GEOMETRIC RULE LEARNING BY PIGEONS

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GEOMETRIC RULE LEARNING BY PIGEONS

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DISSERTATION ABSTRACT

GEOMETRIC RULE LEARNING BY PIGEONS

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In a series of four experiments using an open field search task, pigeons were trained to find a goal located at the midpoint of the hypothetical line connecting two discrete landmarks positioned in a linear array. Pigeons searched in substrate for an initially visible but eventually invisible goal location containing food reward. In Experiment 1, the apparatus was devoid of orienting cues. After reaching performance criteria in training, critical food-absent test trials were conducted by manipulating the distance between the landmarks (interlandmark distance) to determine the nature of encoded spatial information. Search error and location on novel interlandmark distances suggested pigeons learned a relative geometric relationship between the landmarks as opposed to absolute distance and direction. In Experiment 2, orienting cues were introduced and pigeons were again trained to performance criteria. After reaching performance criteria, pigeons were again tested in the absence of food with novel interlandmark distances. In contrast to Experiment 1, results from Experiment 2 suggested pigeons learned absolute distance from the landmarks. In Experiment 3, pigeons continued to search along the hypothetical line connecting the landmark with rotations of the landmark array in both the presence and absence of an orienting cue indicating learning of relative direction from the landmarks and further evidence for the learning of a geometric relationship between the landmarks. Experiment 4 tested pigeons with each landmark from the array individually in both the presence and absence of the orienting cue and revealed that pigeons used the orienting cue and both landmarks for accurate goal localization. Overall, results implicate a stable frame of reference as critical to spatial coding strategies and suggest pigeons are capable of coding location based on both absolute and relative distance and direction. Findings also suggest pigeons are capable of coding location in a manner consistent with that proposed by the multiple-bearings hypothesis (Kamil & Cheng, 2001) and provide evidence for greater flexibility in pigeons' navigation and orientation strategies than revealed by previous research.

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Style manual or journal used

APA Manual

Computer software used

Microsoft Word
SPSS
Sigma Plot

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I. INTRODUCTION

Navigating an environment is a daunting task. One of many problems encountered by navigating animals is returning to a previously visited location. The ability to return to a previously visited location allows for navigation between known locations and increases an animal's chance for procurement of food and other resources. To accomplish this task, mobile animals appear to rely on landmark-based navigation. Landmark-based navigation is the process of determining a position and orientation by using objects in the environment with known positions (Gallistel, 1990). As spatial coding has been suggested to be based on metric relations (Gallistel, 1990), it has been of considerable interest to determine what spatial information is encoded from these objects for later use in returning to a goal location (for a review see Shettleworth, 1998).

A method for determining the spatial information encoded from landmarks during navigation is the *landmark transformation technique* (for a review see Cheng, 1995; Cheng & Spetch, 1998) in which an animal is trained to find an unmarked goal location containing food at a constant distance and/or direction from an individual landmark or landmark array. During training, the spatial location of the landmark or landmark array is varied from trial to trial about the search space while both the orientation and spatial relation of the landmark or landmark array to the goal remain constant. To verify that the landmark or landmark array is the stimulus controlling accurate search behavior, food-absent control trials are conducted to eliminate possible olfactory and/or visual cues. If search behavior during food-absent trials is concentrated in the same areas as search behavior during training trials, location of search behavior is controlled by some aspect(s) of the landmark or landmark array. During intermixed test trials, food is also removed and either an individual landmark and/or the landmark array is manipulated in size, shape, or color and/or by expansion, contraction, or rotation. Measures of search behavior during these manipulations have provided insight into the contents of spatial learning and illuminated species similarities and differences in mechanisms underlying landmark-based navigation.

Landmarks-based navigation is so ubiquitous in the animal kingdom that diverse species ranging from insects to mammals have been shown capable of navigation by this process; however species differences have also emerged with respect to its underlying mechanisms (for a review see Healy, 1998). For example, honeybees (*Apis mellifera*) appear to rely on a process called *image matching* (Cartwright & Collett, 1979, 1982, 1983; Collett & Rees, 1997; for review see Cheng, 2000; Collett & Zeil, 1998). Image matching involves reducing the discrepancy between the bee's current retinal image and a representation stored in memory containing a view of the landmarks from the goal location. Seemingly, bees do not abstract information from an individual landmark or landmark array in order to locate a goal. Instead, these animals rely solely on the projected retinal image; search continues until each landmark in the current retinal image matches those of the image stored in memory. In contrast, adult humans appear to use both absolute and relative distances and directions (Foo et al., 2005; Hartley, Trinkler, & Burgess, 2003; Waller et al., 2000; for review see Cheng & Spetch, 1998). In short, humans are able to abstract information from a landmark array to accurately locate a goal. For example, adults are capable of rapidly forming and using a “middle rule” to find a goal when presented with novel contractions or expansions of a previously learned landmark configuration (MacDonald et al., 2004; Spetch, Cheng, & MacDonald, 1996; Spetch et al., 1997).

Marked inter-species differences in the processes underlying landmark use raise interesting questions concerning ecological versus general-process views of learning (for a review see Papini, 2002). For example, is absolute encoding of spatial information a general process available to all mobile animals? Is relative encoding of spatial information species-specific? To answer these questions diverse species must be tested using identical procedures to permit legitimate and explicit comparisons (Bitterman, 1960). Such a comparative approach has revealed similarities and differences in spatial learning across species and provided an opportunity to differentiate general from specialized processes (for a review see Shettleworth, 1998). Although this approach suffers from ensuring that tasks are equivalent across species, it has served as the best tactic for determining the ubiquity of general learning processes in the animal kingdom.

Adopting a comparative approach necessitates the detailed study of a few diverse species, and the pigeon has conspicuously served as the representative from the aves’ class for decades. Not surprisingly, a substantial amount of literature has accumulated on the spatial behavior of the pigeon (e.g., Cheng, 1988, 1989, 1990, 1994; Cheng & Sherry, 1992; Cheng & Spetch, 1995; Spetch, Cheng, & MacDonald, 1996; Spetch et al., 1997; Spetch, Cheng, & Mondloch, 1992; Spetch & Edwards, 1988; Spetch & Mondloch, 1993; Spetch & Wilkie, 1994), and much of this work has shown that pigeons rely almost exclusively on absolute spatial information and, like honeybees, are relatively inflexible with respect to their search strategies (for a review see Cheng, 1995).

For example, Cheng (1988, 1990) trained pigeons in a square box to locate food in the presence of a single landmark positioned on the rear wall. Transformation tests manipulating one aspect of the landmark (i.e., shortening, elongating, narrowing, or widening) resulted in no changes to pigeons' search distributions, but lateral transformations (left/right) resulted in systematic shifts in search distributions toward the direction and approximately the distance of the landmark shift. Based upon these observations, Cheng (1989) developed the Vector Sum Model of landmark use which specifically purported that pigeons encoded absolute distance and direction information in the form of landmark-to-goal vectors when positioned at the goal location. The model suggests that, in future attempts to return to the goal location, pigeons perceive current self-to-landmark vectors from each landmark and add these vectors to the remembered landmark-to-goal vector (using vector addition). Such a process results in navigation vectors which are then used to compute a weighted average. As a result, the actual path traveled to the goal by a pigeon consists of a weighted average of navigation vectors computed from the addition of perceived current self-to-landmark vectors and remembered landmark-to-goal vectors (Figure 1).

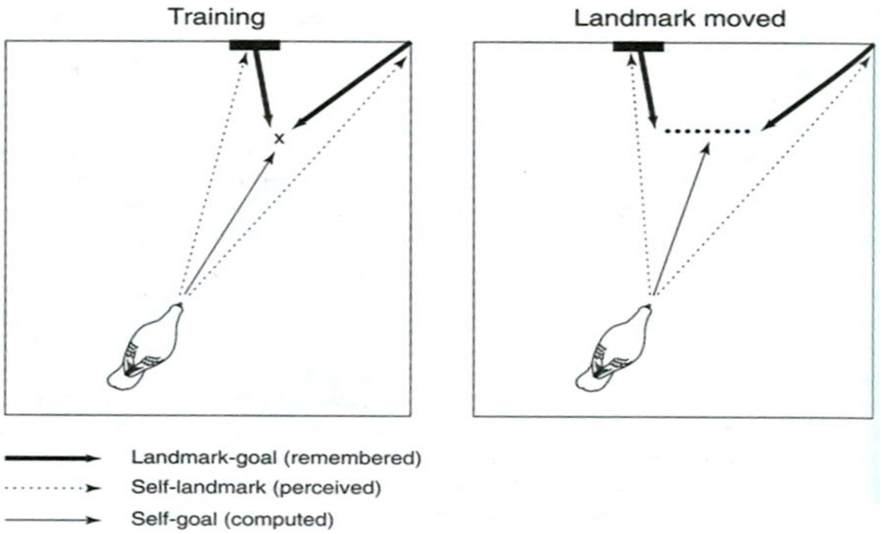


Figure 1. The left panel represents the vectors pigeons perceive, remember, and compute from the goal location during training. The right panel shows the change in these vectors when the landmark is shifted. Please note that an aspect of room geometry (the closest edge of the experimental room to the goal) is used in this process (from Shettleworth, 1998).

The Vector Sum Model adequately accounted for shifts in the peak of pigeons' search distributions resulting from a lateral or horizontal shift in landmark direction: pigeons shifted the peak of their search distribution in the direction of the landmark shift. However, with a simultaneous horizontal and vertical landmark shift (i.e., diagonal shift), pigeons failed to shift the peak of their search distribution in this direction (Cheng, 1990). Instead, search shifted in the horizontal direction of the landmark shift (left/right) but not in the vertical direction (up/down). However, Cheng and Sherry (1992) observed that pigeons encoded the absolute distance from the goal to the closest perpendicular edge of an experimental enclosure and modified the Vector Sum Model: in addition to encoding landmark-goal vectors, pigeons also encode absolute distance from the goal to the nearest edge of the experimental enclosure. The use of a fixed distance in conjunction with vector summation accounts for the changes in pigeons' search distributions when landmarks were shifted in both axes of space.

The Vector Sum Model assumes that pigeons compute both distance and direction, but it does not speak to the way in which this information is computed (e.g., independently or averaged). By creating a directional conflict during testing, Cheng (1990, 1994) provided evidence that pigeons compute direction and distance information independently. During training, pigeons were required to locate a goal in the presence of a single cylindrical landmark with a single vertical stripe. In order to solve this task, pigeons needed to encode a vector from the landmark to the goal location. However, during testing, the stripe was rotated 90º from the training orientation, resulting in two separate but equally plausible goal locations. Thus, during testing, the landmark itself indicated the goal was in the training location whereas the stripe indicated that the

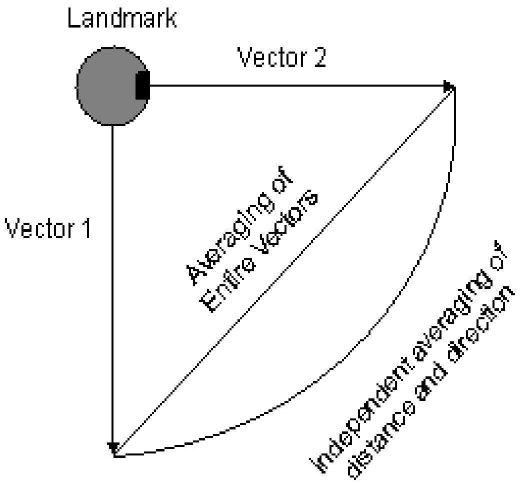


Figure 2. Illustration of the directional conflict presented during testing to pigeons (Cheng, 1994). Initial training allowed vector 1 to be used from the landmark (filled circle) or vector 2 from the stripe on the landmark (black stripe on filled circle) to find the goal. Resulting predictions of search locations are illustrated if pigeons averaged entire vectors or averaged distance and direction independently (reproduced in part from Cheng & Spetch, 1998).

goal was in a novel location. If pigeons averaged entire vectors, search should be concentrated on a line connecting the vectors (according to vector geometry); however, if pigeons averaged direction and distance independently, search should be concentrated on an arc connecting the two trained vectors (Figure 2). Results suggested that pigeons averaged distance and direction independently.

In summary, pigeons encode absolute distance and direction information from individual landmarks that take the form of spatial vectors. These vectors, which are averaged independently, preserve both distance and direction information from a landmark to a goal. A return trip to the goal location is guided by perceived self-to-landmark vectors, remembered landmark-to-goal vectors, remembered goal proximity to an edge, and computed self-to-goal vectors.

Despite its complexity, pigeons' strategy of landmark use has been suggested as solely based on absolute metric information (Spetch et al. 1997; for review see Cheng, 1995; Cheng & Spetch, 1998). Hence, pigeons do not appear to abstract information from a landmark or landmark array and instead appear to rely on individual elements composing the array. Further support for the use of a strategy based on absolute metrics has emerged from research using multiple landmarks. For example, Spetch et al. (1996) trained pigeons in a touch-screen task to locate a hidden goal in the center of a square landmark array composed of four identical white crosses. During transformation tests, pigeons failed to search in the center of a horizontally, vertically, or diagonally expanded array. Instead, regardless of array transformation, pigeons searched an absolute distance from an individual landmark within the array. Search concentrated at an absolute distance from an individual landmark was also obtained in an open-field analog of the touch-screen task (Spetch et al., 1997). Furthermore, pigeons failed to transfer to novel landmark configurations in both the touch-screen and open-field versions of the task. Interestingly, single-landmark tests in which an individual landmark was presented alone revealed that pigeons were unable to locate the goal. Thus, the configuration of the array was likely used for the identification of an individual landmark within the array, a process termed *landmark matching* (Spetch et al.; for a review see Cheng & Spetch, 1998). After identifying a landmark within the configuration, pigeons apparently engage in *search-place matching* which involved determining the location of search relative to the identified landmark.

In contrast to pigeons, nutcrackers (*Nucifraga columbiana*) have been shown to use multiple landmarks during navigation via a process termed the *multiple-bearings hypothesis* (Kamil & Cheng, 2001). Specifically, the multiple-bearings hypothesis suggests that nutcrackers encode directional information from multiple landmarks to a goal location which is then defined by the intersection of these multiple bearings. Any error in encoding and/or recalling these multiple bearings will result in a zone of uncertainty defined by the area of the polygon formed by the intersection of each bearing (Figure 3). The multiple-bearings hypothesis has received modest empirical support as search error has been shown to decrease when the number of landmarks present increases (Kamil, Goodyear, & Cheng, 2001) and when a goal is located inside as opposed to outside a landmark array (Gibson & Kamil, 2001).

Although differences in spatial ability exist between caching and non-caching aves (e.g., Brodbeck, 1994), the complex use of bearings from multiple landmarks shown by nutcrackers may be applicable to pigeons as well. Specifically, Sutton (2002) trained

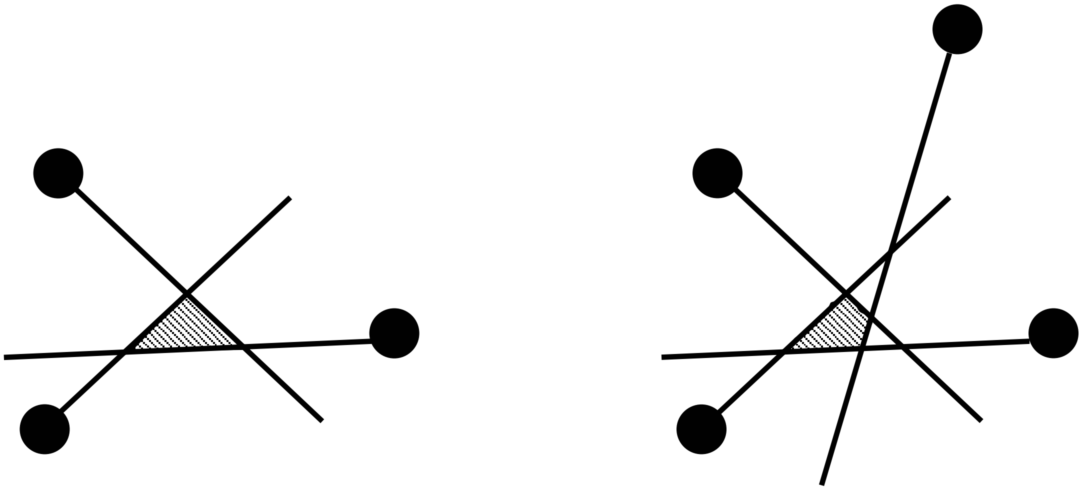


Figure 3. Illustration of the intersection of individual bearings (lines) from individual landmarks (circles) to form the zone of uncertainty (hashed polygon). Notice that the zone of uncertainty becomes smaller with an additional landmark present (reproduced in part from Kamil & Cheng, 2001).

pigeons with two unique configurations of four landmarks. Each configuration was assigned its own goal location with respect to the landmarks. During food-absent trials pigeons concentrated their searches at the goal location appropriate for the individual configurations. Such an outcome indicated that pigeons were relying on the landmark configuration itself as an indication of the location of the goal. Further tests with displacements of single landmarks within the configuration did not disrupt search accuracy, indicating that pigeons must have encoded distance and direction from multiple landmarks. Sutton suggested that pigeons may have been using the same (or a similar) multiple landmark-to-goal bearings mechanism as suggested by Kamil and Cheng (2001) for nutcrackers which indicates a greater flexibility in pigeons' navigational strategies than revealed by previous research.

Further support for flexibility in pigeons' navigational strategies has emerged with respect to environmental geometry. Surprisingly, pigeons do not rely exclusively on absolute spatial information with respect to environmental geometry of the surrounding experimental enclosure in order to locate a hidden goal and have recently been shown capable of using relative geometric cues (Kelly & Spetch, 2001; Gray et al., 2004; for review see Cheng & Newcombe, 2005). For example, Kelly and Spetch (2001), trained pigeons to located food in one corner of a rectangular arena. Only the shape of the environment was available as a spatial cue. Similar to other experiments investigating the use of environmental geometry (e.g., Cheng, 1986), choices were constrained to the trained and diametric corners. After training, pigeons were tested with reductions of the experimental enclosure consisting of a medium- and smaller-sized rectangle and square. If pigeons encoded absolute spatial information then these transformation should disrupt search accuracy, but if they learned some relative spatial rules based on the geometry of the experimental enclosure then search on the medium and small rectangles should be similar to performance within the original training environment. In contrast, performance in the square environment should be at chance as all walls were equal in length and hence could not be used to indicate a geometrically correct corner. During testing, pigeons searched significantly more in the correct and diametric corners of both the medium and small rectangles indicating control by relative geometry. Furthermore, as predicted, performance in the square environment test resulted in chance performance.

Although it is uncertain whether the spatial information encoded from the overall geometry of an experimental environment differs fundamentally from information encoded from landmark configurations (i.e., multiple individual landmarks placed in the form of a square, rectangle, triangle, etc.), it seems that animals encode geometric information from landmark configurations (Cheng & Newcombe, 2005). For example, both rats (Benhamou & Poucet, 1998; Greene & Cook, 1997) and pigeons (Gray & Spetch, 2006; Sutton, 2002) are capable of using individual landmarks composing a configuration and/or the geometric arrangement of these landmarks for accurate goal localization. Thus, despite clear differences between landmark configurations and overall geometry of an environment (e.g., enclosures provide a continuous edge while configurations do not), geometric information is encoded from both types of cues.

It has been suggested that some animals including jackdaws (*Corvus monedula*), nutcrackers, and pigeons form geometric rules by using previously acquired geometric information (Jones et al., 2002; Spetch et al., 2003). A *geometric rule* is defined as "a method of solution based on distance and directional relationships that could be used with a variety of landmark configurations, particularly novel configurations" (Kamil & Jones, 2000, p. 439). Specific geometric rules include halfway, quarter way, constant distance, and constant bearing (Figure 4). For purposes of the present paper, the focus will be concentrated on the halfway rule. For example, Kamil and Jones (1997) trained nutcrackers to search for buried food placed at the midpoint of a two landmark linear array. Distance between the landmarks (interlandmark distance) was varied from trial to trial, but the goal always remained equidistant from, and along the hypothetical line connecting, both landmarks. Error in search from the goal was used to determine accuracy. Training interlandmark distances included 20 to 120 cm in increments of 20 cm, and the birds readily learned the training interlandmark distances requiring 90 trials to average less than 20 cm in search error. However, given this task, the nutcrackers may not have been using a geometric rule but the memorization of an absolute vector from

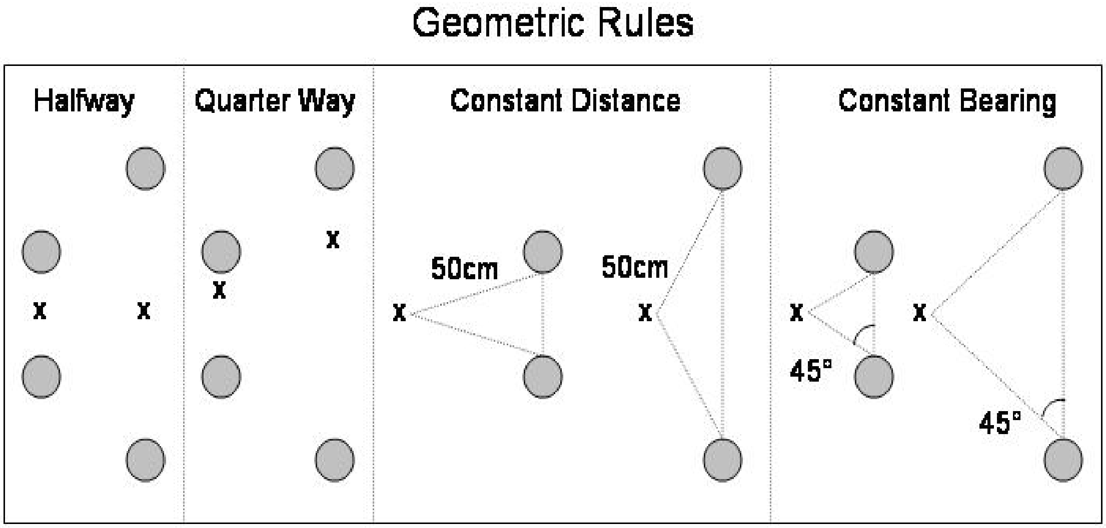


Figure 4. Examples of specific geometric rules with respect to a goal location (x). Landmarks (filled circles) are shown with two different interlandmark distances (reproduced in part from Spetch et al., 2003).

each landmark for each training interlandmark distance. Therefore, novel interlandmark distances ranging from 30 to 110 cm in 20 cm increments were presented during testing to distinguish between these two equally plausible and effective strategies. If the nutcrackers were relying on memorized absolute vectors, error during novel interlandmark distances should be larger than that during training. Yet, performance during presentations of novel interlandmark distances was equivalent to performance during training which suggested that nutcrackers formed and used a relative geometric rule. However, learning of a geometric middle rule by nutcrackers has been criticized on the basis that such a task can be solved by using vector-averaging strategies (Biegler, McGregor, & Healy, 1999). The first vector-averaging strategy (Strategy 1), assumes that nutcrackers learn a landmark-goal vector from each landmark that is the mean of the landmark-goal distances experienced during training. When presented with a novel interlandmark distance, these mean landmark-goal vectors are used to compute self-goal vectors. The average of the computed self-goal vectors will always specify the midpoint between the landmarks as the resulting search location. The second strategy (Strategy 2) assumes that nutcrackers learn separate landmark-goal vectors from each landmark for each training interlandmark distance. When presented with a novel interlandmark distance, the two training interlandmark distances closest to this novel distance are used to compute self-goal vectors. The average of the computed self-goal vectors will always specify the midpoint between the landmarks as the resulting search location. Such strategies would erroneously appear like geometric rule learning because they would also result in searches at the midpoint and produce transfer to novel interlandmark distances (Figure 5). Importantly, however, although these vector-averaging strategies specify the same search location as a middle rule, they produce very different error patterns (Figure 6).

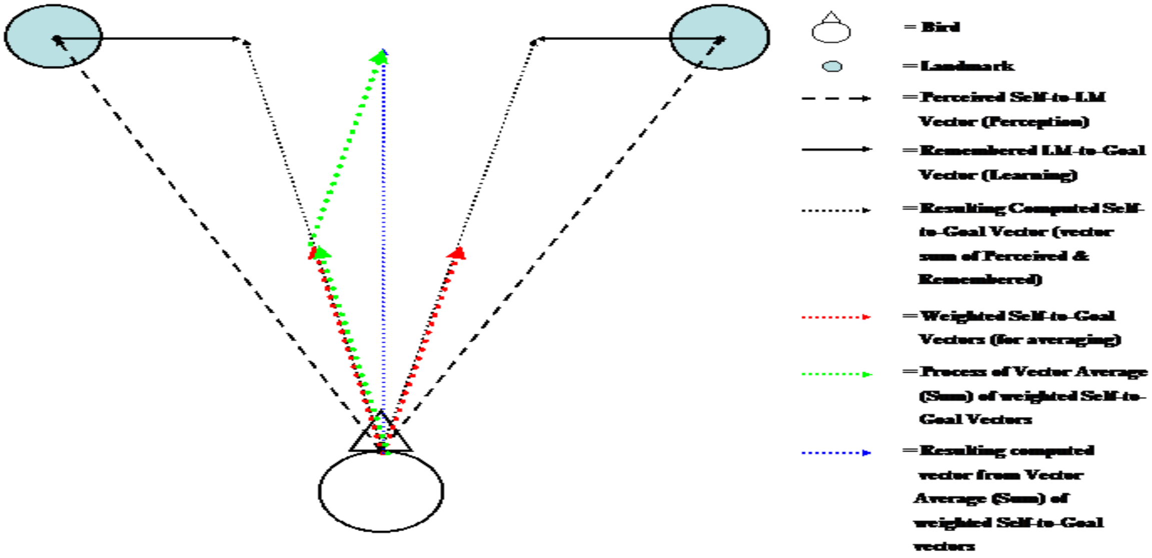


Figure 5. Graphical representation of vector-averaging strategy as proposed by Biegler et al. (1999).

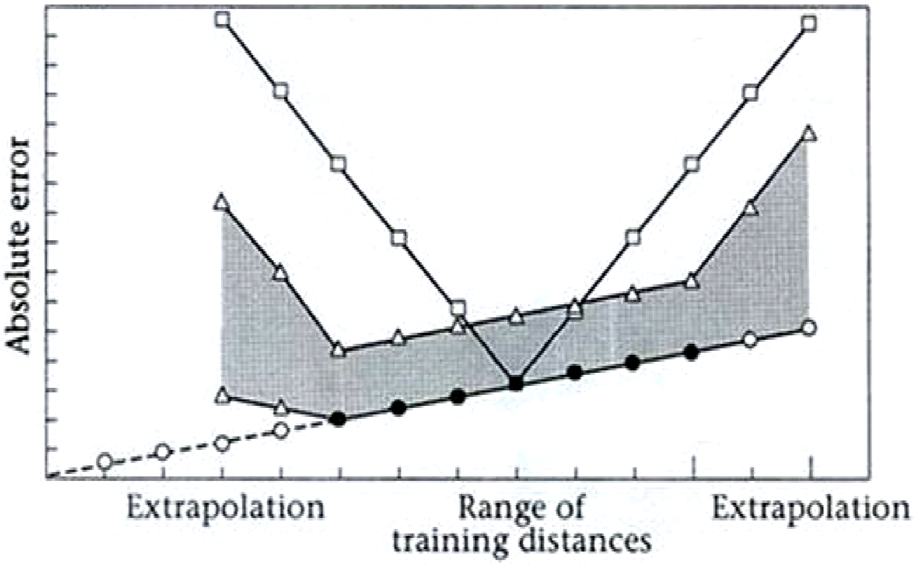


Figure 6. Predictions of search error at interlandmark distances within and beyond those experienced during training for three competing strategies: Middle Rule (circles), Strategy 1 (squares), and Strategy 2 (triangles). Reproduced from Biegler, McGregor, & Healy (1999).

Making these accounts mutually exclusive requires the presentation of interlandmark distances outside the range of training because vector-averaging will predict the most error at these distances whereas a middle rule predicts error equal to that during training (Biegler et al., 1999). To address these competing explanations, Kamil and Jones (2000, Experiment 2) again trained nutcrackers on the middle rule search task with interlandmark distances of 38 to 98 cm with increments of 20 cm. During testing, the birds were presented with novel interlandmark distances within (i.e., interpolated distances, 48, 68, and 88 cm) and beyond (i.e., extrapolated distances, 28 and 108 cm) the training interlandmark distances. Nutcrackers performed with an error amount similar to training distances on both interpolated and extrapolated interlandmark distances, thus supporting the view that they had formed a general geometric rule.

Kamil and Jones (1997, 2000) suggested that two processes were involved in successfully solving the middle rule search task: (1) directional determination - locating the hypothetical line connecting the landmarks, and (2) distance determination – locating the correct location along that line. Evidence for the two separate processes emerged as North-South (NS) error (error parallel the line connecting the landmarks) increased linearly with increased interlandmark distance whereas East-West (EW) error (error perpendicular to the line connecting the landmarks) remained constant across increased interlandmark distance. The process of locating the line connecting the landmarks may be independent of the process of locating the correct location along that line as direction and distance error may result from two separate processes (Kamil & Cheng, 2001). Distance error may follow the psychophysical principle of Weber's Law in that error increases linearly as a function of the to-be-judged distance whereas direction error remains constant at all landmark-goal distances.

Further support of geometric rule learning has been obtained with nutcrackers, pigeons and jackdaws as all have been shown to transfer to both interpolated and extrapolated interlandmark distances during a middle rule search task (Jones et al., 2002). Moreover, pigeons and nutcrackers have been shown to learn other complex relative rules such as constant bearing or constant distance and relative and absolute bearing (Jones & Kamil, 2001; Spetch et al., 2003). Despite evidence for geometric rule learning in these species, results have revealed that pigeons and jackdaws (non-caching aves) not only performed less accurately than nutcrackers (caching aves) during transfer but also did not show preferential weighting of direction over distance information. Specifically, no differences were found between NS and EW errors for pigeons or jackdaws as interlandmark distance increased. In addition, pigeons showed no differences in an ability to learn landmark-goal relationships based on distance or direction (Spetch et al., 2003). Also, because these studies were conducted in the presence of numerous orienting cues, it remains unclear whether pigeons actually coded direction to the goal from both landmarks. In contrast, nutcrackers have shown an increase in NS error but not EW error as interlandmark distance increases (Kamil & Jones, 1997), as well as an ability to learn directional tasks faster than distance tasks (Jones & Kamil, 2001). Additionally, there is mounting evidence that nutcrackers have the capacity to code goal location with respect to multiple landmarks (Kamil & Jones, 1997, 2000).

Although it appears that nutcrackers code the goal location with respect to multiple landmark-goal bearings and rely primarily on this direction information as predicted by the multiple-bearings hypothesis (for a review see Kamil & Cheng, 2001), lack of such evidence with pigeons may have been masked by procedural factors. Specifically, studies investigating preferential weighting of distance or direction information have not controlled for cue availability within the experimental environment. As a result, it remains unknown whether pigeons, like nutcrackers, would also code multiple landmark-goal bearings and rely on directional information over distance information in a middle rule search task if cue availability were controlled. Thus, an initial goal of the present experiments was to further explore the applicability of the multiple-bearings hypothesis to pigeon navigational strategies - specifically to determine if pigeons are able to code multiple-landmark-goal bearings. Presumably, in the absence of external reference cues and informative environmental geometry, the landmark array will serve as the only source of direction information. Given such a set of circumstances, pigeons may be forced to code the direction of the goal location relative to both landmarks or otherwise fail to solve the task.

As geometric rules are based on the relationship between stimuli, they can be viewed as a type of abstract concept - a rule about a relationship. Importantly, abstract concepts are not bound to any specific aspects of the stimulus or stimulus set allowing for flexibility and adaptability when encountering novelty. Outside of the spatial domain, abstract relational concepts such as identity have been extensively investigated in numerous species including gorillas (*Gorilla gorilla*), orangutans (*Pongo pygmaeus*), rhesus monkeys (*Macaca mulatto*), capuchin monkeys (*Cebus Capucinus*), and parrots (*Psittacus erithacus*) with such tasks as matching-to-sample, oddity-from-sample, and same/different (Bhatt & Wright, 1992; Bovet & Vauclair, 2001; Pepperberg, 1987; Wright, Santiago, & Sands, 1984; Wright, Shyan, & Jitsumori, 1990; York, 2003).

Although the case has been made that language-absent animals are incapable of forming abstract concepts (Premack, 1978), recent evidence has emerged to the contrary (Katz & Wright, 2006; Katz et al., 2002; Wright et al., 2003). Results in support of abstract-concept learning have been attributed to a shift from product (i.e., which species do or do not possess abstract-concepts) to process (i.e., mechanisms by which concepts are learned). This shift toward process has revealed parameters critical to abstract-concept learning. For example, utilizing a set-size expansion procedure in a same/different task, Katz et al. (2002), Katz and Wright (2006), and Wright et al. (2003) were able to achieve full concept learning (i.e., transfer performance with novel stimuli equal to baseline training performance) with rhesus monkeys, pigeons, and capuchin monkeys, respectively. The parameter critical to the formation of the abstract concept was an increase in the number of training examples.

Applying this shift toward process to the spatial domain raises important questions concerning the parameters critical to the formation of geometric rules such as *halfway*. Specifically, which parameters lead to item-specific (absolute spatial coding) and relational learning (relative spatial encoding)? To this end, a second goal of the present experiments was to explore parameters critical to geometric rule learning using a middle rule search task with pigeons. Performance on novel interlandmark distances presented during testing will serve as the metric for the extent of rule formation. Complete geometric rule learning will be evidenced if performance on novel interlandmark distances is equivalent to performance on baseline interlandmark distances.

A third goal of the present experiments was to further investigate the flexibility of pigeons' orientation and navigation strategies. Although there is substantial evidence that pigeons use absolute distance and direction strategies (e.g., Spetch et al., 1996, 1997; Gray & Spetch, 2006), there is little evidence that pigeons use relative direction or distance strategies. The notable exceptions have occurred using orientation tasks in enclosed apparatuses devoid of external cues (e.g., Gray et al., 2004; Kelly & Spetch, 2001). Thus, the evidence that pigeons use relative distance and direction strategies with landmark arrays is scarce. However, a few recent studies have indicated that pigeons are capable of using relative distance strategies when trained with multiple exemplars (Jones et al., 2002) and relative direction strategies when tested with small rotations of an array (Gray & Spetch, 2006). Collectively, however, previous research has implicated the importance of external cues in spatial strategy use. As a result, the present experiments were also designed to determine whether pigeons are able to rely on relative distance and directional information when external references cues and informative geometry are eliminated.

II. EXPERIMENT 1

Method

Pigeons. Three adult White Carneaux pigeons (*Columba livia*) aged 3 to 6 years were used as subjects. The pigeons had varying amounts of experience in same/different and/or matching-to-sample touch-screen tasks but no experience within the arena search task. One bird was dropped from the study because of difficulties during pretraining. Pigeons were maintained at 80-85% of their free-feeding weight throughout the duration of the experiment. Pigeons were housed in individual cages with constant access to grit and water. The colony room was on a 14:10 light:dark cycle, and overhead lights were illuminated from 0500 – 1900. Pigeons were tested 4 – 6 days per week with two sessions per day (one morning and one afternoon session). The morning session occurred between 500 – 0800, and the afternoon session occurred between 1600-1900.

Apparatus. The apparatus is depicted in Figure 7. Pigeons were tested in a hexadecagon-shaped arena, 150 cm (length) x 150 cm (width) x 14 cm (height). A hexadecagon-shaped ceiling 150 cm (length) x 150 cm (width) x 5.08 cm (height) was suspended over the center of the arena. The arena and ceiling were painted matte gray and coated with a urethane gloss. Eight individual white vinyl curtains, 186 cm (length) x 96 cm (width), were affixed to the outside of the arena and suspended ceiling via Velcro in an overlapping fashion. Each side of the arena was numbered 1-16 clockwise and could serve as an entrance or exit. A Cartesian grid was marked on the floor of the arena so that individual cells measured 5 cm x 5 cm. The floor of the arena

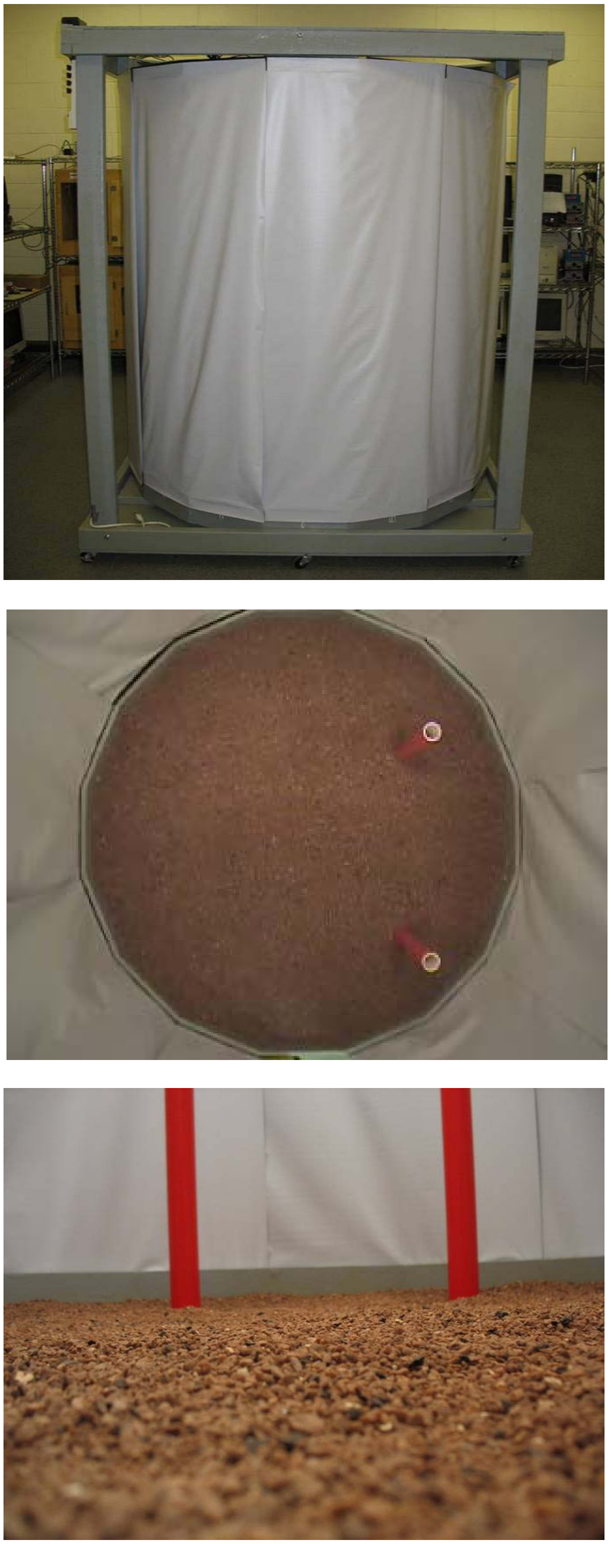


Figure 7. External picture of the apparatus (*top panel*). Internal picture of the apparatus (*middle panel*). Internal picture of the apparatus illustrating the substrate and landmarks from ground-level (*bottom panel*).

was covered with approximately 5 cm of Purgrain Fortified Pigeon Grit (Moyer & Sons Inc., Souderton, PA). The arena was illuminated by 16 circular 10-watt halogen lights 5.4 cm in diameter (Portfolio, Model 59209) that were equidistantly arranged in a circle with a diameter of 76.2 cm from the center of the suspended ceiling. Industrial casters were attached to the underside of the arena which allowed rotation of the entire apparatus with respect to the experimental room. A digital video camera (Sony, Model DCR-TRV22) was centered above the arena and mounted so that the lens was flush with the inside of the suspended ceiling. The camera was connected to a personal computer (Dell Latitude C640, Model PP01L). A dustpan was used to smooth grit between trials. A white noise generator centered above the outside ceiling of the arena was used to mask background noise (68 dB at ground level). A fully enclosed return box, 40.5 cm (length) x 32.5 cm (width) x 40.5 cm (height), with a guillotine door at each end was painted matte gray and coated with urethane gloss. A small flashlight (Rayovac, Model SPSL2AA-B) was mounted externally above the ceiling to provide illumination to a centered food well, 2 cm (length) x 4.5 cm (width) x 0.5 cm (depth), located in the rear of the return box.

Stimuli. Two pieces of PVC pipe each measuring 5 cm in diameter and 40 cm in height were used as landmarks. Both landmarks were painted red. Landmarks were always placed in a linear array that was oriented North and South with respect to the camera view on the Cartesian grid.

Home-Cage Training. Pigeons were initially trained to eat mixed grain from a small, white, cylindrical, plastic container (3.3 cm in diameter and 3.2 cm in height) in their home cages and from the food well when the light was illuminated in the return box. Pigeons were also trained to shuttle into the baited return box when the light was illuminated. Once pigeons were reliably eating from the plastic container and shuttling into the return box preliminary training began.

Preliminary training. Pigeons were familiarized with the apparatus for two days with two sessions of 6 trials per day. For the first session of Day 1, pigeons entered the arena and retrieved two kernels of corn from the inside of the plastic container which was placed completely above the substrate. The location of the container varied randomly from trial to trial. Beginning with Trial 1 of Session 2, the kernels and the sides of the container were progressively covered with substrate until only the top of the container was visible. For the first trial of Session 3 (i.e., Day 2) and all subsequent trials and sessions the kernels and container were covered with substrate so that only the top of the container was visible.

Training. Training consisted of two daily sessions (one morning and one afternoon session) consisting of 6 trials each (total of 12 daily trials). As numerous birds (Wiltschko & Wiltschko, 1996) including pigeons (Mora et al., 2004) are sensitive to geomagnetic fields, the entire apparatus was rotated to one of four randomly determined positions (0º, 45°, 90º, or 135º) with respect to the experimental room prior to each trial to eliminate the use of magnetoreception for orientation. Only four rotations were used with respect to the experimental room because a linear two-landmark array composed of landmarks of identical shape and color displays radial symmetry. As a result, a specific orientation and its 180º rotation were not only visually indistinguishable but also ambiguous with respect to a single magnetic field. In addition, prior to each trial, a goal location was quasi-randomly determined by generating an X and a Y coordinate on the Cartesian grid. Next, one randomly selected landmark was placed 30 cm North (N) while the other landmark was placed 30 cm South (S) of the goal location. Hence, the interlandmark distance was 60 cm, and the goal was always located at the midpoint of the hypothetical line connecting the two landmarks. Pigeons were then transported individually from their home cages to the arena in an opaque container. As pigeons have been shown to use ideothetic cues in determining location (Sutton & Shettleworth, 2005), an attempt was made to disorient subjects by rotation for 1 minute (12 rotations per minute) prior to the start of each trial to eliminate the possibility of inertial navigation/orientation. The arena lights were turned off until each trial began. For each trial, one of the sixteen arena sides was randomly selected as the entrance point, the subject was placed into the arena from this location, the curtain was closed, and the arena lights were illuminated.

Training trials continued until the goal location was found, 60 searches had been made, or 5 minutes had elapsed. A search was defined as the occurrence of the pigeon's beak contacting the substrate. A trial ended if the goal location was not found within 60 searches or after 5 minutes had elapsed. At the end of each trial, the arena lights were extinguished, a random side was selected as an exit, the return box was baited and placed at this exit location, the return box light was illuminated, and pigeons exited the arena by entering the return box.

Trials with the container visible continued for four sessions. Starting with the fifth session, two quasi-randomly selected container-visible trials were replaced with container-invisible trials in which the container was completely covered with substrate for both daily sessions. Food was present on all trials. During the first 12 container-invisible trials, if the goal location was not found within the allotted time or number of searches, the lights were extinguished, the container was made visible, the lights were illuminated, and pigeons were allowed to find the goal location. Training continued until search behavior met the criterion of three successive 6-trial blocks with a mean search error (calculated as described below) of 30 cm or less on container-invisible trials and the goal was found on at least 6 out of the last 12 trials. Upon reaching this criterion, another container-invisible trial was added to each daily session until search behavior met the criterion of three consecutive 6-trial blocks with a mean search error of 25 cm or less and the goal was found on at least 8 out of the last 12 trials. Upon reaching this criterion, a warm-up goal-visible trial was added prior to the start of both daily sessions, the other 6 trials for both daily sessions were converted to container-invisible trials, and 2 randomly selected food-present trials were replaced with food-absent (and container-absent) trials. This training continued until search behavior met the following three criteria: 1) no statistical difference between the last 12 food-present trials and the last 12 food-absent trials, 2) three successive 6 trial-blocks with a mean search error of 20 cm or less collapsed across these 24 trials, and 3) at least 10 of the last 12 trials in which the goal was found.

Testing. Once the food-absent criterion had been met, testing began. Testing consisted of two Test Blocks of 6 sessions each. Each session consisted of a container-visible warm-up trial prior to the presentation of 4 food-present goal-invisible training trials, 1 food-absent training trial (baseline), and 1 food-absent transfer trial. The trial location of the food-absent trials was quasi-randomly determined within each session. For each transfer trial, one novel interlandmark distance was randomly selected until each novel interlandmark distance had been presented. The two novel interlandmark distances used in the first Test Block were 40 cm and 80 cm. Upon completion of the first Test Block, a second test Block was conducted. Test Block 2 was conducted identically to Test Block 1 with the exception that the novel interlandmark distances used were 20 cm and 100 cm.

Determination of Search Locations. Search locations were determined using a procedure similar to that used by Jones et al. (2002). Specifically, each trial was viewed frame-by-frame through a custom videograph system. The videograph system allowed the recording of an East-West (EW) and North-South (NS) coordinate for the goal and search locations. During training, the coordinates for the first 5 searches of food-present goal-invisible and food-absent trials were subtracted from those of the goal location and converted to centimeters. During testing, the coordinates for all 60 searches for both baseline and transfer trials were subtracted from those of the goal location and converted to centimeters. An average was then taken of the absolute coordinate values. The NS and EW errors were used to determine mean search error using the Pythagorean Theorem.

Results

Training

All pigeons completed training in less than 100 goal-invisible/goal-absent trials. These trials were divided into six-trial blocks. Figure 8 shows mean search error for each subject and averaged across subjects plotted by block. Search error decreased across blocks indicating that search behavior came under the control of the landmarks. This result was confirmed by a repeated measures ANOVA on mean search error with Block (1-15) as a factor and revealed a main effect $F(14, 154) = 4.08$, $p < .001$. A trend analysis

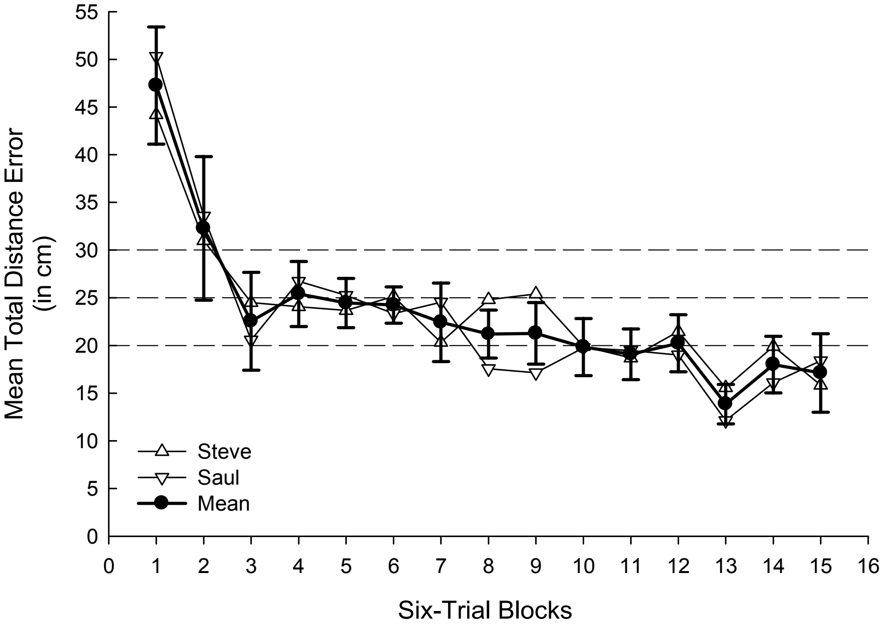


Figure 8. Mean total distance error (in cm) from the goal location on goal-invisible/goal-absent trials plotted across trial blocks for each bird (*unfilled symbols*) and averaged (*filled symbols*). Dashed lines indicate training performance criteria. Error bars represent standard errors of the mean.

yielded significant linear, *F*(1, 11) = 28.51, *p* < .001, quadratic, *F*(1, 11) = 5.51, *p* < .05, and quartic components, *F*(1, 11) = 8.96, *p* < .05. The alpha level was set at .05 for these and all subsequent analyses.

To determine whether pigeons relied on directional information over distance information during training, error was parsed into NS (error parallel the hypothetical line connecting the landmarks) and EW error (error perpendicular to this line) for all 15 trial-blocks of training. Figure 9 shows mean NS and EW search error collapsed across birds plotted by block. NS and EW search error initially decreased at different rates, but converged around trial-block 5. A repeated measures ANOVA on mean search error with Axis (ns, ew) and Block (1-15) as a factors revealed only a main effect of Block, *F*(14,

154) = 4.08, $p < .001$. A trend analysis on the Block factor revealed significant linear, $F(1, 11) = 26.51$, $p < .001$, quadratic, $F(1, 11) = 6.27$, $p < .05$, and quartic components, $F(1, 11) = 9.65$, $p < .05$. However, a repeated measures ANOVA on mean search error for the first 5 trial blocks revealed a main effect of Axis, $F(1, 11) = 5.31$, $p < .05$, and a main effect of Block, $F(4, 44) = 3.48$, $p < .05$. The interaction was not significant. A trend analysis on the Block factor revealed significant linear, $F(1, 11) = 8.37$, $p < .05$ and quadratic components $F(1, 11) = 11.15$, $p < .01$.

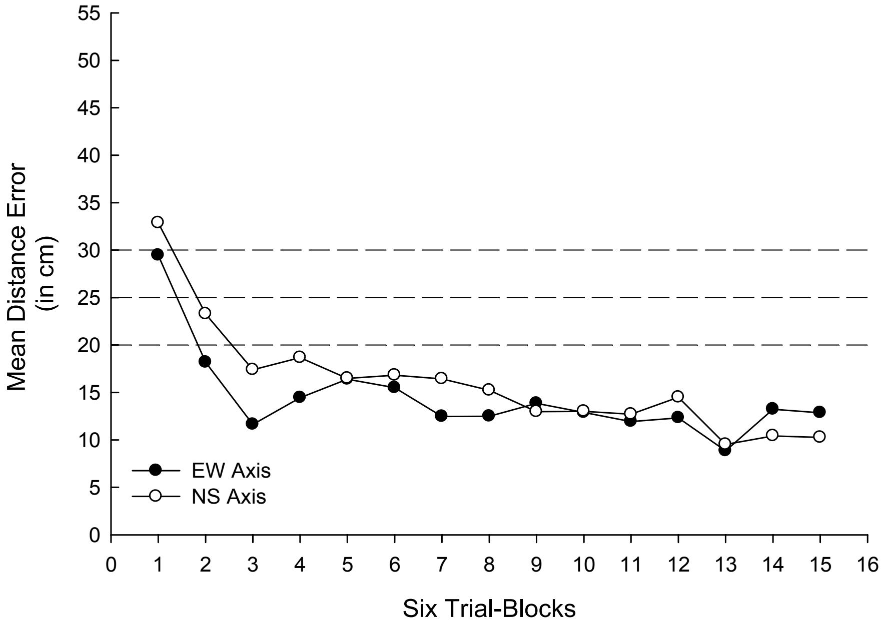


Figure 9. Mean distance error (in cm) from the goal location across trial blocks for EW and NS axes. Dashed lines indicate training performance criteria.

Testing

Three separate analyses were used collectively as converging evidence to determine search strategy during testing and to differentiate use a vector-averaging strategy from use of geometric rule learning: 1) search error on baseline and transfer, 2) search error functions plotted across interlandmark distance, and 3) spatial distribution of searches.

Search Error: Baseline and Transfer. Performance on transfer compared to that of baseline was of primary interest. Equivalent mean search error on baseline and transfer trials at novel interlandmark distances would provide evidence that pigeons had learned a relative relationship (geometric rule) between the landmarks. However, differences in performance on baseline and transfer trials at novel interlandmark distances would indicate use of a vector-averaging strategy or simply memorized vectors from each landmark. In an attempt to fully illustrate the search strategies used during testing, the error from the first 5 searches (as in training) was used to determine initial search strategy and error from all 60 searchers was used to determine the overall search strategy. Figure 10 shows mean search error on baseline and transfer trials collapsed across birds plotted by interlandmark distance for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). For the first 5 searches, baseline performance was equal to transfer performance at all novel interlandmark distances. Similarly, for all 60 searches, baseline performance was equal to transfer performance at all novel interlandmark distances with the exception of 20 cm. These results were confirmed by two separate repeated measures ANOVAs on mean search error with Type (baseline, transfer) and Interlandmark Distance (20 cm, 40 cm, 80 cm, 100 cm) as factors. Error from the first 5 searches revealed no significant

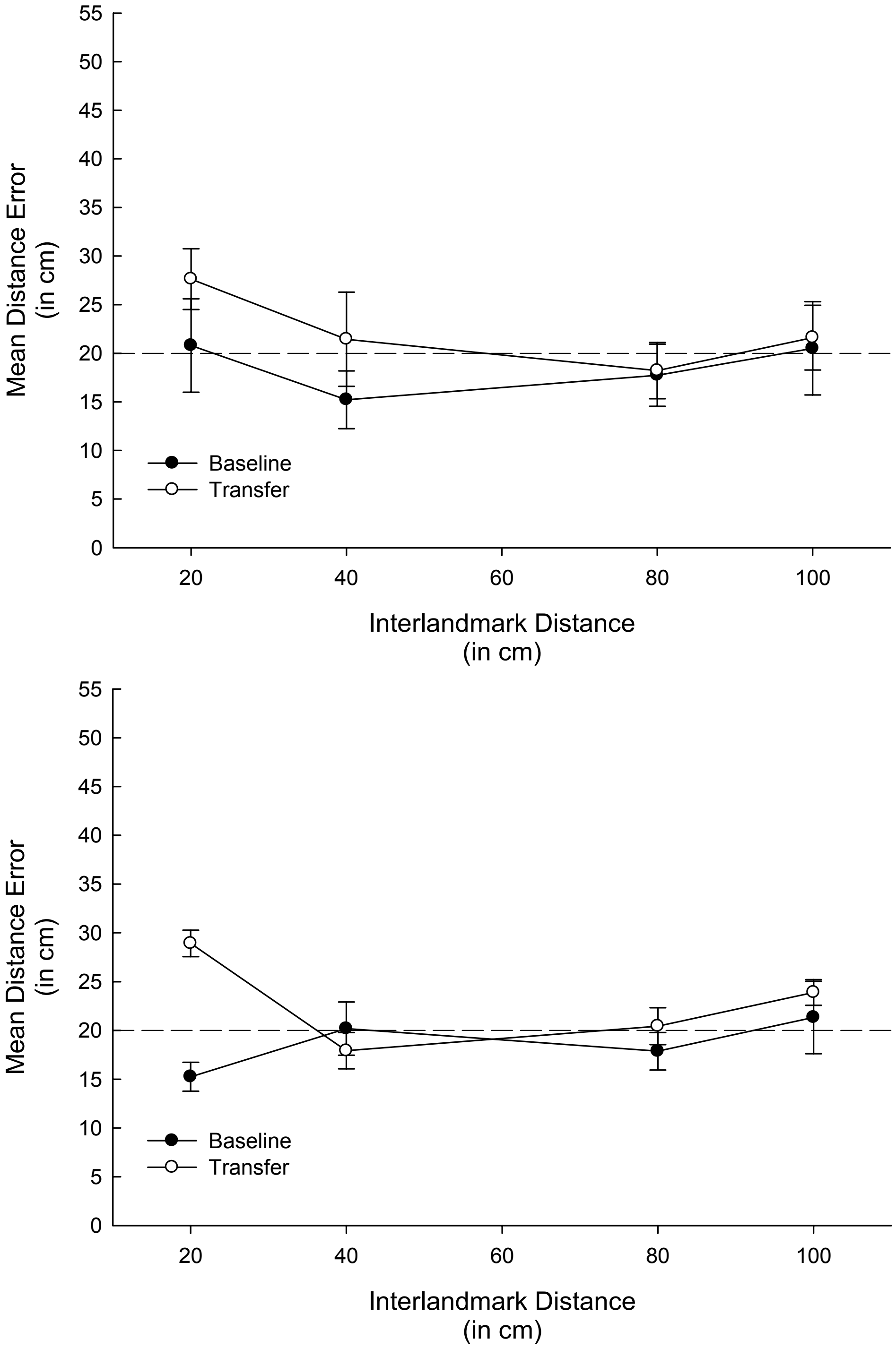


Figure 10. Mean distance error (in cm) from the goal location on baseline and transfer trials collapsed across birds plotted by interlandmark distance for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). Dashed line indicates the performance criterion required in training prior to testing. Error bars represent standard errors of the mean. *Note*. Interlandmark distance was not manipulated for baseline trials and remained at 60 cm throughout testing and is plotted across interlandmark distance only for comparative purposes.

effects or interactions. Error from all 60 searches revealed a main effect of Type, $F(1, 5) = 14.23$, $p < .05$, and a significant Type x Interlandmark Distance interaction, $F(3, 15) = 6.67$, $p < .01$. In order to isolate the source of the interaction, planned comparisons were performed. Baseline performance was compared to transfer performance at each interlandmark distance. The only significant difference between baseline and transfer performance was found at an interlandmark distance of 20 cm, $F(1, 5) = 51.53$, $p < .01$.

Search Error: Interlandmark Distances. To further distinguish use of a vector-averaging strategy from the use of a geometric rule, mean search error was plotted for each interlandmark distance. According to Biegler et al. (1999), use of a vector averaging strategy should result in a V-shaped function, whereas use of a geometric rule should result in a linear function. Figure 11 shows mean search error collapsed across birds plotted by interlandmark distance for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). For the first 5 searches, there appears to be a linear function with no change in search error across interlandmark distance. For all 60 searches, search error increased linearly with interlandmark distance (with the exception of 20 cm). These results were confirmed by two separate repeated measures ANOVAs on mean search error with Interlandmark Distance (20 cm, 40 cm, 60 cm, 80 cm, 100 cm) as a factor. Error from the first 5 searches revealed no significant effects. Error from all 60 searches revealed a main effect of Interlandmark Distance, $F(4, 20) = 11.46$, $p < .001$. Post hoc tests were conducted to determine the differences across interlandmark distances and results are displayed in Table 1. A trend analysis revealed only a significant quadratic component, $F(1, 5) = 49.54$, $p < .001$. Importantly, however, with the removal of the 20 cm interlandmark distance, a repeated measures ANOVA on mean search error also

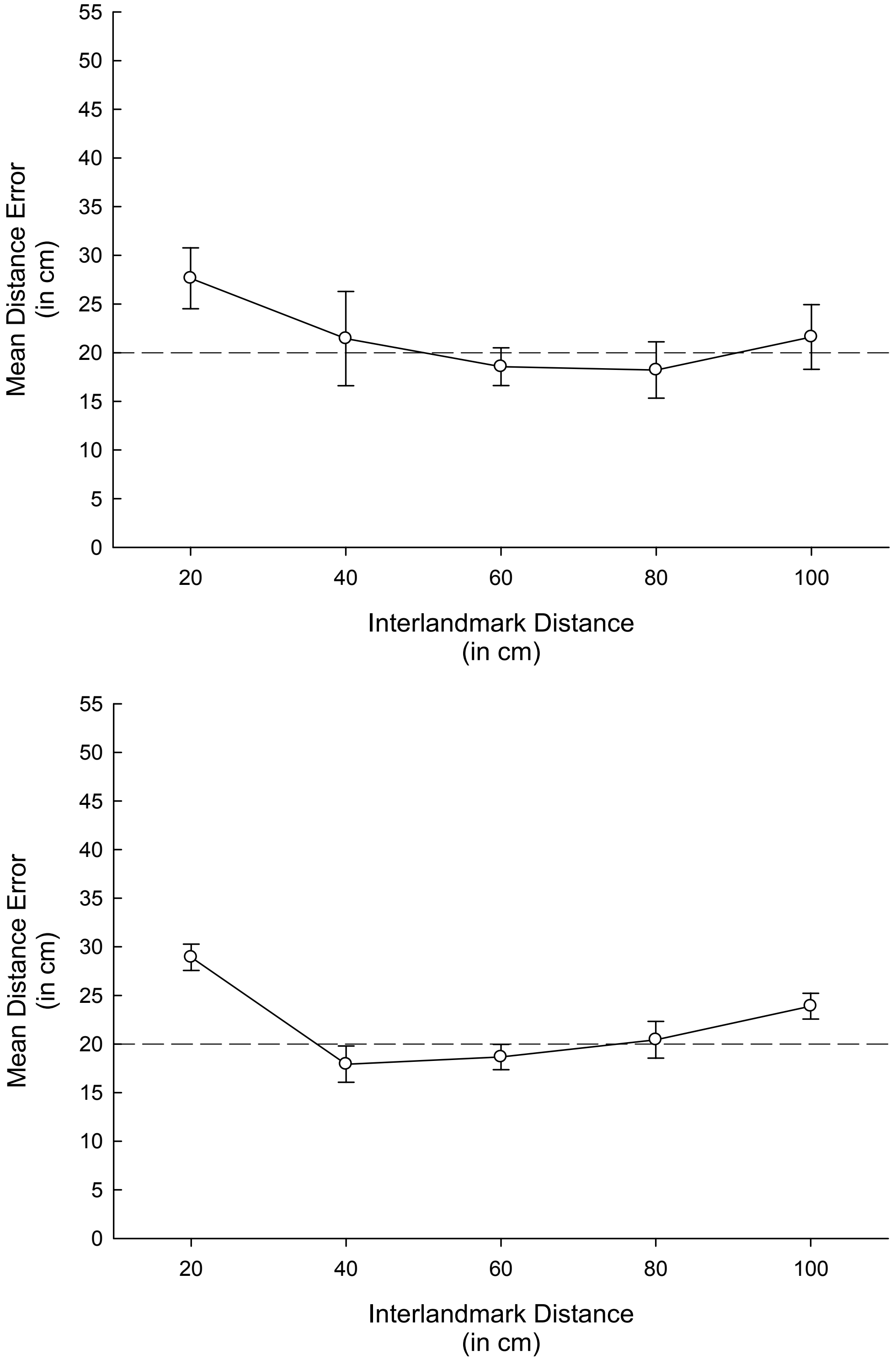


Figure 11. Mean distance error (in cm) from the goal location collapsed across birds plotted by interlandmark distance for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). Dashed line indicates the performance criterion required in training prior to testing. Error bars represent standard errors of the mean.

Table 1. *Post Hoc Tests for Each Interlandmark Distance for All 60 Searches.*

Least-Squares-Difference (LSD) post hoc tests for interlandmark distances (ILMD)

(I) ILMD	(J) ILMD	Mean Differences (I-J)	Standard Error	Significance
20 cm	40 cm**	11.00	2.49	.007
	60 cm***	13.67	1.90	.001
	80 cm**	8.48	1.92	.007
	100 cm*	5.03	1.69	.031
40 cm	20 cm**	---	---	---
	60 cm	2.67	2.24	.287
	80 cm	-2.51	3.36	.488
	100 cm*	-5.96	2.15	.039
60 cm	20 cm***	---	---	---
	40 cm	---	---	---
	80 cm*	-5.19	2.00	.048
	100 cm**	-8.64	2.02	.008
80 cm	20 cm**	---	---	---
	40 cm	---	---	---
	60 cm*	---	---	---
	100 cm	-3.45	2.04	.152
100 cm	20 cm*	---	---	---
	40 cm*	---	---	---
	60 cm**	---	---	---
	80 cm	---	---	---

Note. Single asterisk (*) indicates a significant difference at $p < .05$. Double asterisk (**) indicates a significant difference at $p < .01$. Triple asterisk (***) indicates a significant difference at $p < .001$.

revealed a main effect $F(3, 15) = 4.89$, $p < .05$, and a trend analysis yielded only a significant linear component $F(1, 5) = 8.32$, $p < .05$.

Search Error: NS versus EW Axes. To determine the sources of error contributing to total search error and to determine whether pigeons relied on directional information over distance information during testing, error was parsed into NS and EW error for each interlandmark distance. Figure 12 shows mean NS and EW search error collapsed across birds plotted by block for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). For the first 5 searches, there appears to be no change in search error across interlandmark distance or axis. However, for all 60 searches, NS error appears to increase linearly with interlandmark distance whereas EW error remains constant across interlandmark distance. These results were confirmed by two separate repeated measures ANOVAs on mean search error with Axis (ns, ew) and Interlandmark Distance (20 cm, 40 cm, 60 cm, 80 cm, 100 cm) as factors. Error from the first 5 searches revealed no significant effects or interactions. Error from all 60 searches revealed a main effect of Interlandmark Distance, $F(4, 20) = 9.15$, $p < .001$, and a significant Axis x Interlandmark Distance interaction, $F(4, 20) = 12.69$, $p < .001$. Custom contrasts were performed to isolate the source of the interaction and are shown in Table 2.

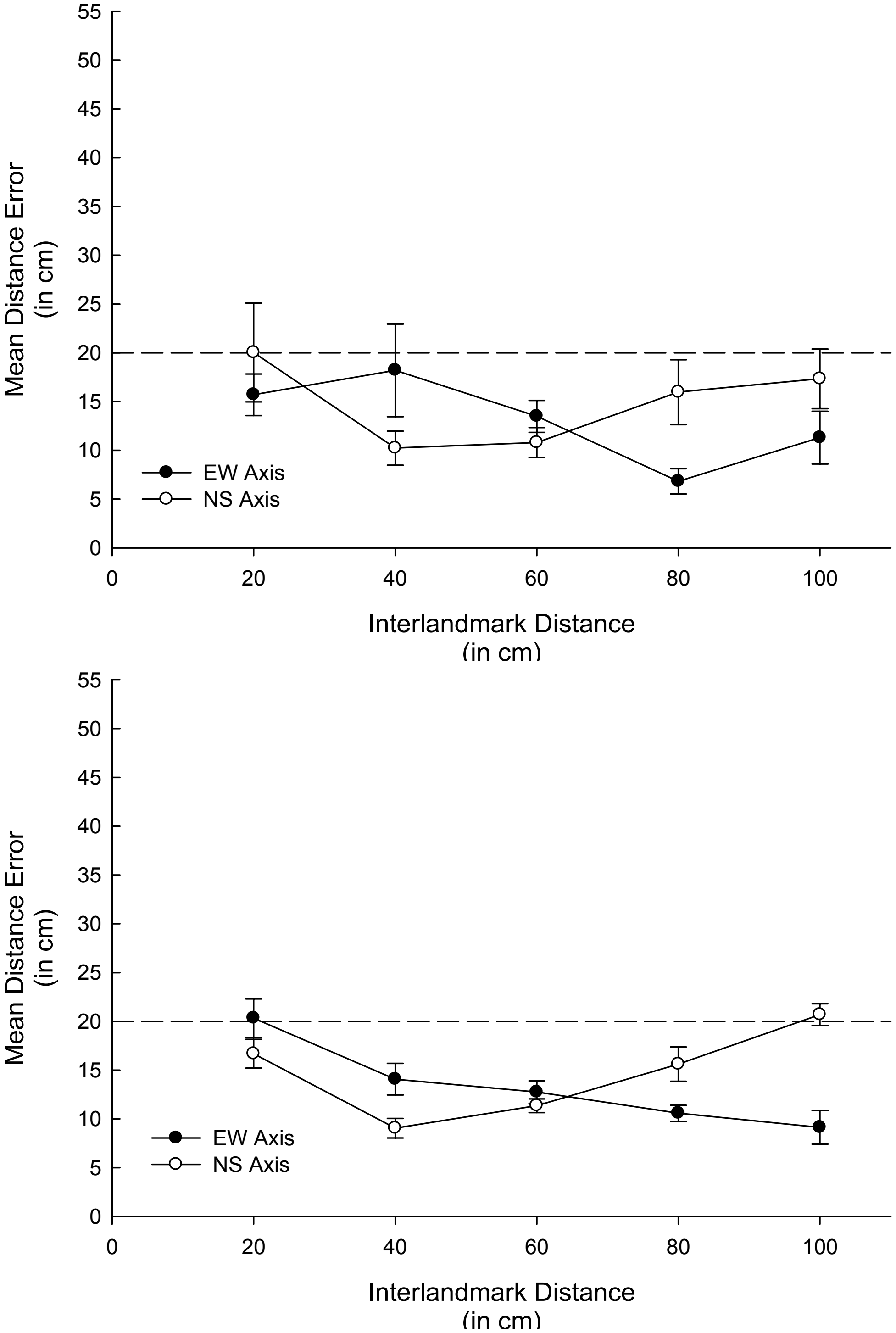


Figure 12. Mean distance error (in cm) from the goal location in the EW Axis and the NS Axis collapsed across birds plotted by interlandmark distance for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). Dashed line indicates the performance criterion required in training prior to testing. Error bars represent standard errors of the mean.

Table 2. *North-South (NS) and East-West (EW) Axis Comparisons for All 60 Searches.*

Custom Contrasts (p-values) for Interlandmark Distance Comparisons in the NS Axis

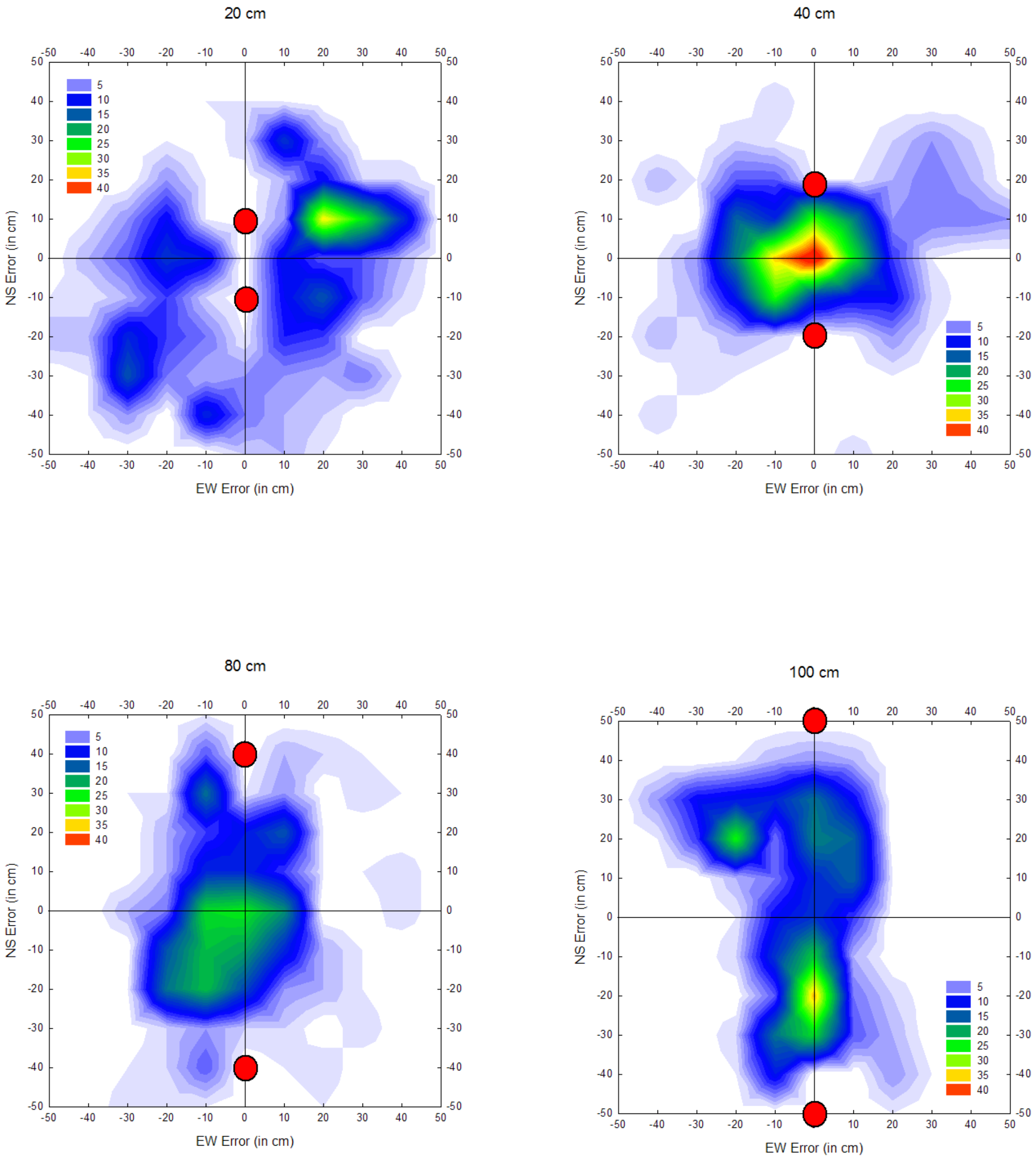
ILMD	20 cm	40 cm	60 cm	80 cm	100 cm
20 cm	---	.015*	.011*	.661	.046*
40 cm		---	.696	.045*	.001***
60 cm			---	.019*	.001***
80 cm				---	.079
100 cm					---

Custom Contrasts (p-values) for Interlandmark Distance Comparisons in the EW Axis

ILMD	20 cm	40 cm	60 cm	80 cm	100 cm
20 cm	---	.043*	.001***	.003**	.018*
40 cm		---	.151	.161	.167
60 cm			---	.913	.643
80 cm				---	.393
100 cm					---

Note. Single asterisk (*) indicates a significant difference at $p < .05$. Double asterisk (**) indicates a significant difference at $p < .01$. Triple asterisk (***) indicates a significant difference at $p < .001$.

Spatial Distribution of Searches. To more fully illustrate the pigeons' performance on transfer trials, Figure 13 shows the spatial distribution of all 60 searches at each test interlandmark distance (i.e., 20 cm, 40 cm, 80 cm, and 100 cm) collapsed across birds. Search distributions are centered at the goal location (0, 0). As shown, responding was unimodal and concentrated at the goal location for the majority of the test interlandmark distances. However, test performance at the 20 cm interlandmark distance is worthy of further discussion because of the seemingly peculiar search performance (with respect to search error and location) at this distance. Interestingly, although search was not concentrated *at* the midpoint of the hypothetical line between the landmarks, it seemed to be concentrated *along* the hypothetical line. Importantly, search was not concentrated at the locations specified by the endpoints of the vectors (which would lie outside of the array). Thus, performance at this interlandmark distance does not provide support for either vector-averaging or geometric rule learning. The most likely explanation of search performance (especially with respect to search location) is evident in visual inspection of the video files and related to reluctance on the part of the pigeons to move close enough to the array to place their heads between the landmarks at such a close interlandmark distance. Specifically, as interlandmark distance was measured from center-to-center of the landmarks, the distance from landmark edge to landmark edge was only 15 cm. As pigeons themselves measured about 9 cm in width across the breast, little room was left for maneuvering in between the landmarks. Visual inspection of the contour plot at this distance supports this speculation as search was mostly concentrated in the area between the landmarks in the NS axes but not in the EW axis.



20 cm

40 cm

80 cm

100 cm

Figure 13. Cumulative spatial distribution of searches at each novel interlandmark distance: 20 cm (*top-left*), 40 cm (*top-right*), 80 cm (*bottom-left*), and 100 cm (*bottom-right*). Search distributions are centered at the goal location (0, 0).

Discussion

Pigeons were able to solve the middle rule search task and eventually located the goal with relatively high frequency and accuracy. The simple fact that pigeons searched at or near the goal location on food-absent trials provides tentative evidence that pigeons coded multiple landmark-goal bearings as proposed for nutcrackers by the multiple-bearings hypothesis. Specifically, in an environment devoid of orienting cues and informative geometry, pigeons would have been unable to solve the task had they not been able to code direction with respect to both landmarks. As great care was taken to eliminate or render useless all known sources of orientation information, it is unlikely that some orientation cue other than the landmarks themselves were used by pigeons for accurate goal localization. An ability to code direction with respect to both landmarks is extremely important as pigeons would be unable to use a vector-averaging strategy, and perhaps, more importantly for the purposes of the present discussion, a geometric rule.

During initial training trials, pigeons were more accurate in the EW axis than the NS axis. This result is consistent with an interpretation that pigeons were learning a geometric rule as it suggests that two separate processes were involved in successfully solving the middle rule search task: (1) directional determination - locating the hypothetical line connecting the landmarks, and (2) distance determination – locating the correct location along that line (Kamil & Jones, 1997, 2000). Surprisingly, pigeons were engaging in these separate processes during initial acquisition which suggests that they may have been learning a relative relationship between the two discrete landmarks from the onset of training. Accordingly, search error on novel interlandmark distances during Testing indicated that baseline performance was equivalent to transfer performance at 40 cm, 80 cm, and 100 cm. Such equivalent performance at extrapolated distances below (i.e., 40 cm) and above (i.e., 80 cm, 100 cm) that experienced during training (i.e., 60 cm) is also consistent with the notion that pigeons learned a relative relationship between the landmarks.

As only one interlandmark distance was presented during training, a vector averaging strategy predicts differences in search error at any novel interlandmark distance (Biegler et al., 1999). Thus, present results are inconsistent with a vector-averaging explanation of pigeons' search performance. However, present results are consistent with those previously reported with both nutcrackers (Kamil & Jones, 1997, 2000) and pigeons (Jones et al., 2002; Spetch et al., 2003) suggesting the learning of a geometric rule unbound by specific aspects of the landmark or landmark configuration.

Finally, differences in NS and EW error were dependent on interlandmark distances. Search error increased in the NS axis with increased interlandmark distances whereas EW error remained relatively constant across interlandmark distances. Such differences suggest that pigeons relied on directional information over distance information in the present apparatus. Although this result is in contrast to previous results with pigeons (Jones et al., 2002), it is consistent with results obtained with nutcrackers (Jones & Kamil, 2001). Presumably, the most likely explanation for obtaining such results with pigeons is related to the nature of the apparatus. Specifically, in the absence of external or inertial reference cues, landmarks served as the only source of directional information, and, given these circumstances, pigeons were forced to attend to direction over distance information to successfully locate the goal.

Perhaps, most surprisingly, pigeons transfered to novel interlandmark distances after single exemplar training. Although pigeons (Jones et al., 2002), nutcrackers (Kamil & Jones, 1997, 2000; Jones et al.), and jackdaws (Jones et al.) have been shown capable of learning geometric rules, the learning of these relative relationships has been attributed to multiple exemplar training with discrete landmarks. Importantly, however, this is not the first time learning of relative relationships has emerged after single-exemplar training in the spatial domain. Specifically, training with a single exemplar of environmental geometry has been shown to produce relational learning on multiple occasions (e.g., Gray et al., 2004; Kelly & Spetch, 2001). Although such differences in performance may be the result of differences in spatial information extracted from landmark arrays and environmental geometry (for a review see Cheng & Newcombe, 2005), the present results suggest that this difference may be the result of procedural factors. Such speculation concerning the critical role of procedural factors such as orienting cues in spatial strategies is consistent with recent studies that have found relational learning after single-exemplar training when eliminating orienting cues (Gray et al., 2004; Kelly & Spetch, 2001). Not surprisingly, others have argued for the importance of orienting cues in spatial coding (Gray & Spetch, 2006; Kelly & Spetch, 2001). For example, Gray and Spetch suggested that "…the availability of external cues may be an important determinant of how spatial information is coded" (p. 478).

In summary, the current results speak to the fact that the present apparatus and procedure created an extremely impoverished environment by eliminating or rendering useless numerous orientation cues usually present in previous studies of spatial cognition. Specifically, enclosing the entire arena, eliminating global orienting cues, rotating the apparatus between trials, rotating subjects prior to each trial, randomly selecting entrance and exit points, and using an array with ambiguous radial symmetry either eliminated or rendered useless experimental room cues, apparatus cues, magnetic cues, environmental shape, subjective inertial cues, and entrance or exit cues for determining orientation. Unlike numerous studies in which these types of orienting cue were held constant (Kamil & Jones, 1997, 2000; Jones et al., 2002; Spetch et al., 1996, 1997), the present study eliminated cues other than the landmark array for orientation. Presumably, in the absence of these external orientation cues pigeons were unable to form a stable frame of reference and, as a result, were unable to code the goal location in absolute terms. Thus, presence or absence of a stable frame of reference (as provided by an orienting cue) may be especially influential in determining how pigeons code spatial location. Experiment 2 was designed to address this issue.

III. EXPERIMENT 2

Results from Experiment 1 implicate the importance of numerous parameters involved in spatial coding strategies – especially relative spatial coding strategies. These include experimental room cues, apparatus cues, magnetic cues, environmental shape, subjective inertial cues, and entrance or exit cues. The purpose of Experiment 2 was to provide a stable frame of reference by introducing a select few of the orienting cues absent in Experiment 1 to determine their influence in spatial coding. If the aforementioned parameters are critical in providing a stable frame of reference, then the same subjects who showed evidence of relational learning (relative coding) in Experiment 1 may show item-specific learning (absolute coding) under these modified environmental conditions.

Method

Subjects, Apparatus, and Stimuli. The same two pigeons used in Experiment 1 served as subjects in Experiment 2. Pigeons were housed and maintained as in Experiment 1. The apparatus was the same as used in Experiment 1 with the exception that a black stripe (180 cm in length x 32 cm in width) was painted directly onto the curtain behind the North entrance/exit (side 9). As a result, the black stripe served as a cue indicating North within the experimental apparatus. Stimuli were the same as those used in Experiment 1 except that one landmark was painted yellow and the other blue. The yellow landmark was always placed 30 cm North of the goal location, and the blue landmark was always placed 30 cm South of the goal location (Figure 14). Landmarks were given distinct colors so that the array itself would also serve as an unambiguous source in determining orientation.

Preliminary Training and Training. Preliminary training and training were conducted following the same specifications as those used in Experiment 1 with two exceptions. First, prior to each trial, the entire apparatus was rotated to one of eight randomly determined positions (0º, 45°, 90º, 135º, 180º, 225°, 270º, 315º) with respect to the experimental room . The additional four positions not used in Experiment 1 (i.e., 180º, 225°, 270º, 315º) were required as an array with two distinct landmarks no longer exhibits ambiguous radial symmetry. Second, side 1 which was located directly opposite the orienting cue served as both the entrance and exit point for all trials. Thus, subjects entered and exited the apparatus from the same location for the duration of Experiment 2.

Testing. Testing was conducted identically to that of Experiment 1.

Determination of Search Locations. Search locations were determined the same as in Experiment 1.

Figure 14. Picture of the inside of the apparatus illustrating the orienting cue (black stripe) and different colored landmarks (yellow = North; blue = South) used in Experiment 2.

Results

Training

All pigeons completed training in the minimum number of goal-invisible/goal-absent trials (72). These trials were divided into six-trial blocks. Figure 15 shows mean search error collapsed across birds plotted by block. Search error remained stable below the 20 cm training criterion across blocks. This result was confirmed by a repeated measures ANOVA on mean search error with Block (1-12) as a factor and revealed no main effect, *F*(11, 121) = 1.39.

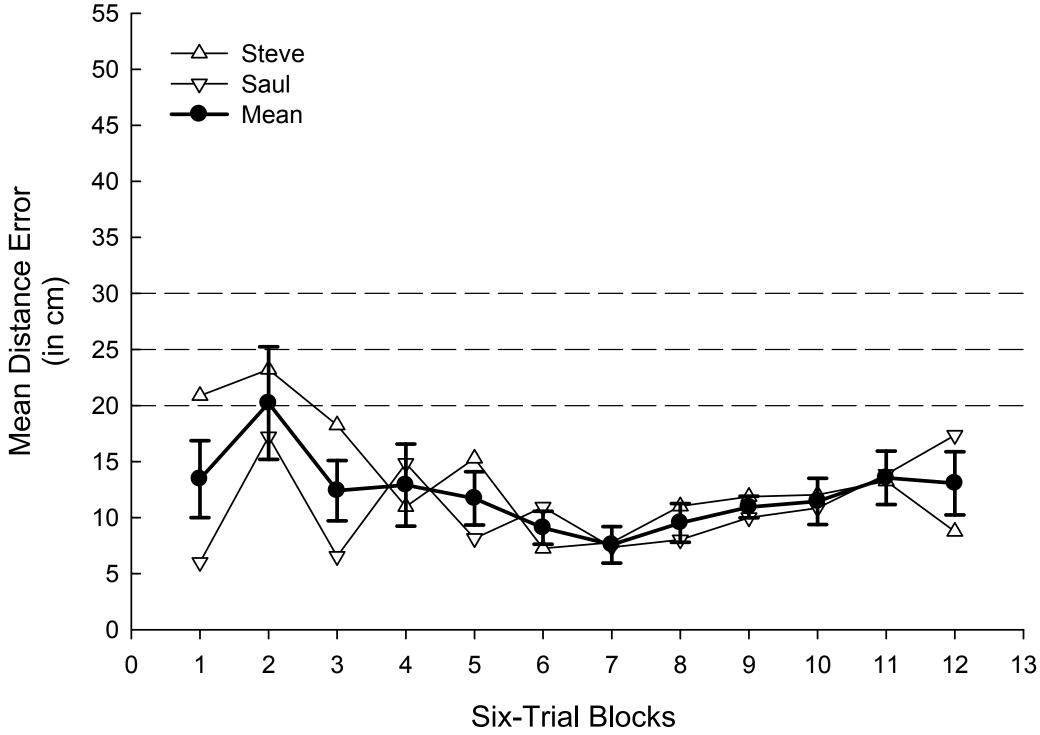


Figure 15. Mean total distance error (in cm) from the goal location on goal-invisible/goal-absent trials plotted across trial blocks for each bird (*unfilled symbols*) and averaged (filled symbols). Dashed lines indicate training performance criteria. Error bars represent standard errors of the mean.

Testing

As in Experiment 1, three separate analyses were used collectively as converging evidence to determine search strategy during testing and to differentiate use a vector-averaging strategy from use of geometric rule learning: 1) search error on baseline and transfer, 2) search error functions plotted across interlandmark distance, and 3) spatial distribution of searches.

Search Error: Baseline and Transfer. Performance on transfer compared to that of baseline was of primary interest. As in Experiment 1, equivalent mean search error on baseline and transfer trials at each tested interlandmark distance would provide evidence that pigeons had learned a geometric rule. However, differences in performance on baseline and transfer trials at tested interlandmark distance could indicate use of a vector-averaging strategy or fixed distance and direction from one or both landmarks. In either case, item-specific information would be used to determine search location. In an attempt to fully illustrate the search strategies used during testing, the error from the first 5 searches was used to indicate initial search strategy and error from all 60 searches was used to indicate the overall search strategy. Figure 16 shows mean search error on baseline and transfer trials collapsed across birds plotted by interlandmark distance for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). For the first 5 searches, baseline performance appeared different from transfer performance at interlandmark distances of 20 cm and 100 cm. Similarly, for all 60 searches, baseline performance appeared different from transfer performance at all novel interlandmark distances with the exception of 80 cm. Overall, baseline performance was different from transfer performance which suggested the learning of item-specific information. These results

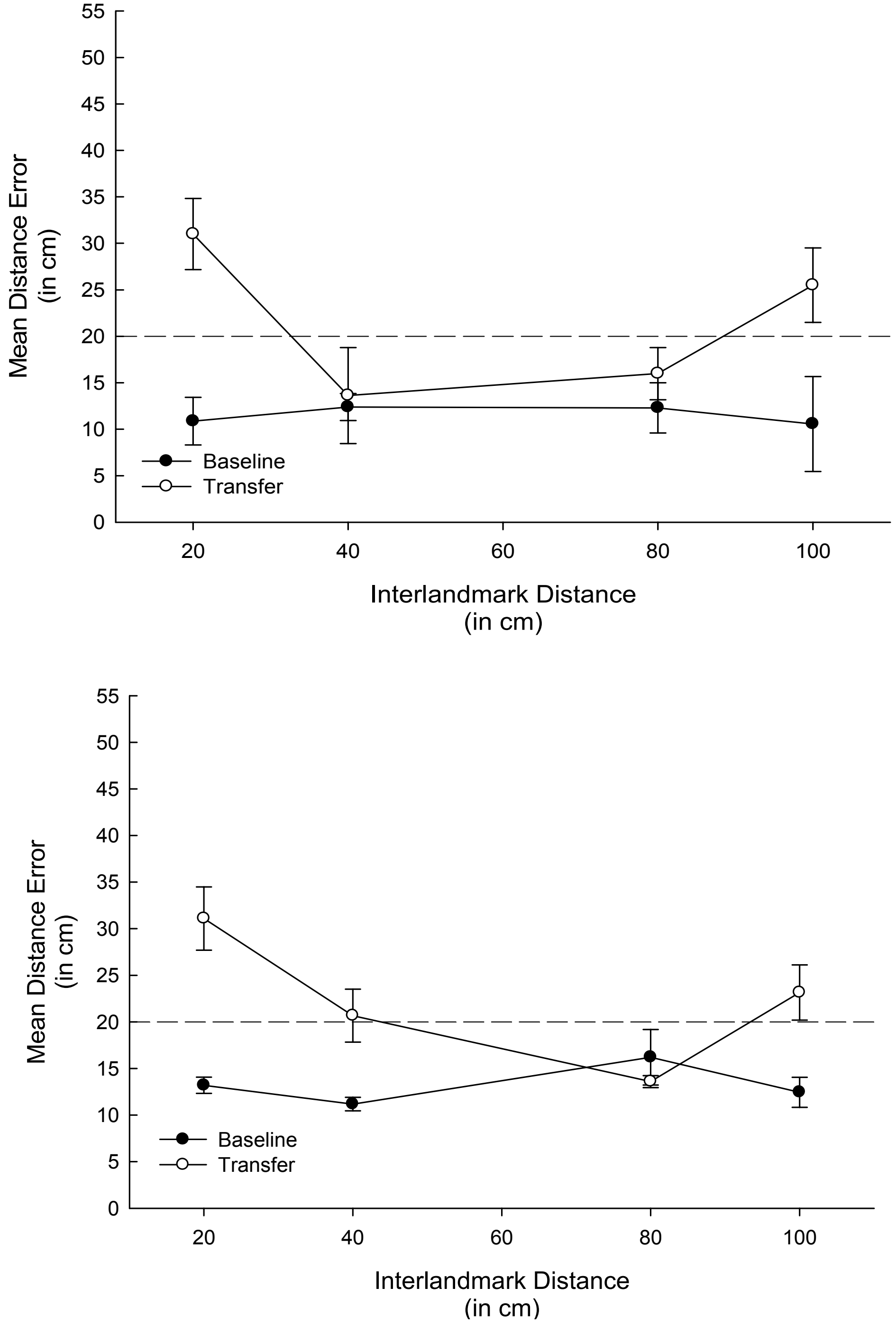


Figure 16. Mean distance error (in cm) from the goal location on baseline and transfer trials collapsed across birds plotted by interlandmark distance for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). Dashed line indicates the performance criterion required in training. Error bars represent standard errors of the mean. *Note*. Interlandmark distance was not manipulated for baseline trials and remained at 60 cm throughout testing and is plotted across interlandmark distance only for comparative purposes.

were confirmed by two separate repeated measures ANOVAs on mean search error with Type (baseline, transfer) and Interlandmark Distance (20 cm, 40 cm, 80 cm, 100 cm) as factors. Error from the first 5 searches revealed only a main effect of Type, $F(1, 5) = 36.69, p < .01$. The interaction was not significant. Error from all 60 searches revealed a main effect of Type, $F(1, 5) = 36.69, p < .01$, a main effect of Interlandmark Distance, $F(3, 15) = 4.2, p < .05$, and a significant Type x Interlandmark Distance interaction, $F(3, 15) = 6.5, p < .01$. In order to isolate the source of the interaction, planned comparisons were performed. Baseline performance was compared to transfer performance at each interlandmark distance. Significant differences between baseline and transfer performance were found at an interlandmark distances of 20 cm, $F(1, 5) = 41.19, p < .01$, 40 cm, $F(1, 5) = 8.38$, $p < .05$, and 100 cm, $F(1, 5) = 8.22, p < .05$. No significant difference was found at an interlandmark distance of 80 cm.

Search Error: Interlandmark Distances. To further distinguish use of a vector-averaging strategy from the use of a geometric rule, mean search error was plotted for each interlandmark distance. According to Biegler et al. (1999), use of a vector-averaging strategy should result in a V-shaped function, whereas use of a geometric rule should result in a linear function. Figure 17 shows mean search error collapsed across birds plotted by interlandmark distance for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). For the first 5 searches, there appears to be non-linear changes in search error across interlandmark distance. Similarly, for all 60 searches, search error differed in a non-linear fashion across interlandmark distance. These results were confirmed by two separate repeated measures ANOVAs on mean search error with Interlandmark Distance (20 cm, 40 cm, 60 cm, 80cm, 100 cm) as a factor. Error from the first 5 searches revealed

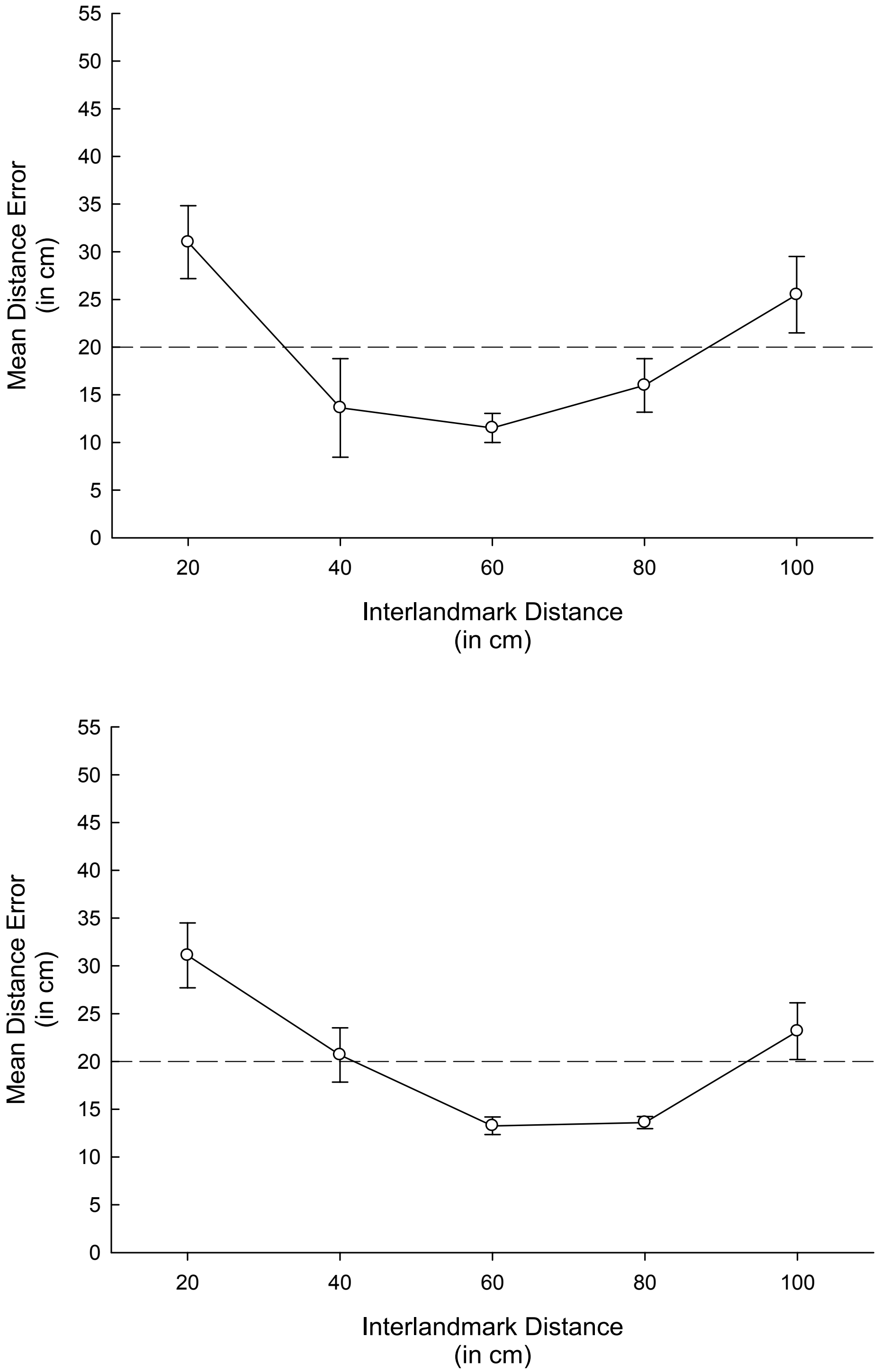


Figure 17. Mean distance error (in cm) from the goal location collapsed across birds plotted by interlandmark distance for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). Dashed line indicates the performance criterion required in training prior to testing. Error bars represent standard errors of the mean.

a main effect of Interlandmark Distance, $F(4, 20) = 4.39$, $p < .05$. A trend analysis revealed only a significant quadratic component, $F(1, 5) = 14.34$, $p < .05$, and post hoc tests were conducted to determine the differences across interlandmark distances and are shown in Table 3. Error from all 60 searches revealed a main effect of Interlandmark Distance, $F(4, 20) = 9.46$, $p < .001$. A trend analysis revealed only a significant quadratic component, $F(1, 5) = 50.87$, $p < .001$, and post hoc tests were conducted to determine the differences across interlandmark distances and are shown in Table 4.

Search Error: NS versus EW Axes. To determine the sources of error contributing to total search error and determine whether pigeons relied on directional information over distance information during testing, error was parsed into NS and EW error for each interlandmark distance. Figure 18 shows mean NS and EW search error collapsed across birds plotted by block for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). For both the first 5 searches and all 60 searches, NS error appeared to change non-linearly while EW error remained constant across interlandmark distance. These results were confirmed by two separate repeated measures ANOVAs on mean search error with Axis (NS, EW) and Interlandmark Distance (20 cm, 40 cm, 60 cm, 80 cm, 100 cm) as factors. While error from the first 5 searches revealed no main effects or interactions, error from all 60 searches revealed a main effect of Interlandmark Distance, $F(4, 20) = 8.09$, $p < .001$, and a significant Axis x Interlandmark Distance interaction, $F(4, 20) = 3.92$, $p < .05$. Custom contrasts were performed to isolate the source of the interactions and are shown in Table 5.

Table 3. *Post Hoc Tests for Each Interlandmark Distance for the First 5 Searches.*

Least-Squares-Difference (LSD) post hoc tests for each interlandmark distance (ILMD)

(I) ILMD	(J) ILMD	Mean Differences	(I-J)Standard Error	Significance
20 cm	40 cm	17.38	7.75	.075
	60 cm**	20.14	4.03	.004
	80 cm*	15.02	5.33	.037
	100 cm	5.51	6.28	.420
40 cm	20 cm	---	---	---
	60 cm	2.76	5.33	.627
	80 cm	-2.36	6.20	.720
	100 cm	-11.87	6.74	.139
60 cm	20 cm**	---	---	---
	40 cm	---	---	---
	80 cm	-5.12	2.61	.107
	100 cm	-14.63	5.75	.052
80 cm	20 cm*	---	---	---
	40 cm	---	---	---
	60 cm	---	---	---
	100 cm	-9.51	5.77	.160
100 cm	20 cm	---	---	---
	40 cm	---	---	---
	60 cm	---	---	---
	80 cm	---	---	---

Note. Single asterisk (*) indicates a significant difference at $p < .05$. Double asterisk (**) indicates a significant difference at $p < .01$. Triple asterisk (***) indicates a significant difference at $p < .001$.

Table 4. *Post Hoc Tests for Each Interlandmark Distance for the All 60 Searches.*

Least-Squares-Difference (LSD) post hoc tests for each interlandmark distance (ILMD)

(I) ILMD	(J) ILMD	Mean Differences	(I-J)Standard Error	Significance
20 cm	40 cm	10.42	4.19	.055
	60 cm***	17.89	2.79	.001
	80 cm**	17.49	3.40	.004
	100 cm	7.93	5.40	.202
40 cm	20 cm	---	---	---
	60 cm*	7.48	2.64	.037
	80 cm*	7.07	2.33	.029
	100 cm	-2.49	4.06	.567
60 cm	20 cm***	---	---	---
	40 cm*	---	---	---
	80 cm	-0.40	0.95	.692
	100 cm*	-9.97	3.12	.024
80 cm	20 cm**	---	---	---
	40 cm*	---	---	---
	60 cm	---	---	---
	100 cm*	-9.56	3.28	.033
100 cm	20 cm	---	---	---
	40 cm	---	---	---
	60 cm*	---	---	---
	80 cm*	---	---	---

Note. Single asterisk (*) indicates a significant difference at $p < .05$. Double asterisk (**) indicates a significant difference at $p < .01$. Triple asterisk (***) indicates a significant difference at $p < .001$.

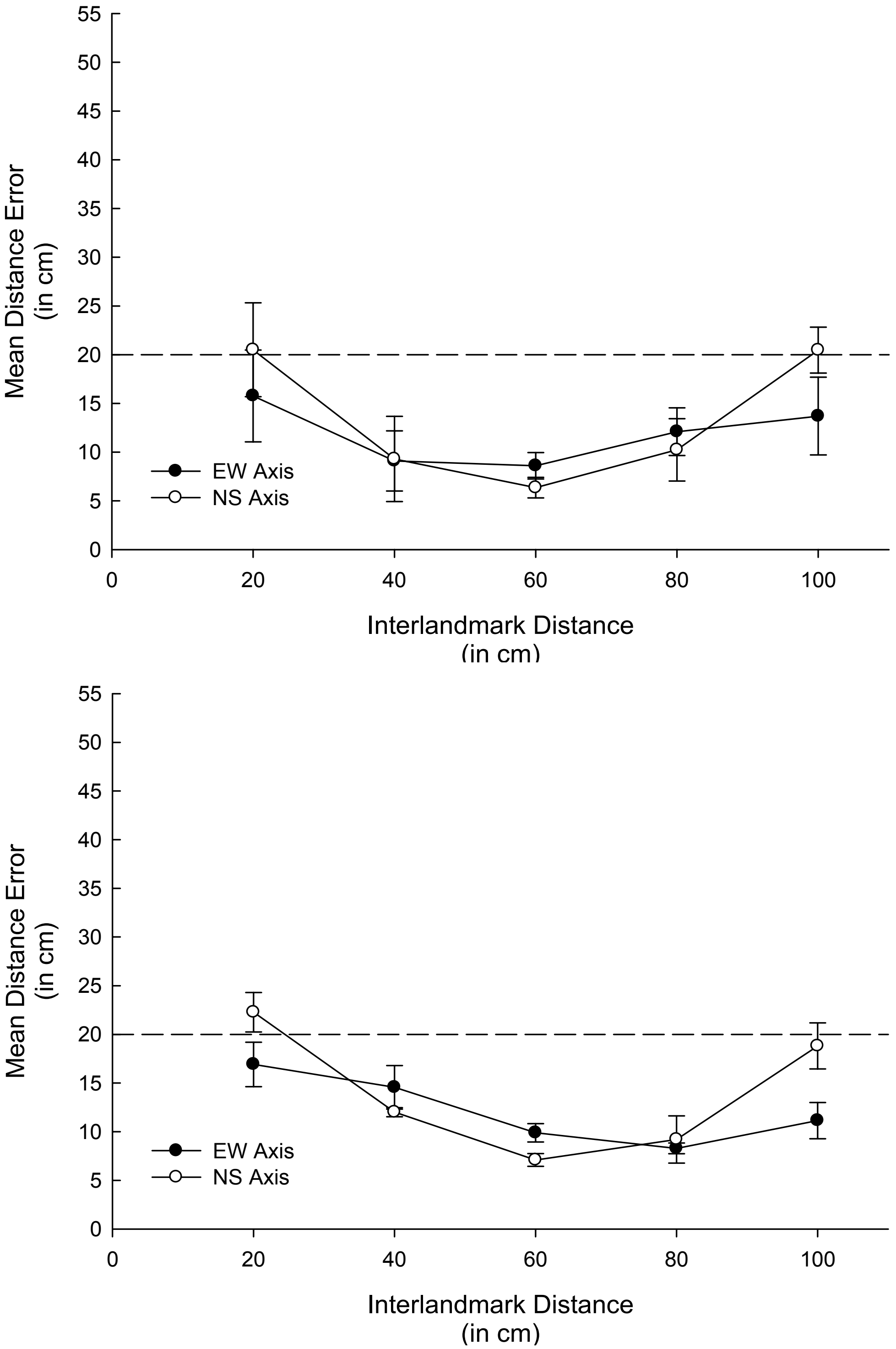


Figure 18. Mean distance error (in cm) from the goal location in the EW Axis and the NS Axis collapsed across birds plotted by interlandmark distance for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). Dashed line indicates the performance criterion required in training prior to testing. Error bars represent standard errors of the mean.

Table 5. *North-South (NS) and East-West (EW) Axis Comparisons for All 60 Searches.*

Custom Contrasts (p-values) for Interlandmark Distance Comparisons in the NS Axis

ILMD	20 cm	40 cm	60 cm	80 cm	100 cm
20 cm	---	.064	.013*	.030*	.489
40 cm		---	.042*	.257	.033*
60 cm			---	.022*	.005**
80 cm				---	.022*
100 cm					---

Custom Contrasts (p-values) for Interlandmark Distance Comparisons in the EW Axis

ILMD	20 cm	40 cm	60 cm	80 cm	100 cm
20 cm	---	.262	.028*	.013*	.171
40 cm		---	.092	.024*	.368
60 cm			---	.126	.615
80 cm				---	.229
100 cm					---

Note. Single asterisk (*) indicates a significant difference at $p < .05$. Double asterisk (**) indicates a significant difference at $p < .01$. Triple asterisk (***) indicates a significant difference at $p < .001$.

Spatial Distribution of Searches. To more fully illustrate pigeons' performance on transfer trials, Figure 19 shows the spatial distribution of all 60 searches at each novel interlandmark distance (i.e., 20 cm, 40 cm, 80 cm, 100 cm) collapsed across birds. Search distributions are centered at the goal location (0, 0). As shown, responding was unimodal and concentrated at a distance of 30 cm from the blue landmark for all of the novel interlandmark distances.

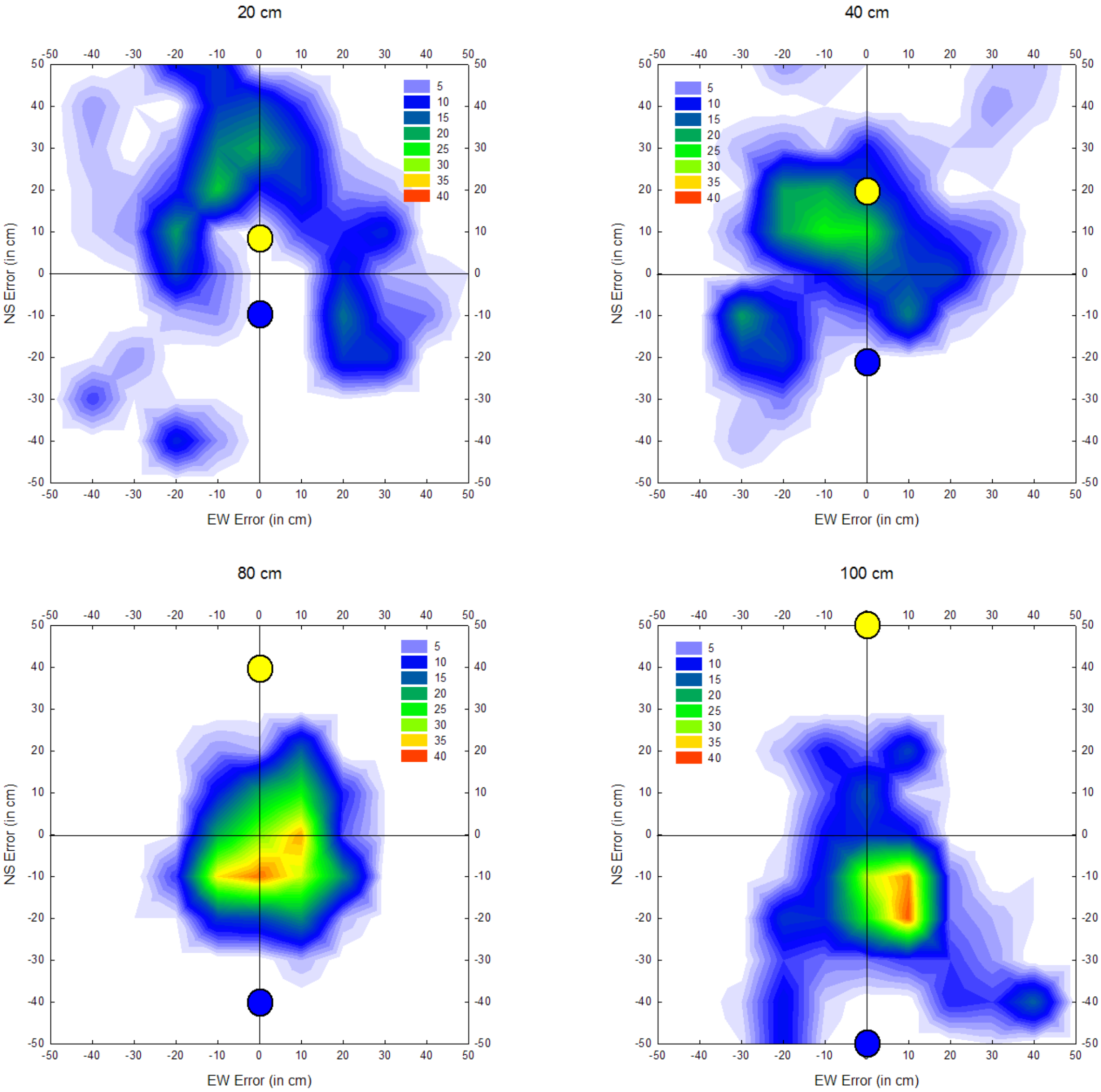


Figure 19. Cumulative spatial distribution of searches at each novel interlandmark distance: 20 cm (*top-left*), 40 cm (*top-right*), 80 cm (*bottom-left*), and 100 cm (*bottom-right*). Search distributions are centered at the goal location (0, 0).

Discussion

Despite the introduction of the orienting cue and novel landmarks, pigeons maintained relatively high levels of frequency and accuracy in locating the goal during training. Initial test performance (i.e., first 5 searches) indicated that search error on baseline and transfer were equivalent only at 40 cm and 80 cm, and overall test performance (i.e., all 60 searches) indicated that search error on baseline and transfer were significantly different at 20 cm, 40 cm, and 100 cm. Although these search error results suggest that pigeons may have initially used a geometric rule to solve the task, differences at extrapolated distances below (i.e., 20 cm, 40 cm) and above (i.e., 100 cm) that experienced during training (i.e., 60 cm) suggest use of a vector-averaging strategy. Importantly, spatial distributions indicated that search was not concentrated at the midpoint of novel interlandmark distances and instead was concentrated at roughly 30 cm North of the blue landmark. Thus, search error and location indicate that pigeons learned absolute distance in presence of the orienting cues.

Whereas relative distance was learned from the landmarks in the absence of orienting cues (i.e., Experiment 1), absolute distance was learned from the landmarks in the presence of orienting cues (Experiment 2). In combination, these data point to the importance of reference cues in spatial strategy formation. Although other researchers have suggested the importance of cue availability in determining how spatial information is coded (e.g., Gray & Spetch, 2006; Kelly & Spetch, 2001), the present results specifically implicate a stable frame of reference as critical in coding distance in absolute terms. Specifically, as global orientation could have been determined from either the black stripe or entrance/exit cues, pigeons may have been able to maintain a stable frame of reference. Not surprisingly, absolute strategies have been shown to dominate in well-oriented search spaces (Spetch et al., 1996, 1997).

Given the conditions of Experiment 2, another important question arises concerning how pigeons coded direction. Specifically, it is unknown whether pigeons coded direction in absolute or relative terms in an environment with a stable frame of reference. For example, pigeons could have coded goal direction using absolute bearings (i.e., direction was determined with respect to the orienting cue) or relative bearings (i.e., direction was determined with respect to the landmark array). Visual inspection of the contour plots suggests that pigeons were relying exclusively on the blue landmark during transfer tests of Experiment 2 as searches were concentrated at roughly 30 cm North of this landmark on all transfer trials. An inability to code distance and direction from the yellow landmark would prove problematic in accounting for pigeons' search behavior by a mechanism that codes multiple landmark-to-goal bearings (i.e., multiple-bearings hypothesis).

Fortunately, the source of the directional information can be revealed through rotational manipulations of the landmark array. If subjects were using the environment in determining directional information (absolute bearings), then rotations of the array (90º clockwise, 90º counter-clockwise, and 180º) will no longer result in search concentrated along the line connecting the landmarks. Instead searches would be concentrated in the appropriate cardinal direction from one or both of the individual landmarks (i.e., North of the blue landmark and/or South of the yellow landmark). In contrast, if subjects were using array geometry to determine directional information (relative bearings), then rotations of the array would continue to result in concentrated search along the line connecting the landmarks. However, it is possible that pigeons would not rely exclusively on absolute or relative bearings and perform similarly to nutcrackers who showed evidence of using absolute bearings with small (i.e., 90º clockwise, 90º counter-clockwise) rotations and relative bearings with a large (180º) rotation of the array (Kamil & Jones, 2000).

Experiment 3 was designed to determine whether pigeons relied on absolute and/or relative bearings by testing them with rotations of the landmark array. These rotational tests were conducted in both the presence and absence of the black stripe to fully explore the sources of the directional information and determine the influence of the orienting cue in pigeons’ spatial strategies. For example, pigeons may show use of absolute bearings in the presence of the cue but relative bearings in its absence. Alternatively, pigeons may show use of absolute or relative bearings exclusively and hence have equivalent performance in both the presence and absence of the cue.

IV. EXPERIMENT 3

Method

Subjects, Apparatus, and Stimuli. The same two pigeons used in Experiments 1 and 2 served as subjects in Experiment 3. Pigeons were housed and maintained as in Experiments 1 and 2. The apparatus and stimuli were the same as used in Experiment 2 with the exception that the curtain containing the black stripe was replaced with a plain white curtain on test trials in which the cue was absent so that all curtains were identical.

Testing. Upon completing Experiment 2, pigeons were immediately tested with three types of rotations of the array (90º clockwise, 90º counter-clockwise, and 180º) each presented in the presence and absence of the black stripe (cue). As a result, there were a total of 6 unique combinations. Each combination was presented twice during Testing for a total of 12 rotational test trials. Testing consisted of a container-visible warm-up trial prior to the presentation of 4 food-present training trials, 1 food-absent training (baseline) trial, and 1 food-absent test (rotation) trial. The trial location of the food-absent trials was quasi-randomly determined within each session. For each test trial, one of the six unique rotational combinations was randomly selected without replacement until each rotational combination had been presented. An interlandmark distance of 60 cm was used for all trials during Experiment 3 (including test trials).

Determination of Search Locations. Search locations were determined as described in Experiment 1.

Results

Testing

Search Error. Performance on test trials compared to that of baseline trials was of primary interest. Such a comparison served to indicate the source of the directional information used to determine goal location. Specifically, equivalent mean search error on baseline and rotational tests (with and without the presence of the cue) would provide evidence that pigeons learned the geometric relationship of the landmark array. Importantly, this would also indicate that pigeons' searches were controlled by the array for orientation and either ignored or failed to encode information about the black stripe. In contrast, differences in performance on baseline and test trials would indicate pigeons' searches were controlled by the black stripe and either ignored or failed to encode the geometric relationship of the landmark array. Figure 20 shows mean search error collapsed across birds and rotation type plotted by trial type (i.e., baseline, cue present, cue absent) for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). Performance on rotational tests (both in the presence and absence of the cue) was identical to baseline performance and suggests pigeons learned the geometric relationship of the landmark array. These results were confirmed by two separate repeated measures ANOVAs on mean search error with Type (baseline, cue present, cue absent) as a factor, and neither revealed any significant effects. This suggests that pigeons used the landmark array itself for determining orientation. As such, it also suggests that pigeons either ignored the conspicuous orienting cue (black stripe) during rotational tests or failed to encode any information about it.

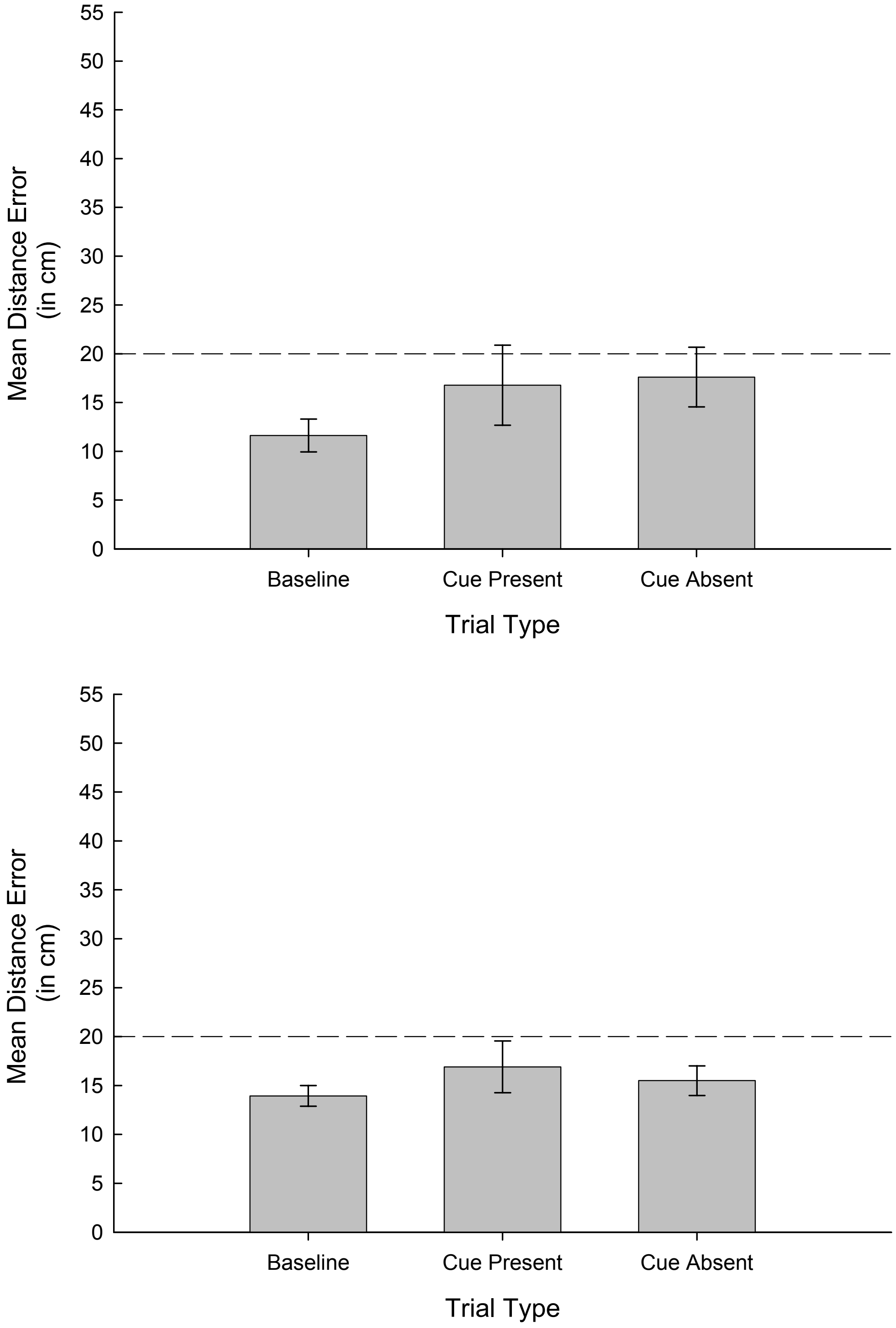


Figure 20. Mean distance error (in cm) from the goal location collapsed across birds and rotation type plotted by trial type for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). Dashed line indicates the performance criterion required in training. Error bars represent standard errors of the mean.

Spatial Distribution of Searches. To more fully illustrate performance on rotational test trials, Figure 21 shows the spatial distribution of searches for each rotational test (i.e., 90º clockwise, 90º counter-clockwise, and 180º) both in the presence (*left column*) and absence (*right column*) of the cue collapsed across birds. Search distributions are centered at the goal location (0, 0). As shown, responding was mostly unimodal and concentrated at or near the goal location for all rotational tests.

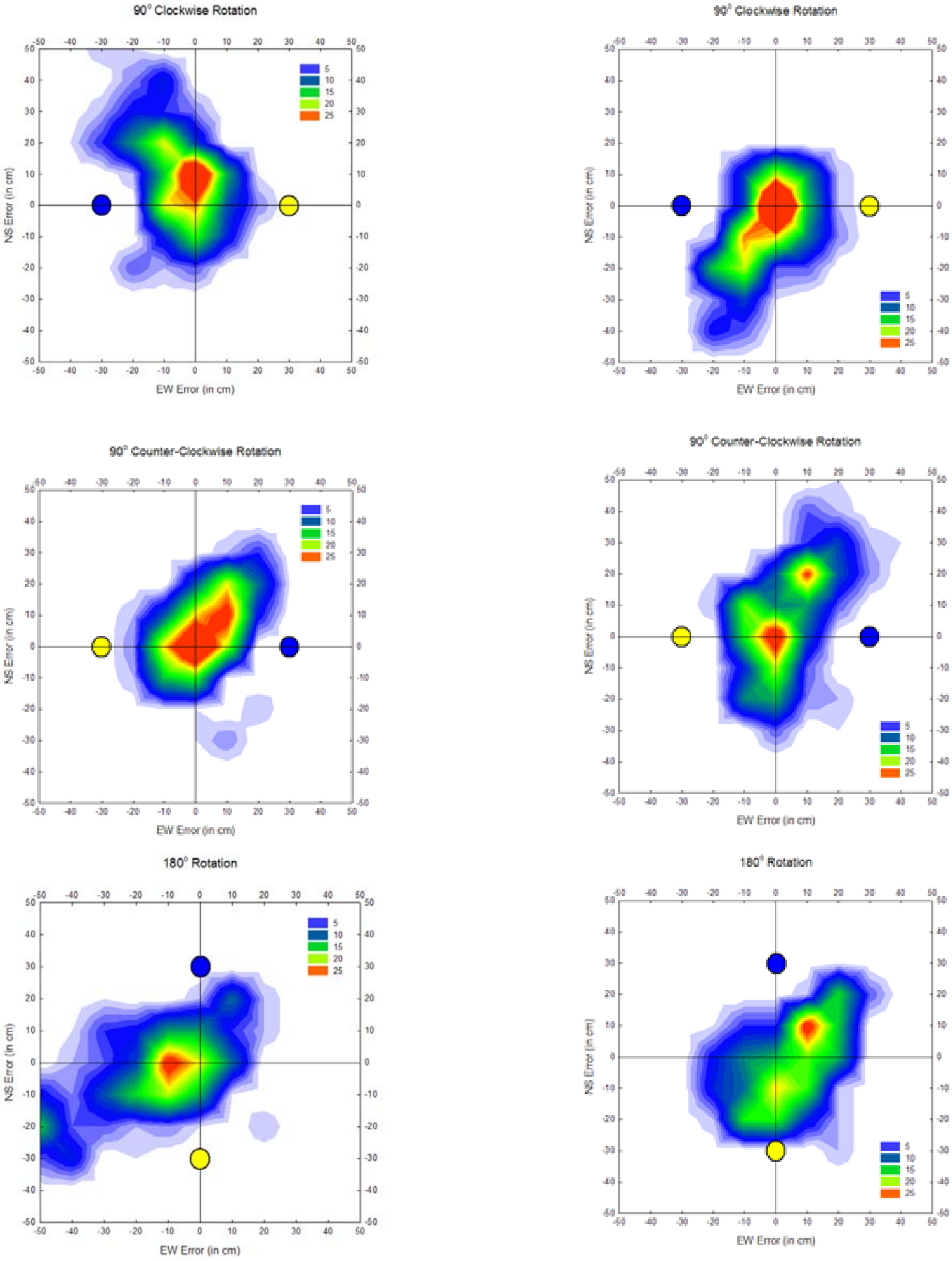


Figure 21. Cumulative spatial distribution of searches at each test rotation when the cue was present (*left column*) and absent (*right column*): 90º clockwise (*top row*), 90º counter-clockwise (*middle row*), and 180º (*bottom row*). Search distributions are centered at the goal location (0, 0).

Discussion

Search performance was unaffected by rotational manipulations of the landmark array or presence/absence of the black stripe as search error on all rotational tests was equivalent to that of baseline trials and search location was concentrated at the goal location across all rotations of the array regardless of cue presence/absence. These results support an interpretation that pigeons learned the geometric relationship between the landmarks and coded location in relative terms; pigeons used the landmark array itself as the source of directional information. As a result, equivalent performance in the presence versus absence of the cue is not surprising given that it was not used to determine orientation.

Results from Experiment 3 demonstrate that pigeons relied on the relationship between the landmarks to determine goal direction. Use of the landmark array for determining direction is consistent with comparative research with both gerbils (*Meriones unguiculatus*) and nutcrackers (Collet, Cartwright, & Smith, 1986; Kamil & Jones, 2000). Specifically, gerbils' searches were concentrated at the appropriate goal location during 180º rotational tests when trained with multiple orientations of a linear two-landmark array (Collet et al., 1986), and nutcrackers responded in a similar manner during the 180º rotational tests performed by Kamil and Jones (2000, Experiment 3). However, it should be noted that although this relative coding of direction by pigeons is consistent with the performance of these species, both pigeon and gerbil performance is inconsistent with the same nutcrackers' performance on 90º clockwise and 90º counter-clockwise rotation tests. On the 90º clockwise and 90º counter-clockwise rotation tests, nutcrackers used absolute cardinal direction to determine goal direction evidenced by both their failure to continue to search along the line connecting the landmarks and their concentrated searches North and South of the appropriate landmarks (Kamil & Jones, 2000, Experiment 3). Thus, while nutcrackers showed evidence of coding direction both in absolute and relative bearings, pigeons in the present experiment coded direction exclusively by relative bearings. Importantly, however, these species difference could also be due to procedural factors as nutcrackers were not trained with multiple rotations of the array (like gerbils) and did not have previous training in the absence of orienting cues (like the pigeons in the present experiments).

Although results from Experiment 3 suggest that pigeons relied exclusively on relative bearings, absence of evidence for absolute coding in the presence of the cue raises important questions about what was learned (if anything) about the orientation cue and landmark colors. Specifically, initial training in the absence of an orienting cue with identical landmarks may have prevented pigeons from learning any spatial information about the orienting cue or landmark colors once they became available. As a result, pigeons may have simply treated the landmark array as a configuration without learning anything about the orienting cue or the individual landmarks composing the array. Experiment 4 was designed to assess this possibility.

V. EXPERIMENT 4

Although Experiment 3 suggested that pigeons used directional information from the yellow landmark, it is also possible that pigeons did not learn any information about the individual landmark colors and exclusively relied on information from the array. Such learning would explain the absence of evidence for the use of absolute bearings during rotational tests in the presence of the black stripe (Experiment 3). However, even if pigeons learned to discriminate the landmark colors, failure to learn spatial information about the black stripe would also result in reliance on relative bearings. Thus, it is unclear whether results of rotational tests were due to preferential use of relative bearings or an inability to use absolute bearings because the relevant information about the landmarks or black stripe was not learned. Specifically, initial training in the absence of orienting cues and identical landmark colors (i.e., Experiment 1) may have prevented pigeons from learning additional information about the orienting cue or the distinctness of the landmark colors. Unfortunately, to complicate matters further, pigeons may have learned information about the orientation cue but simply ignored this source of information during the rotational tests.

Fortunately, single landmark tests can be conducted to provide further information concerning the nature of distance and direction information extracted from both landmarks. Thus, the purpose of Experiment 4 was to determine whether pigeons encoded information about the black stripe and landmark colors by presenting each landmark from the array individually in both the presence and absence of the cue. Such manipulations would not only reveal if pigeons learned information about the black stripe and landmark colors but also reveal if pigeons coded distance information from the yellow landmark. Specifically, if pigeons encoded information about the black stripe and were able to use it as a source of directional information and learned about individual landmark colors (and hence, distance and direction to the goal location), then searches on single landmark tests with this cue present should be more accurate (with respect to both search error and location) than searches with this cue absent. However, if no information was encoded about the black stripe or the individual landmark colors, search performance should be identical in both the presence and absence of the cue and deficient with respect to baseline. In addition, poor performance on single-landmark tests could also result not from a failure to encode information about the black stripe or individual landmarks but because pigeons relied exclusively on the array as a configuration. It follows that if pigeons only learned the landmarks as a configuration, performance on all single landmark tests (both in the presence and absence of the black stripe) should be identical and deficient with respect to baseline.

Method

Subjects, Apparatus, and Stimuli. The same two pigeons used in Experiments 1-3 served as subjects in Experiment 4. Pigeons were housed and maintained as in the previous experiments. The apparatus and stimuli were the same as used in Experiment 3.

Testing. Upon completing Experiment 3, pigeons were immediately tested with two types of single landmarks tests (yellow only and blue only) each presented in both the presence and absence of the black stripe (cue). As a result, there were a total of 4 unique combinations. Each combination was presented twice during Testing for a total of 8 single-landmark test trials. Testing consisted of a container-visible warm-up trial prior to the presentation of 4 food-present training trials, 1 food-absent training (baseline) trial, and 1 food-absent test (single-landmark) trial. The trial location of the food-absent trials was quasi-randomly determined within each session. For each test trial, one of the four unique single-landmark combinations was randomly selected without replacement until each single-landmark combination had been presented. An interlandmark distance of 60 cm was used for all trials in which two landmarks were present. For single-landmark tests, the position of the goal location and landmarks were determined as specified in Experiment 2 and then the appropriate landmark was removed from the apparatus for each respective single-landmark test.

Determination of Search Locations. Search locations were determined as described in Experiment 1.

Results

Testing

Search Error. Performance on test trials compared to that on baseline trials was of primary interest. Such a comparison served to indicate the nature of the information (if any) learned about the orienting cue and the individual landmarks. Specifically, if pigeons encoded information about the landmarks and cue but simply ignored this information during the rotational tests of Experiment 3, then performance on single landmark tests would be better when the cue is present than when the cue is absent. However, if pigeons failed to encode information about the cue, then performance on single landmark tests would be identical in both the presence and absence of the cue.

Figure 22 shows mean search error collapsed across birds and landmark type plotted by trial type (i.e., baseline, cue present, cue absent) for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). Performance on single landmark tests was different from baseline performance and affected by the presence or absence of the cue. These results were confirmed by separate repeated measures ANOVAs on mean search error with Type (baseline, cue present, cue absent) as a factor. The ANOVA on the first 5 searches revealed a main effect, $F(2, 14) = 5.16, p < .05$. Likely due to variability, Fisher's least significant difference (LSD) tests only revealed that error on baseline trials was significantly less than error on cue absent trials ($p < .05$). However, as shown, the trend in search error for the first 5 searches is the same as that for all 60 searches, and the ANOVA for all 60 searches also revealed a main effect, $F(2, 14) = 14.62, p < .001$, and Fisher's LSD tests revealed that error on baseline trials was significantly less than error on both cue present ($p < .05$) and cue absent ($p < .001$) trials. Additionally, error on cue present trials was significantly less than error on cue absent trials ($p = .05$).

Spatial Distribution of Searches. To more fully illustrate performance on single-landmark test trials, Figure 23 shows the spatial distribution of searches for each single-landmark test (i.e., yellow only + cue present, yellow only + cue absent, blue only + cue present, blue only + cue absent) collapsed across birds. Search distributions are centered at the landmark (0, 0). As shown, responding was unimodal and concentrated at or near the goal location when the cue was present but multimodal and roughly 30 cm from the landmark in various directions when the cue was absent.

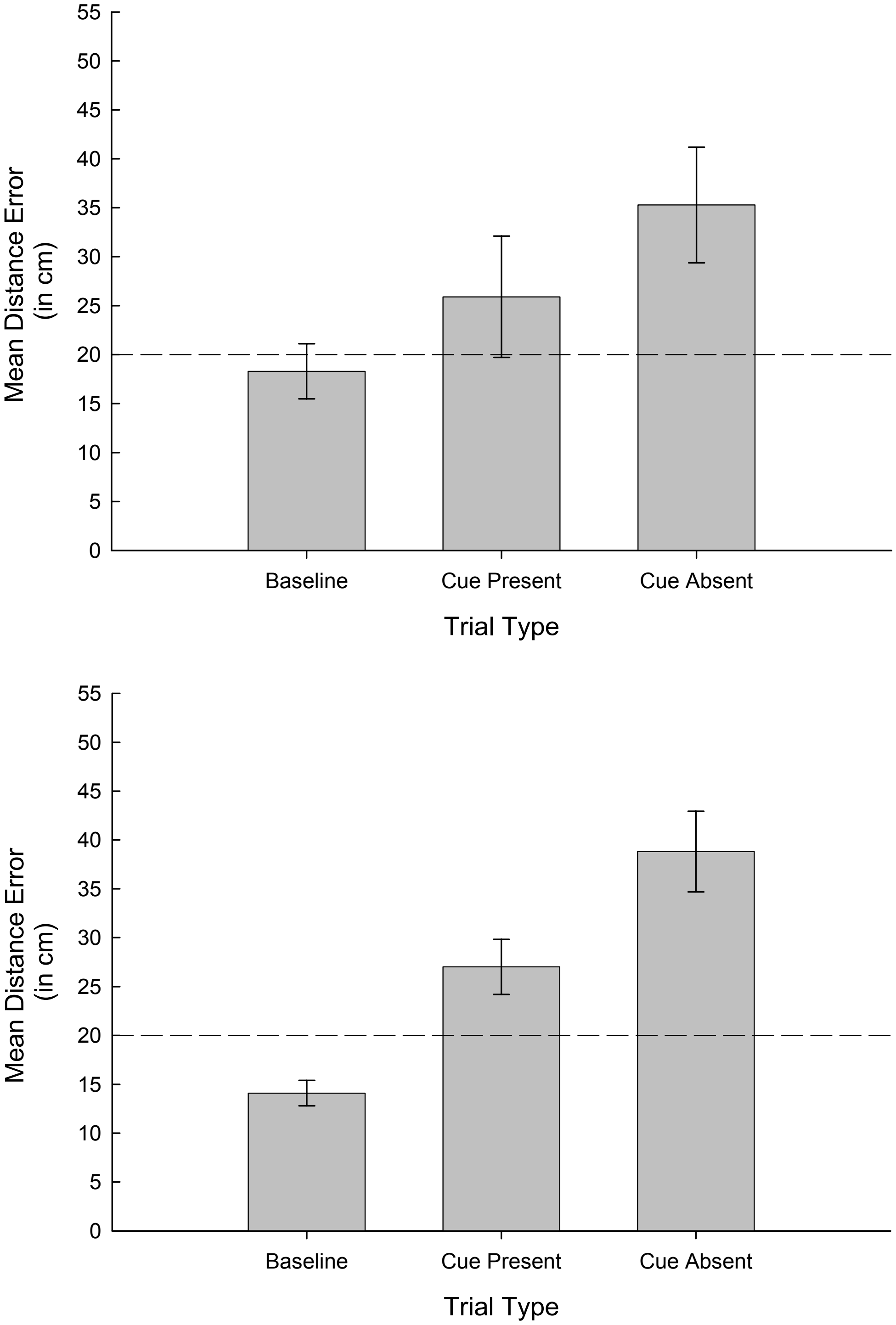


Figure 22. Mean distance error (in cm) from the goal location collapsed across birds and landmark type plotted by trial type for the first 5 searches (*top panel*) and all 60 searches (*bottom panel*). Dashed line indicates the performance criterion required in training. Error bars represent standard errors of the mean.

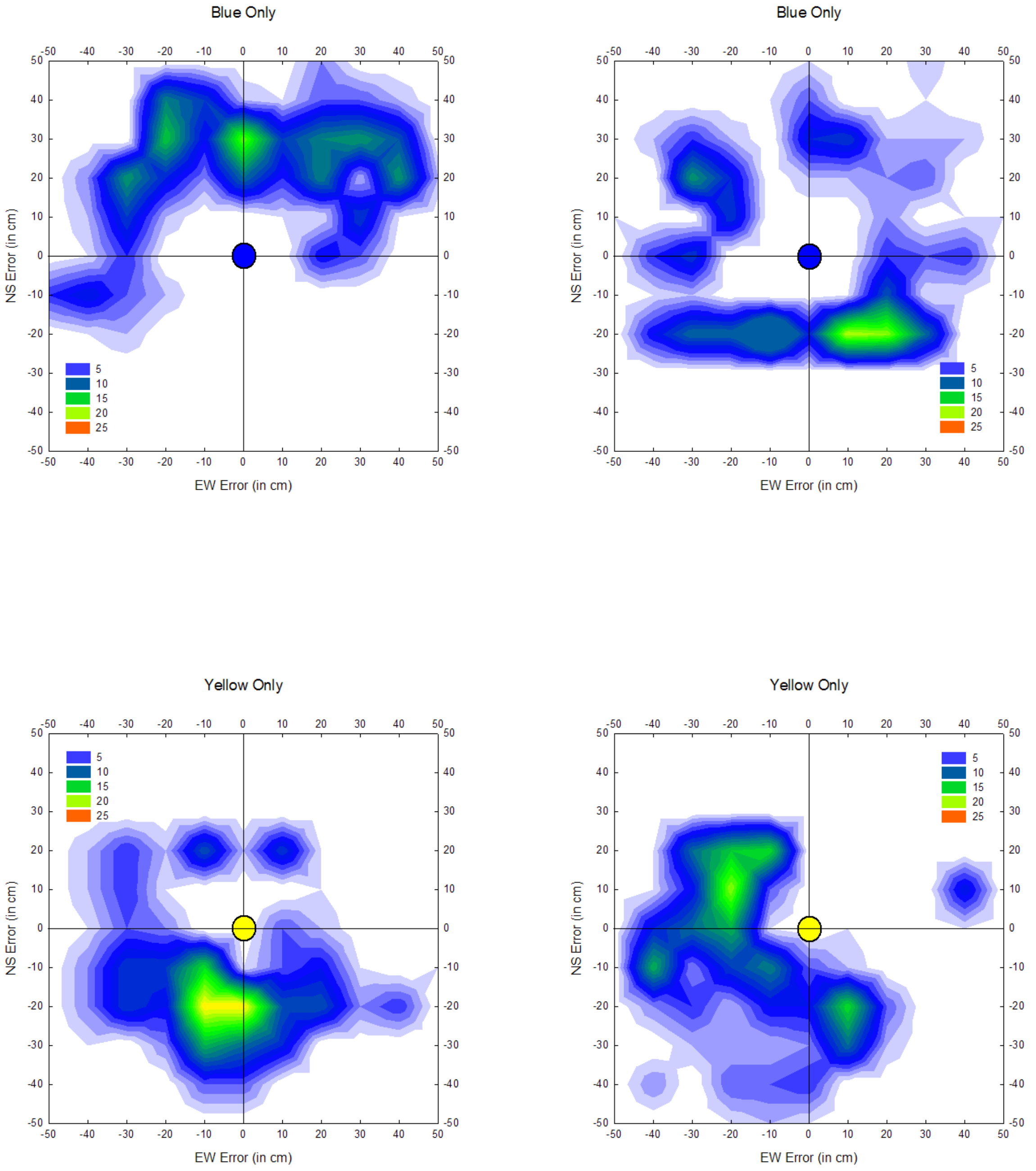


Figure 23. Cumulative spatial distribution of searches for each single landmark when the cue was present (*left column*) and absent (*right column*): yellow only (*top row*), blue only (*bottom row*). Search distributions are centered at the landmark (0, 0).

Discussion

In the presence of a single landmark, mean search error was lower when the cue was present than when the cue was absent and search location was concentrated in the appropriate direction only when the cue was present. Interestingly, this suggests that pigeons had encoded information about the orienting cue and distance and direction of the goal from both landmarks but ignored these sources of directional information during the rotational tests of Experiment 3. Such a result is especially interesting because despite training with identically colored landmarks in Experiment 1, pigeons were able to discriminate the color of the landmarks evidenced by the concentration of searching in the appropriate cardinal direction in the presence of the cue. In other words, learning a landmark array with identically colored landmarks did not prevent the pigeons from later discriminating between the two landmarks once they differed with respect to this attribute. Moreover, mean search error during single landmark tests with the cue present was greater than mean search error on baseline trials. This decrement in performance with the removal of one of the landmarks from the array is consistent with results obtained with nutcrackers (Kamil et al., 2001) and suggests that pigeons also relied on information from both landmarks for accurate goal localization.

Evidence that pigeons relied on information from both landmarks has important implications for the applicability of the multiple-bearings hypothesis to the pigeons' navigational strategies. As both landmarks were used in locating the goal, present results are also consistent with those obtained with pigeons by Sutton (2002) and support her conclusion that pigeons may be capable of using the same or a similar mechanism as nutcrackers that relies on multiple landmark-goal bearings.

Results from Experiment 4 are also reminiscent of studies documenting latent learning (for a review see Davidson, 2000) in the sense that learning about the black stripe and individual landmarks was not evident in the rotational tests of Experiment 3 but was only revealed when environmental conditions were modified (i.e., single landmark tests). Such a result indicates that initial training did not prevent pigeons from learning information about the orienting cue (black stripe) and landmarks once they became available and have important wide-spread implications for learning/performance distinctions with respect to landmark-based navigation.

Single-landmark tests unequivocally revealed that pigeons encoded spatial information from the both the black stripe and individual landmarks. These tests were crucial in illustrating the multiple spatial cues encoded by the pigeons that would have otherwise gone undetected. Such rich coding of spatial information on the part of the pigeon naturally raises questions about competition among these spatial cues. For example, it remains unclear whether control by the landmark array and the black stripe competed for control of search behavior in the rotational tests of Experiment 3. Although a group of pigeons receiving training in opposite order from that experienced by subjects in the present experiments is required to make definitive statements concerning cue competition, it appears that initial learning about the landmark array when composed of identically colored landmarks in the absence of an orienting cue did not block or overshadow later learning about the black cue or distinct landmark colors. At first blush, such a result would have important implications for recent research suggesting that spatial learning can be accounted for by the same mechanisms as that of classical and instrumental conditioning as it has revealed evidence of blocking and overshadowing in the spatial domain (e.g., Cheng & Spetch, 2001; Chamizo, Aznar-Casanova, & Artigas, 2003; Jacobs, Laurance, & Thomas, 1997; Rodrigo et al., 1997; Sawa, Leising, & Blaisdell, 2005; Spetch 1995).

VI. GENERAL DISCUSSION

As transfer performance was equal to baseline performance at nearly all interlandmark distances in Experiment 1, the present results suggests that pigeons learned the relative relationship (*halfway*) between the landmarks with only a single training example. Such a result is in stark contrast to other studies within (e.g., Jones et al., 2002; Kamil & Jones, 1997, 2000) and beyond (e.g., Katz & Wright, 2006; Katz et al., 2002; Wright et al., 2003) the spatial domain requiring multiple training examples to produce relational learning. However, although this is the first known evidence of single exemplar training resulting in relational learning with discrete visual landmarks, it is not the first time a single exemplar training has resulted in relational learning in the spatial domain. With respect to environmental geometry, both chickens (Tommasi, Vallortigara, & Zanforlin, 1997) and pigeons (Gray et al., 2004; Kelly & Spetch, 2001) have been shown to search in the center of expanded, contracted, and novel environmental shapes after training with only a single environmental shape.

Although this difference raises important questions concerning the nature of spatial information extracted from environmental geometry and that extracted from landmark arrays, it also raises important questions concerning the nature of the training environment. Specifically, Kelly and Spetch (2001) suggested that the success of pigeons to demonstrate relative encoding of environmental shape after single exemplar training in their barren environment may have been due to the fact that geometric shape was the only source of information available for orientation. In addition, they speculated that the failure of pigeons in previous studies (Spetch et al., 1996, 1997) to demonstrate relative encoding of landmark arrays after single exemplar training may be due to the fact that numerous extraneous cues were available that could have been used to determine a directional heading. Furthermore, they suggested that such a stable frame of reference may facilitate absolute encoding. Present results support such speculation as pigeons in the present experiments used the landmark array itself to determine orientation when the training environment was devoid of orienting cues.

Presumably, in an environment devoid of orienting cues (as in Experiment 1), pigeons would not need to learn to ignore irrelevant sources of direction or distance information. Not surprisingly, Kamil and Jones (2000) commented on the importance of ignoring irrelevant information with respect to the performance of their nutcrackers in the middle-rule search task, “What may be most impressive is not what stimuli come to control the animal's search behavior, but rather how many aspects of the situation the animal learns to ignore (pg. 452)”. Such speculation is at least consistent with that suggested by Kelly and Spetch (2001) and Gray and Spetch (2006) in that access to external cues may play a prominent role in how spatial information is coded. Certainly, an inability to ignore irrelevant cues would explain previous studies of landmark-based navigation in which pigeons almost exclusively coded location with respect to absolute distance and direction.

In summary, the present results show that pigeons are capable of encoding relative distance and direction from two discrete visual landmarks in an environment devoid of orienting cues after single exemplar training. In such a disorienting environment, increases or decreases of the interlandmark distances resulted in continued search by pigeons in the middle of the array. Although changes to the apparatus and procedure from Experiment 1 to Experiment 2 make it difficult to determine which specific variable(s) was (were) the most critical, these changes certainly specify a select few for the focus of future research. Not surprisingly, when the environment was no longer devoid of orienting cues, pigeons relied on absolute distance from the landmarks. Surprisingly, however, this absolute encoding did not prevent pigeons from using relative bearings from the landmark array during rotational tests. Perhaps even more surprisingly, orientation by the array did not prevent pigeons from learning elemental information about each individual landmark which was revealed during single landmark tests. As such, the present results have important implications for a learning/performance distinction with respect to the landmark-based navigation and for classical and instrumental accounts of spatial learning.

Taken collectively, the current results offer evidence for greater flexibility in pigeons' navigational strategies than revealed by previous research as they were shown to code location from multiple landmarks using both absolute and relative distances and directions. These results offer further support for the conclusions that distance and direction are coded independently (Cheng, 1994) and that spatial coding is based on metric relations (Gallistel, 1990). Furthermore, an ability to code location from multiple landmarks using both absolute and relative direction suggests that pigeons are capable of coding location in a manner consistent with that proposed by the multiple-bearing hypothesis (Kamil & Cheng, 2001) as suggested previously by Sutton (2002).

Such conclusions have important implications for investigating and accounting for the search strategies of pigeons. Specifically, if pigeons search by a mechanism that codes multiple landmark-to-goal bearing (as suggested by present results and Sutton, 2002), the area of locational uncertainty defined by the intersection of multiple bearings may play a prominent role in the process of determining search location. For example, in the present study, coding location only in absolute bearings would result in two separate (and equally probable) potential areas for the goal location during the rotational tests of Experiment 3. Presumably, it is quite costly (in terms of both time allocation and physiological resources) to search at multiple locations during times of uncertainty. Perhaps more problematic, such uncertainty would increase exponentially with the introduction of additional landmarks. For example, an array composed of three landmarks will result in six possible goal locations in need of search if only rotated by 60º. Any mechanism that could reduce this uncertainty would seem to serve an extremely adaptive advantage. Specifically, if location is coded as the intersection of multiple landmark-goal bearings (as suggested by the multiple-bearings hypothesis), then search effort during rotational tests (or in approaching an array from a novel orientation) will be substantially reduced as the number of possible goal locations is drastically reduced. For example, in the present experiment, use of such a strategy would reduce the number of possible goal locations by half.

In conclusion, the present results add to a growing body of literature suggesting flexibility in the spatial coding strategies of pigeons. Importantly, this evidence of such flexibility has emerged due to recent efforts to explicitly manipulate important procedural factors (e.g., Gray & Spetch, 2006; Gray et al., 2004; Kelly & Spetch, 2001). Such a research approach should prove invaluable in identifying necessary and sufficient conditions to determine how spatial information is coded. Ultimately, this approach should continue to advance an understanding of the mechanisms underlying these navigation strategies in pigeons and illuminate their similarities and differences to those used by other mobile organisms.

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