretations as to how both human and non-human animals cope with cue conflict (e.g., Pfuhl et al., 2011; Cheng et al., 2007; Körding et al., 2007). Specifically, if multiple cues occur closely in either space or time, like in our near-shift tests, animals will interpret the cues as coming from a single source (i.e., a compound source). Thus, in such a situation, animals would be more likely to predict a single goal location relative to the compound source than when the two cues were separated by a larger amount and perceived to be unrelated. In such a situation, as in our far-shift tests, animals are more likely to predict two unique goal locations, each relative to a single cue (Pfuhl et al., 2011; Cheng et al., 2007; Körding et al., 2007). Thus, our results on both near- and far-shift tests are congruent with theoretical predictions regarding how animals cope with cue conflict.

5.5.4 Pure hierarchical models

When pooled-subject analyses were conducted on pigeons' search distributions, our pure hierarchical model (HierBest; also known as a winner-take-all or take-the-best model Gigerenzer & Brighton, 2009; Gigerenzer & Goldstein, 1999; Morgan et al., 1998; Palmer, 1994; Palmer et al., 1993) performed very poorly on all tests (see Table 5.1). With the exception ParaN tests, the HierBestmodel had the worst model fit for every shift test. Thus, while the HierBest model was the simplest strategy pigeons' could use to search for a goal when cues provided conflicting information, results from our model fitting reveal pigeons

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[3] Pfuhl et al. (2011) also extend this logic to cases where the cost to travel between unrelated cues is prohibitive (e.g., the distance between cues is very large or the environment is extremely dangerous for travel). In such cases, Pfuhl and colleagues suggest that animals will switch to using a hierarchical search strategy whereby an animal will only search relative to the most preferred cue.

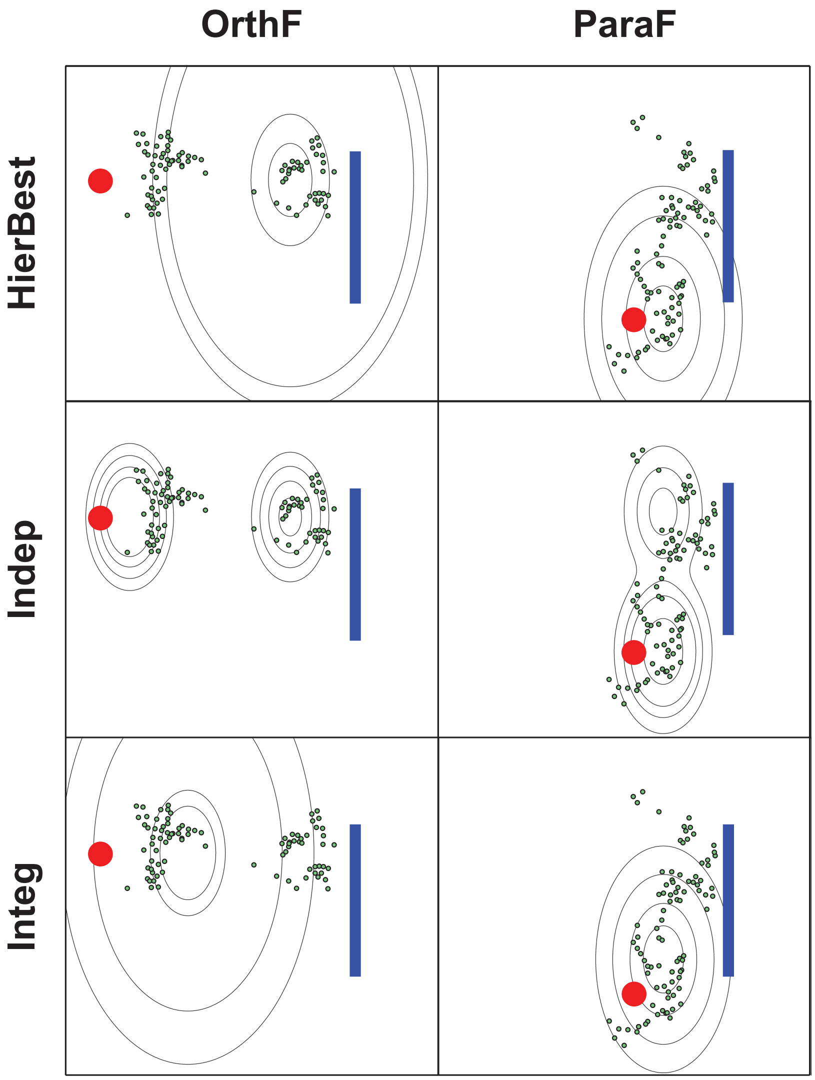

Figure 5.4: Graphical representation of model fits for pigeon responses on Far-shift tests. Responses (small green dots) on far-shift tests plotted relative to the two cues. Note that the width of the blue cue, and the diameter of the red cue were enlarged for illustrative purposes. Contour plots in the background denote model likelihoods. Each ring of the contour plot captures 20% of a pigeons' responses, up to a maximum of 80%. Plotted data is from bird 887. Response data are replicated in each column to highlight model predictions.

were very unlikely to use this strategy on either near- or far-shift tests.

These findings contrast sharply with other studies where pigeons demonstrated hierarchical strategy use (e.g., Legge et al., 2009; Spetch & Edwards, 1988). However, unlike the present study, investigations demonstrating hierarchical strategy use by pigeons used discrete-choice tasks. In such tasks, integrative strategies were not always viable due to the arrangement of potential goal locations. Furthermore, many studies that demonstrate hierarchical strategy use (e.g., Legge et al., 2009; Spetch & Edwards, 1988) did not allow subjects to make more than a single choice on test trials, thus preventing pigeons from using a win-stay/lose-shift strategies. Thus, in such situations, pigeons may have only used hierarchical strategies because more preferred strategies were not viable.

Overall, our results indicate that pigeons do not use pure hierarchical strategies for goal localization when other options are available (e.g., integrative or independent source strategies). Hierarchical strategies, however, may still be of use to animals in some situations due to their computational simplicity (e.g., relatively small number of parameters to be considered and computations to be performed). For example, it is an open question whether animals such as pigeons would prefer to use hierarchical strategies for goal localization when they have a very short window of time to search, or when trying to escape a predator. In these situations, the computational simplicity of hierarchical strategies may allow animals to make a decision more quickly than more computationally complex strategies (e.g., an integrative strategy) and thus provide a survival advantage when a delay may be deadly (Pfuhl et al., 2011). Thus, while hierarchical strategies did not control pigeons' search behaviour in our study, they may be used by pigeons in circumstances where a quick response provides a large survival advantage.

5.5.5 Conclusion

The results of our study demonstrate that pigeons use both integrative and independent (i.e., win-stay/lose-shift) strategies for coping with spatial cue conflict and that their strategy preference is context dependent. On trials where the amount of cue conflict was small (OrthN and ParaN tests), an integrative model best fit pigeons' search behaviour (**Integ**). Conversely, when the amount of cue conflict was large (i.e., the OrthF and ParaF tests), an Independent Source (**Indep**) model best predicted pigeons' search behaviour. Interestingly, while there was a high degree of homogeneity amongst pigeons' strategy use on near-shift tests, this was not the case on far-shift tests. Specifically, pigeons were much more likely to display individual strategy preferences when searching for the goal on far-shift tests than on near-shift tests (i.e., on far-shift tests birds were just as likely to use an independent source strategy as an integrative strategy for coping with cue conflict).

Our results are highly congruent with recent theoretical discussions as to how animals cope with cue conflict (Pfuhl et al., 2011; Cheng et al., 2007; Körding et al., 2007). One such model by Pfuhl et al. (2011), predicts that animals will change their strategy for coping with cue conflict as the amount of conflict increases. Specifically, they predict that when the amount of cue conflict is small, animals will attempt to integrate the information from all cues to identify a single goal location; as we observed in our near-shift tests. Pfuhl and colleagues' model also predicts that as the amount of cue conflict increases, animals will switch from an integrative strategy to one where both cues predict individual goal locations. This is because a very large amount of cue conflict suggests that the cues are unrelated. Animals will still search relative to both cues however, because the cost of travelling between them is not prohibitive (i.e., no significant use of time or energy involved in travelling between cues). We observed this same behaviour in pigeons on far-shift tests[4]. Finally, as the amount of conflict increases further, Pfuhl and colleagues predict that animals will eventually switch to searching relative to only a single, preferred cue, as would be predicted by hierarchical models. This is because, when the cues are separated by such a degree that there will be a significant cost to travel between them, searching relative to both cues is no longer a viable option. While such a final strategy makes functional sense, we did not observe any evidence of this in our experiment. Likely, this is because the cues were never separated by a large enough distance to incur a significant cost of travel (the search space was only 2 m^2 and could not be extended further due to space constraints).

Additionally, it is worth noting that, while our models were very deterministic and rigid by traditional model standards (e.g., the Integ and Indep models did not have any free parameters, and the HierBest model had only a single free parameter), they still accounted for pigeons' data relatively well; particularly for near-shift tests. It is impressive that these models accounted for the data as well as they did, and the relative success of our models is a testament to the strength and accuracy of the individuals who developed the theories upon which our models are based. Now that we have developed and tested these models, it would be it would be a worthwhile area of future research to expand on our work by incorporating parameter search and developing more accurate and flexible models of animal spatial localization.

In conclusion, our results show that pigeons can use both integrative and independent strategies to resolve spatial cue conflict. Because pigeons' responded to small and large amounts of cue conflict by relying on fundamentally different strategies, integrative strategies on near-shift tests and Indep strategies on far-shift tests, our results confirms some aspects of recent theoretical discussions of how animals cope with cue conflict (e.g., Cheng et al., 2007; Pfuhl et al., 2011) and highlights that pigeons can select strategies based on context. Of particular interest is that the Integ and Indep models we used were based on Bayesian inference, and as such, based the location (the Integ model) or number of searches to a given location (the Indep model) on an individual pigeons' determination of each cue's relative reliability. Because model fits were fairly accurate and homogenous among subjects on near-shift tests, as well as for some subjects on far-shift tests, it is reasonable to assume that pigeons can encode the relative reliability of important spatial cues for weighting the information provided by each cue at a later time. That pigeons can weight multiple spatial cues according to their relative reliably should open up many new avenues of research into cue integration and discussions of optimal

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[4] Note that the first two predictions made by Pfuhl and colleagues' model (Pfuhl et al., 2011) have previously been made in Cheng et al. (2007) and Körding et al. (2007).

foraging, both within- and between- species. Finally, that pigeons' responded to small and large amounts of cue conflict by relying on fundamentally different strategies, integrative strategies on near-shift tests and win-shift/lose-stay strategies on far-shift tests, confirms some aspects of recent theoretical discussions of how animals cope with cue conflict (e.g., Cheng et al., 2007; Pfuhl et al., 2011) and highlights that pigeons can select strategies based on context.

5.6 Supplementary Information

Bird	Model	OrthN	ParaN	OrthF	ParaF
61	HierBest	25.19	**0**	34.46	193.97
	Integ	**0**	22.56	**0**	23.80
	Indep	23.99	26.60	6.82	**0**
85	HierBest	169.87	8.63	396.75	63.78
	Integ	**0**	**0**	**0**	298.11
	Indep	150.83	21.30	5.39	**0**
473	HierBest	24.01	6.36	23.40	**0**
	Integ	**0.11**	**0**	9.88	20.97
	Indep	**0**	4.15	**0**	21.91
887	HierBest	265.69	21.84	1880.50	509.44
	Integ	**0**	**0**	1174.60	229.70
	Indep	18.09	31.77	**0**	**0**
943	HierBest	45.09	26.02	129.87	24.65
	Integ	**0**	**0**	**0**	**0**
	Indep	28.39	18.36	41.51	17.40
948	HierBest	94.60	21.23	114.59	104.57
	Integ	**0**	**0**	167.71	13.92
	Indep	64.92	8.40	**0**	**0**
975	HierBest	27.61	**0**	154.72	58.64
	Integ	**0**	**0.48**	**0**	**0**
	Indep	23.93	20.86	65.91	8.66
2767	HierBest	73.76	34.17	**0**	152.64
	Integ	**0**	**0**	44.55	**0**
	Indep	42.21	21.72	14.04	20.47

Table 5.3: Individual ΔBIC values for each bird and each test. Bolded values are significantly different from unbolded values.

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Chapter 6

General Discussion

As detailed throughout my dissertation, animals often redundantly encode multiple cues to aid in navigation and goal localization (Shettleworth, 2010; Spetch & Kelly, 2006). While encoding multiple cues can help animals navigate and localize goals (e.g., using multiple cues can increase an animals' search accuracy and robustness, Kamil & Cheng, 2001; Kamil et al., 2001), it can also create problems for animals when one or more cues become displaced. In such situations, the displaced cue(s) provide information that conflicts with other nearby cues (creating what is commonly referred to as cue conflict). Cue conflict is not uncommon in the natural world, as many animals use small, easily displaced objects as landmarks for localizing goals. As such, animals have developed a number of strategies to cope with cue conflict, and the study of these strategies in both pigeons (*Columba livia*) and desert ants (*Melophrous bagoti*) has been the focus my dissertation.

As we have seen throughout my dissertation, animals can use hierarchical, win-stay/lose-shift (independent source), and integrative strategies to cope with cue conflict. Briefly, these three classes of strategies are outlined below.

Hierarchical strategies, also known as winner-take-all or take-the-best strategies, (Gigerenzer & Brighton, 2009; Morgan et al., 1998), require animals to rank order cues according to preference. When cues conflict, animals primarily respond by relying on information from the most preferred cue. In the spatial domain, evidence of animals using a hierarchical strategy for goal localization has been limited to discrete choice tasks in which animals can only make a single response per trial (e.g., Legge et al., 2009; Spetch & Edwards, 1988). While hierarchical strategies require little computation on the part of an animal to implement, often these strategies will not provide an optimal solution to cue conflict because they do not take into account all available information (e.g., information provided by non-preferred cues).

Similar to hierarchical strategies, independent source strategies require an animal to only use information provided by a single cue to search for a goal (Hodges, 1985; Kamil, 1983; Gaffan & Davies, 1981). However, unlike hierarchical strategies, animals using an independent source strategy will switch from searching relative to one cue to another after finding (win-shift strategies) or failing to find a goal. While more flexible than hierarchical strategies, independent sources strategies will not always provide an animal with an optimal solution to cue conflict, as they often require an animal to search over a dispersed area. Thus animals using an independent source strategy are likely to expend much more time and energy searching for a goal than other strategies.

Unlike either hierarchical or independent sources strategies, integrative strategies require animals to combine the information provided by multiple cues to predict a single, intermediate goal location (Pfuhl et al., 2011; Cheng et al., 2007). Thus, integrative strategies utilize the information provided by all cues to predict a single goal location. While integrative strategies can provide animals with a more optional solution for resolving cue conflict, they require more computation than independent or hierarchical strategies.

Throughout my dissertation, I have found evidence showing that animals can use all three of these strategies, and that the strategy an animal uses can vary according to the context in which cue conflict occurs. Briefly, I review the experiments presented in Chapters 2–5 below.

6.1 Review of Experiments

6.1.1 Chapter 2

In Chapter 2, my colleagues and I tested how pigeons responded to cue conflict in a spatial, discrete choice task. Specifically, pigeons were trained to select the middle of three squares within an array on touch screens in an operant chamber. Pigeons were then tested by placing the local, positional cues (a square's location within the array), in conflict with the global spatial cues present within the operant box (a square's location on the screen).

We conducted three experiments whereby pigeons (*Columba livia*) were trained and tested with specifically oriented arrays. In Experiments 1 and 2, we trained and tested pigeons with vertically and horizontally aligned arrays, respectively. In Experiment 3, we trained and tested pigeons with three array alignments simultaneously: horizontal, vertical, and diagonal. Our results indicated that when local and global cues conflicted, pigeons used a hierarchical strategy to resolve the conflict. Specifically, in all three experiments, pigeons resolved the cue conflict by searching according to their most preferred cue.

Notably, pigeons' preference for using local or global cues to resolve cue conflict was modulated by the alignment of the array. When the array was vertically or diagonally aligned, pigeons preferred to use global cues (Experiments 1 and 3). However, when the array was horizontally aligned, pigeons preferred to use local cues to resolve cue conflict (Experiments 2 and 3). In all experiments, pigeons could accurately respond using either local or global cues if their preferred cue type for a given array orientation was unavailable. Thus, our results indicate that pigeons were relying on a hierarchical response strategy to resolve spatial cue conflict, and that the type of information they preferred was context-dependent

To extend and provide continuity with previous research (e.g., Spetch & Edwards, 1988), these experiments were designed as discrete choice tasks. Thus, they did not provide animals with an opportunity to respond multiple times within a single trial, nor to respond to intermediate locations within specific arrays (e.g., on conflict trials where three squares were presented as an array, the midpoint between the centre of the globally-correct and locally-correct squares fell in the area between the two squares). Thus, our experiment did not provide an opportunity to respond to the conflict using independent or integrative strategies. Thus, while our experiment clearly shows that pigeons can respond to conflict in a discrete choice task using a hierarchical strategy, it does not provide a comprehensive test of strategy preference when there are many valid response strategies. We address this issue by testing pigeons in an open-field task in Chapter 5.

6.1.2 Chapter 3

In Chapter 3, my colleagues and I tested how foraging desert ants (*M. bagoti*) located the exit of an arena after obtaining food inside. The arena provided ants with an undifferentiated visual panorama by blocking all natural skyline cues. To help ants locate the exit inside the arena, a single landmark was placed near the exit. Thus, once inside the arena, ants only had access to three sources of information to locate the exit: the landmark, stored path integration information, and information derived from the ants' celestial compass (e.g., the pattern of polarized light, Wehner & Müller, 2006; Wehner & Srinivasan, 2003).

While ants had access to path integration information during training, we ensured they did not have access to this information during testing by capturing foragers at the end of their inbound journey near their nest[2]. Once captured, we transferred ants to a test arena that replicated the training arena with one exception: it did not contain an exit. Additionally, on some test trials we repositioned the landmark inside the arena so that it conflicted with information provided by ants' celestial compass.

On conflict tests, ants did not use the landmark to search for the arena exit. Instead, ants relied on information provided by their celestial compass to enact a learned response strategy cued by the context of the arena (commonly referred to as a learned local vector, e.g., Collett et al., 1998). Specifically, because ants' celestial compass naturally has 180° of ambiguity (e.g., ants cannot differentiate North and South, or East and West, Wehner & Müller, 2006; Wehner & Srinivasan, 2003), the ants may have learned to combine the ambiguous information from their celestial compass with other sources of information inside the arena (e.g., spectral or proprioceptive cues) to determine their heading direction after obtaining food from the feeder. For example, it is possible that in our experiments, ants used a celestial compass to determine the 180° axis along which the exit should be located and then used spectral cues such as the ambient luminosity of the arena wall to determine a direction of travel along the axis indicated by their celestial compass. Our results provided the first evidence that *M. bagoti* foragers could learn context-specific local vectors (Legge et al., 2010).

While this experiment was not designed to explicitly test whether ants

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[2] Previous research has shown that desert ants do not maintain a permanent record of stored path integration information. Instead, path integration information is only stored for the current outbound (nest-to-food source) path, and is discarded as an ant travels along its inbound (food source-to-nest) path. Thus, an ant captured outside its nest along its inbound journey will not have any stored path integration information (Graham & Cheng, 2009; Narendra, 2007).

would rely on hierarchical, independent, or integrative strategies, it is possible that ants were using a hierarchical strategy to cope with the cue conflict presented in the test arena. If ants had encoded the location of the exit relative to both the landmark and a learned local vector, ants' exclusive reliance on their local vector in conflict tests would be consistent with a hierarchical strategy where the local vector was the preferred cue. However, because this experiment was not designed to test whether ants were using a hierarchical strategy to cope with cue conflict, we did not conduct a test where ants did not have access to celestial compass information. Thus, we cannot be certain that ants learned anything about the location of the exit relative to the landmark. It is possible that ants either could not use the landmark for navigation (e.g., ants may not have been able to discriminate the landmark from the background of the arena wall), or that learning about the landmark was blocked by learning the context-specific local vector. Thus, instead of using a hierarchical strategy for coping with cue conflict, ants may have simply been relying on the only available source of encoded information to locate the goal. We follow up on the question of whether desert ants will rely on a hierarchical strategy for coping with cue conflict in Chapter 4.

6.1.3 Chapter 4

In Chapter 4, my colleagues and I tested how foraging desert ants (*M. bagoti*) would cope with cue conflict between: (1) view-based navigation and a learned celestial local vector along a familiar route (Experiment 1), and (2) ants' path integrator and view-based navigation when displaced off their familiar route (Experiment 2).

In Experiment 1, we trained ants to a feeder in the centre of an arena that provided directional information via an artificial skyline cut into the arena wall. After obtaining food within the arena, ants had to locate the arena exit to return to their nest. This exit was positioned so that it pointed away from the nest. Thus, ants could not use path integration to exit the arena, and instead had to rely on the artificial skyline provided by the arena wall and/or a learned local vector based on ants' celestial compass. Similar to the experiments reported in Chapter 3, ants ran off their path integration vector and were captured outside their nest before being moved to a test arena. The test arena, which was similar to the training arena with the exception that it did not contain an exit, was used to place ants' learned local vector in conflict with the arena's artificial skyline (view-based navigation). Conflict tests revealed that ants did not seem to rely on view-based navigation or their learned celestial local vector in a hierarchical manner, but instead integrated the information provided by both cues to select a compromise direction home.

In Experiment 2, we trained ants to a feeder approximately 10 m from their nest in their natural habitat. Unlike in Experiment 1, in this experiment, ants' view of the surrounding natural panorama was unrestricted. After ants were trained to the feeder for at least one day, they were captured and tested either with ("Full-vector"; Fv) or without ("Zero-vector"; Zv) path integration information at three release points. The three release points varied in their distance from ants nest entrance, and consequently how closely the visual surround matched the view at the nest entrance. Results from this experiment revealed that when view-based navigation and path integration information conflicted, ants integrated the information provided by each cue. Furthermore, this integration was somewhat consistent with the principles of Bayesian integration, whereby each cue was weighted according to its familiarly (c.f. Cheng et al., 2007).

In sum, this experiment demonstrated that ants prefer to integrate multiple conflicting sources of information, rather than respond using a hierarchical strategy. Specifically, these experiments demonstrated that ants could integrate view-based navigation and local vector information (Experiment 1), as well as view-based navigation and path integration information (Experiment 2). When these results are used to re-evaluate the results presented in Chapter 3, it is likely that in Chapter 3, ants did not learn anything about the landmark when it was presented against an undifferentiated panorama (the arena wall). If they had, the results from Chapter 4–Experiment 1 suggests that the ants tested in Chapter 3 would have integrated the information provided by both cues, which was not the case. Thus, my experiments do not provide evidence that *M. bagoti* foragers use hierarchical strategies to cope with cue conflict. Finally, it is worth noting that we did not provide ants with the opportunity to make multiple choices within the test arenas in the experiments presented in Chapters 3 or 4. Thus, we did not test whether ants could respond to cue conflict using an independent source strategy. Further research will be required to determine whether ants will always cope with cue conflict using integrative strategies, or whether they can switch to using independent source strategies when an integrative strategy is unlikely to lead to a goal (e.g., when two sources of information indicate drastically different locations, Pfuhl et al., 2011).

6.1.4 Chapter 5

In Chapter 5, my colleagues and I tested how pigeons would respond to cue conflict in an open-field task. Here, we trained pigeons to locate a hidden food well relative to two cues (landmarks). On test trials, these landmarks were placed in conflict by shifting one cue along the parallel or orthogonal axis of the second cue. We varied the degree of cue conflict by shifting the cue either a relatively short or long distance from its position during training (referred to as near- and far-shift tests, respectively). Thus, our design tested whether pigeons' method of resolving cue conflict would change as a function of the distance (near; far) and/or axis (parallel; orthogonal) of shift. To do this, we gave pigeons the following four shift tests: orthogonal-near (OrthN), parallel-near (ParaN), orthogonal-far (OrthF), parallel-far (ParaF). We then fit pigeons' response data to three theoretically motivated models: a hierarchical, an independent (e.g., win-stay/lose-shift), and an integrative model.

Model analysis revealed that pigeons overwhelmingly relied on an integrative strategy to cope with cue conflict when the amount of shift was relatively small (near-shift tests). Furthermore, on near-shift tests, the axis of shift did not appear to influence pigeons' strategy choice. In contrast, when cues were shifted by a relatively large amount (far-shift tests), pigeons tended to rely on an independent strategy for resolving cue conflict. While there was much more individual variability as to the strategy a particular bird preferred to use for resolving cue conflict on far-shift tests than near-shift tests, there was once again no evidence that the axis of shift influenced pigeons' strategy preference. On both near- and far-shift tests, hierarchical strategies did a very poor job of fitting pigeons' response data.

Thus, the results of Chapter 5 indicate that pigeons can use both integrative and independent strategies to resolve cue conflict in non-discrete choice tasks. These results contrast sharply with the findings reported in Chapter 2, whereby pigeons were shown to use hierarchical strategies for resolving cue conflict. However, unlike the study described in Chapter 5, the experiments reported in Chapter 2 used a discrete-choice task. In such tasks, integrative strategies were not always viable due to the arrangement of potential goal locations, and the experiments did not allow subjects to make more than a single response on test trials, thus preventing pigeons from using an independent strategy. Overall, the results from Chapter 2, coupled with the results from Chapter 5 suggest that pigeons may only use hierarchical strategies to resolve cue conflict when more preferred strategies are unavailable.

6.2 Summary of Novel Findings

Individually, my dissertation research has advanced our understanding of how both pigeons and desert ants cope with cue conflict. However, when taken together, my research reveals some commonalities that are useful for researchers studying comparative spatial cognition. I discuss each of these below.

6.2.1 Context specific spatial cue use

First, the particular context in which information is presented can significantly influence how pigeons and desert ants utilize spatial cues. In Chapter 2, pigeons' preference for local or global cues changed as a function of the orientation of a presented array. Specifically, if the array was oriented vertically or diagonally, pigeons preferred global cues (location on the screen) to local cues (location within the array), whereas when the array was horizontally aligned, pigeons cue preferences were reversed. Thus, the orientation of an array significantly influenced the type of spatial information pigeons preferred to use to for resolving cue conflict.

The fact that context in which information is presented could influence pigeons' response strategy was also reported in Chapter 5. Specifically, Chapter 5 revealed that pigeons' response strategy could be influenced by the distance two cues were shifted relative to one another, and thus how much cue conflict they presented to the animal. When the landmarks were shifted by only a small amount, pigeons responded to the resulting cue conflict by integrating the information provided by both cues. However, when the two cues were shifted by a large amount, pigeons responded to the resulting cue conflict by searching relative to each cue independently.

Taken together, the results of Chapters 2 and 5 indicate that the strategy pigeons use to cope with spatial cue conflict is malleable, and can be modulated by contextual factors such as the orientation of an array or the distance one encoded cue is shifted relative to another.

Similarly, the results of my experiments with desert ants (reported in Chapters 3 and 4) also provide evidence that contextual factors play an important role in navigation and goal localization. Specifically, in both chapters, ants were found to use the context an artificial arena to determine a direction of travel based on their celestial compass, thus demonstrating that ants could learn a context-specific local vector.

Overall, the results from the experiments reported in this dissertation provide strong evidence across two diverse species that contextual factors can modulate how animals utilize certain types spatial information and the strategies animals use to resolve spatial cue conflict.

6.2.2 Integration of Spatial information

To cope with cue conflict, animals may combine (integrate) the information provided by multiple cues to identify a "best guess" location that is close enough to the true goal for success. In my dissertation, particularly in Chapters 4 and 5, I show evidence that both pigeons and desert ants can integrate multiple sources of spatial information to cope with cue conflict.

The experiments presented in Chapter 4 provide evidence that ants can: (1) integrate a learned heading direction based on a celestial compass (local vector) with view-based navigational information derived from the panoramic skyline (Experiment 1), and (2) integrate information from their path integrator with view-based navigational information derived from the panoramic skyline (Experiment 2). Thus, my results indicate that a small-brained invertebrate, namely ants, can integrate the dictates different navigational systems to cope with cue conflict, and that this integration can take place across sensory inputs (e.g., integration of view-based navigation information derived from visual cues with path integration information derived from proprioceptive cues).

Similarly, pigeons tested in Chapter 5 integrated multiple sources of spatial information to resolve small amounts of cue conflict. Specifically, pigeons were found to integrate information from two landmarks when the landmarks were experimentally separated by a small amount relative to their positions in training.

That both pigeons and ants have been shown to integrate multiple sources of conflicting spatial information is informative, as it shows that two highly divergent species use similar strategies for coping with cue conflict. Thus, even though ants and birds exploit very different ecological niches, have different methods of navigation (e.g., terrestrial vs. airborne), and have very different neurological structures, both birds and ants can cope with cue conflict by integrating information from multiple sources. Such convergent strategy use between two species as distantly related as ants and pigeons can provide researchers with valuable insight into how these traits evolved, as well as help researchers understand the neurological basis for integrating information from multiple cues.

6.2.3 Hierarchical strategy use in continuous space

While many species have been shown to use a hierarchical search strategy for coping with cue conflict in discrete choice tasks (e.g., black-capped chickadees: Brodbeck, 1994, dark-eyed juncos: Brodbeck & Shettleworth, 1995; squirrels:

Nesterova, 2007; dogs: Fiset et al., 2000; among others), to my knowledge, there is little, if any, evidence to suggest non-human animals can use a hierarchical search strategy to resolve cue conflict in tasks requiring them to localize a goal in continuous space. The experiments reported in this manuscript do not contradict this fact. Specifically, while Chapter 2 reports findings that are consistent with hierarchical strategy use in pigeons, the task involved discrete choices. Conversely, there was no evidence to suggest animals used hierarchical strategies for resolving spatial cue conflict when tasks required animals to locate a goal in continuous space (see Chapters 3–5).

Thus, taken together, the results from Chapters 3–5 suggest that neither pigeons or ants use hierarchical strategies for goal localization when other options are available (e.g., integrative or independent strategies), and reports of animals using hierarchical strategies for goal localization may be a byproduct of testing procedures in which alternative strategies cannot be used (e.g., discrete choice tasks).

While this is one possibility, it is also possible that the studies reported in Chapters 3–5 simply did not impose a large enough cost of travel, or provide enough cue conflict for animals to rely on a hierarchical search strategy. Specifically, it is possible that when searching in continuous space, animals will only rely on a hierarchical search strategy as a last resort, to be used when other options are either extremely unlikely to predict the correct goal location (e.g., integrative strategies where there is a large amount of cue conflict), or when there is a significant cost to searching relative to each cue independently (e.g., the cost to travel between the locations predicted by each cue is extremely high, e.g., Pfuhl et al., 2011). While the experiments reported here provide a starting point for researchers interested in investigating whether animals can use hierarchical strategies for resolving cue conflict in continuous space, future studies will be required to ascertain whether this is indeed the case.

6.3 Conclusion

The work reported in my dissertation has focused on testing how pigeons (*Columba livia*) and desert ants (*Melophorous bagoti*) resolve spatial cue conflict. Towards this end, I tested animals in a number of experimental paradigms, ranging from discrete choice and continuous navigation tasks conducted in a laboratory (pigeons: Chapters 2 and 5), to continuous navigation tasks conducted in animals' natural environment (desert ants: Chapters 3 and 4). My results indicate that while pigeons and desert ants are physiologically very different, exploit different ecological niches and methods of navigation (e.g., terrestrial vs. airborne), and have very different neurological structures, both species utilize similar strategies for resolving spatial cue conflict. Specifically, both ants and pigeons utilized integrative strategies for resolving relatively small amounts of spatial cue conflict (see Chapters 4 and 5). Additionally, while integrative strategies are computationally complex relative to hierarchical or independent strategies (Pfuhl et al., 2011), the results from my work with navigating desert ants (Chapter 4) demonstrate that a relatively large brain and/or complex central nervous system is not required to accomplish this task (Wehner, Fukushi, & Isler, 2006; Wehner, 2003). Even though ants have a relatively simple nervous system when compared to mammals and birds (Wehner et al., 2006), they were still able to integrate information across navigational systems (i.e., view-based navigation and path integration, Chapter 4).

Thus, because such disparate species use similar strategies for resolving cue conflict, it is likely that integration is an efficient and effective strategy. Because of this, and because my work has shown that two very different species, namely pigeons and desert ants, can use integrative strategies to resolve cue conflict, the ability to integrate the information provided by multiple spatial cues may be widespread across animals. It is my hope that future work with other animal species will validate this hypothesis.

6.4 References

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