

Landmark-Based Search Memory in the Domestic Dog (*Canis familiaris*)

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Recent studies have suggested that any animal that relies on landmark-based search memory encodes and uses metric properties of space to navigate. So far, however, metric information provided by landmarks has been predominantly investigated in avian species. In the present study, I investigated whether the domestic dog (*Canis familiaris*), a mammalian species, encodes the distance and direction from landmarks. Dogs were trained to find a ball hidden next to an array of two distinct landmarks that remained at a constant location in a room from trial to trial. After training, the dogs were occasionally tested on unrewarded conditions where the array was either left in its usual position or shifted laterally, perpendicularly, or diagonally relative to the rear wall of the room. Although the dogs significantly shifted their search as a function of the displacement of the landmarks, they did not search at the predicted coordinates of the goal relative to the shift of the landmarks, suggesting that the global cues available in the testing room were also encoded and used by dogs to locate the position of the goal.

Keywords: landmark, distance, direction, global cues, domestic dogs

Returning to a site visited before is one of the most widespread spatial problem encountered by animals for survival. The site might be a home, a food cache, a hunting territory, a route, and so forth. Among the diverse mechanisms available to animals for solving this kind of spatial problem, the use of visual landmarks is a very common strategy. An efficient method to demonstrate that visual landmarks control an animal's search behavior is to systematically move the landmarks surrounding a desired location and note if the animal shifts its searching in the same direction and distance in regards to the shift of the landmarks. This transformational approach was pioneered by Tinbergen (1972) when he showed that the digger wasp uses landmarks to locate its nest. In his classic work, Tinbergen placed pinecones around the entrance of the nest dug out in the ground by a digger wasp. As the digger wasp flew away to collect food, she apparently encodes and memorizes the relationships between the pinecones and her nest. Before the digger wasp was returned, Tinbergen moved the array

a short distance to a new location. On her return, the digger wasp searched in the center of the array of pinecones and not where her nest actually was, revealing that she had used the pinecones as landmarks to encode and remember her nest location.

Contemporary laboratory studies mainly used two variations of this approach to investigate the metric properties (distance and direction) underlying landmark-based search memory in animals (for an extensive review, see Cheng & Spetch, 1998; Cheng, Spetch, Kelly, & Bingman, 2006; Spetch & Kelly, 2006). In the computerized version (called the touch-screen spatial task), animals are trained to find an unmarked position on the surface of a computer monitor (e.g., Lechelt & Spetch, 1997; Spetch, Cheng, & MacDonald, 1996; Spetch, Cheng, & Mondloch, 1992; Spetch & Wilkie, 1994). In the open-field task, a piece of food is hidden under a fluffy surface (e.g., sawdust) covering either the floor of a small search arena or the floor of a testing room and the animal moves freely about in search of the food location (e.g., Cheng, 1989, 1990; Cheng & Sherry, 1992; Della Chiesa, Pecchia, Tommasi, & Vallortigara, 2006; Della Chiesa, Speranza, Tommasi, & Vallortigara, 2006; Gould-Beierle & Kamil, 1996, 1998, 1999; Tommasi, Gagliardo, Andrew, & Vallortigara, 2003; Tommasi & Vallortigara, 2001, 2004). In both tasks, the target position is located a certain distance and direction from one or several landmarks and on unrewarded tests, the landmark or the array of landmarks is translated, expanded, contracted, or removed.

In some studies, animals are trained in a situation in which the landmarks and goal move without rotation within the search area from trial to trial (e.g., Cartwright & Collett, 1987; Collett, Cartwright, & Smith, 1986; Gould-Beierle & Kamil, 1996, 1998; Spetch, Cheng, & McDonald, 1996; Spetch & Wilkie, 1994). This approach is generally used when researchers investigate whether animals encode and memorize absolute or relative distance from a configuration of identical landmarks to locate a spatial position. In other studies, the landmarks and target position remain at a constant position relative to the global cues of the room (Cheng, 1989, 1990; Cheng & Sherry, 1992; Della Chiesa et al., 2006; Gould-

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This research was supported by an operating research grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) and by a research grant from the Faculté des Études Supérieures et de la Recherche (FESR) of Université de Moncton. The experiment received approval from the Comité de protection des animaux from the Faculté des études supérieures et de la recherche de l'Université de Moncton, which is responsible for the application and enforcement of rules of the Canadian Council on Animal Care. I am thankful to Claude Beaulieu, Lucie Dubé and Manon Ouellette for assistance with the research and to the owners of the dogs who participated in this study. I am also very grateful to the anonymous reviewers who have provided valuable suggestions on a previous version of this article.

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Beierle & Kamil, 1996, 1998, 1999). This approach is of particular interest when researchers explore whether animals encode and use distance and direction from one landmark or an array of landmarks and/or examine the effect of global cues on the processing of metric information. In the current study, I used this later approach to investigate landmark-based search memory in the domestic dog.

In one particular study, Cheng and Sherry (1992) investigated how pigeons and chickadees encode distance and direction from landmarks to find hidden food. The target location (called *the goal*) was next to one edge of a square arena placed on the laboratory floor and a single landmark was located inside the arena near the target position. In training, the tray, landmark, and goal remained in a constant position relative to the global room. On tests, the landmark was shifted 10 cm laterally, perpendicularly, or diagonally relative to the nearest edge of the tray. This experiment was designed to test the vector sum model, which was initially proposed by Collett et al. (1986) and developed and extended by Cheng (1988, 1989) to explain how animals use landmarks to navigate. This model assumes that an animal learns the location of a goal by encoding in reference memory a single vector (distance and direction) between each landmark in the vicinity of the goal and the goal itself (landmark-to-goal vectors). The model also claims that when approaching the goal the animal perceives vectors between its current position in space and each landmark (self-to-landmark vectors). By adding landmark-to-goal and self-to-landmark vectors, the animal computes a self-to-goal vector that points directly to the goal. It is interesting to note that the vector sum model makes a testable prediction when a landmark is shifted from its usual position. If the landmark is shifted on x cm in one direction, the directional vector is also shifted between 0 and x cm in the direction the landmark is shifted and not in the orthogonal direction. Unfortunately, the results of Cheng and Sherry partially contradicted this prediction. Their pigeons and chickadees shifted their search in the lateral condition, but not in the perpendicular condition. Moreover, the birds shifted their search more in the lateral than in the perpendicular direction when the landmark was shifted diagonally. These results, therefore, suggest that birds encode two kinds of vector from local landmarks: they encode distance and direction from distinct landmarks, but perpendicular distance from extended surfaces, such as a nearby edge. These results supported those primarily observed by Cheng (1988, 1989) in pigeons, and they were later replicated in three storing-bird species (Gould-Beierle & Kamil, 1996, 1998). Using the touch-screen task, Spetch et al. (1992) also found that pigeons encode and use both kinds of vectors.

Additional evidence revealed that birds weighted landmarks near the target location more than those far from the target location (Bennett, 1993; Cheng, 1989; Goodyear & Kamil, 2004; Letchelt & Spetch, 1997; Spetch, 1995; Spetch & Wilkie, 1994). For example, Gould-Beierle and Kamil (1999) showed that Clark's nutcrackers initially trained with two landmarks far away from the target location were less accurate than those trained with the landmarks closer to the target location. Moreover, the birds trained with landmarks closest to the target location were much more sensitive to the shift of the landmarks than the birds trained with the landmarks far away from the target location.

Although numerous studies suggested that proximity to the goal is an important determinant of landmark use in animals, as pointed

out by Gould-Beierle and Kamil (1996), it is not excluded that distal landmarks can also control search behavior in the landmark-based search paradigm. To test this hypothesis, Gould-Beierle and Kamil (1999) trained Clark's nutcrackers to find hidden food with two local landmarks placed far away (72 and 90 cm respectively) from the target location. When the landmarks were removed from the room, the birds still searched at the target location even if the closest wall was 110 cm away from the target position, suggesting that under specific conditions Clark's nutcrackers are less dependent on local cues and are able to use global cues to maintain their search accuracy. This later conclusion is consistent with other studies (Gould-Beierle & Kamil, 1996; Spetch & Edwards, 1986) that have already shown the importance of global cues on birds' search behavior. Recently, Della Chiesa, Speranza, Tommasi, and Vallortigara (2006) also found that chicks' encoding of metric information is determined both by local distinct landmarks and distal extended surfaces (walls of a small enclosure).

In the current study, I investigated the metric properties of landmark-based search memory in the domestic dog. Although recent studies revealed that dogs can use landmark information to locate a disappearing object (Fiset, Gagnon, & Beaulieu, 2000; Fiset, Beaulieu, Leblanc, & Dubé, in press) or discriminate a spatial position (Milgram et al., 1999; Milgram et al., 2002), how they encode and use spatial information provided by the landmarks is unclear. Furthermore, most of the studies that have investigated the metric properties of landmark-based search memory in animals have used avian species with a few exceptions, such as bees (Cartwright & Collett, 1987; Cheng, Collett, Pickhard, & Wehner, 1987; Collett & Kelber, 1988), gerbils (Collett et al., 1986), humans (Spetch, 1995; Spetch et al., 1996; Spetch et al., 1997), marmoset monkeys (MacDonald, Spetch, Kelly, & Cheng, 2004) and squirrel monkeys (Sutton, Olthof, & Roberts, 2000). From a comparative perspective, however, more mammal species need to be tested in the landmark-based search paradigm before claiming, as suggested by Spetch et al. (1997), that all creatures that rely on landmark-based memory encode and use metric properties of space.

Specifically, I tested whether domestic dogs encode the distance and direction from an array of landmarks that were centrally located in a rectangular room, providing a further test of the vector sum model in a mammalian species. Dogs were first trained in an open-field environment to find a ball hidden a constant distance and direction from two distinct landmarks that remained at the same location in the center of a room from trial to trial. The two landmarks were placed near the target position and the global cues, defined by the walls of the room, were over 150 cm from the target position. On unrewarded tests, the array of landmarks was shifted lateral, perpendicular, or diagonal to the rear wall of the testing room. If dogs rely on the distance and direction provided by the array of landmarks, they might be expected to shift their search by the same extent and direction as the shift of the landmarks. However, if dogs encode the target position relative to the global cues provided by the room at large, they should search at the initial target position in the room. Finally, if dogs simultaneously encode both sources of information, they should search somewhere between the initial target position and the predicted coordinates of the target position relative to the shift of the landmarks.

Method

Participants

The participants were five purebred Labrador retrievers (*Canis familiaris*, 1 female and 4 males, mean age = 2 years and 5 months, range = 1 to 6 years) that belonged to private owners. According to the American Kennel Club (AKC, 1992), the Labrador retriever is classified as a sporting dog. The dogs were selected on the basis of the criterion that they had to be highly motivated by the opportunity to interact with the experimenters and play with a ball. All dogs showed a strong interest in the target object.

Apparatus

The experimental room (362 cm wide \times 604 cm long) was painted white. An opaque gray curtain (600 cm wide \times 200 cm high) separated the room in two parts (see Figure 1). One part (362 cm wide \times 320 cm long \times 258 cm high) served as the search area. The floor of the search area was covered by a layer (15 cm) of woodchips. An orange fluorescent rubber ball (4.8 cm-diameter) served as the target object. The task was to find the target object buried at a specific position in the room (which was labeled "the goal"). The goal was marked on the floor by a plus-shaped cross that was invisible to the dog at the time of searching. In the search area, the goal was located 180 cm from the rear wall, 150 cm from

the left wall, and 150 cm from the right wall. The left wall had a smoked glass observation window (90 cm high \times 120 cm large) mounted in it. Two black PVC cylinders that differed in their diameter (5 cm diameter \times 35.5 cm high; 10 cm diameter \times 35.5 cm high) served as landmarks. Each cylinder was filled with dry sand in order to increase inertia. The landmarks were arrayed parallel to the rear wall of the search area at a distance of 40 cm from each other. The goal was 20 cm in front of each landmark and centered (20 cm) between the two landmarks. Consequently, the goal was at 28.28 cm from the nearest point of each landmark. From the encoding position of the dog, the smaller landmark was on the left side of the goal and the larger landmark was on its right side. The dog's search behavior was monitored by a camera (Panasonic camcorder Model PV-A208-K) that was fixed to the ceiling above the goal, and it was recorded on a VHS video recorder (Panasonic Model PV-8664-K) located in an adjacent room. Overhead fluorescent lights lit the search area.

The encoding position of dogs was located in the second part of the room (362 cm wide \times 284 cm long \times 210 cm high). Five potential positions where the dogs could be positioned were marked with tape on the floor of the encoding area. One position (A) was 250 cm from the goal; two positions (B and C) were 271 cm from the goal; and two positions (D and E) were 307 cm from the goal. One of these positions (A) was directly in front of the goal; two positions (B and D) were on the left side of the goal; and two positions (C and E) were on its right side. To prevent the dogs from using the camera and/or overhead fluorescent lights as landmarks, a second opaque gray curtain (362 cm large \times 100 cm long) hung from the ceiling of the room.

Finally, an opaque screen made of Masonite (150 cm wide \times 156 cm high) was used to prevent dogs from seeing the manipulation of the curtain separating the room. The opaque screen was manipulated by a plastic L-shaped handle screwed to the top edge. One experimenter (E1) performed the manipulations in the search area and a second experimenter (E2) restrained the dog during the manipulations and stood to the right side of the dog. All dogs were unfamiliar to both experimenters.

Procedure

The dogs were brought to the laboratory by the experimenters. On few occasions (five visits), the owner of one dog was present in the laboratory. She was allowed to observe her pet through the smoked observation window from the adjacent room, but did not interact with the dog. To prevent the use of olfaction by the dogs, every five trials, rose water (diluted 1/10 in water) was uniformly sprayed over the woodchips and the landmarks. In addition, to prevent the use of audition by the dogs, white noise (78 dB) was played back by two speakers standing against the right and left walls of the encoding area.

Shaping. During shaping, the dogs were trained to touch the target object, which was visibly exposed at the goal. From trial to trial, the position of the landmarks and the goal remained the same in the search area. Although the dogs were highly motivated by the opportunity to play with the target object, we introduced a food reinforcement procedure to prevent any motivation decline during the experiment.

In each trial of shaping, E1 stood up about 25 cm behind the two landmarks in the search area and the curtain separating the encod-

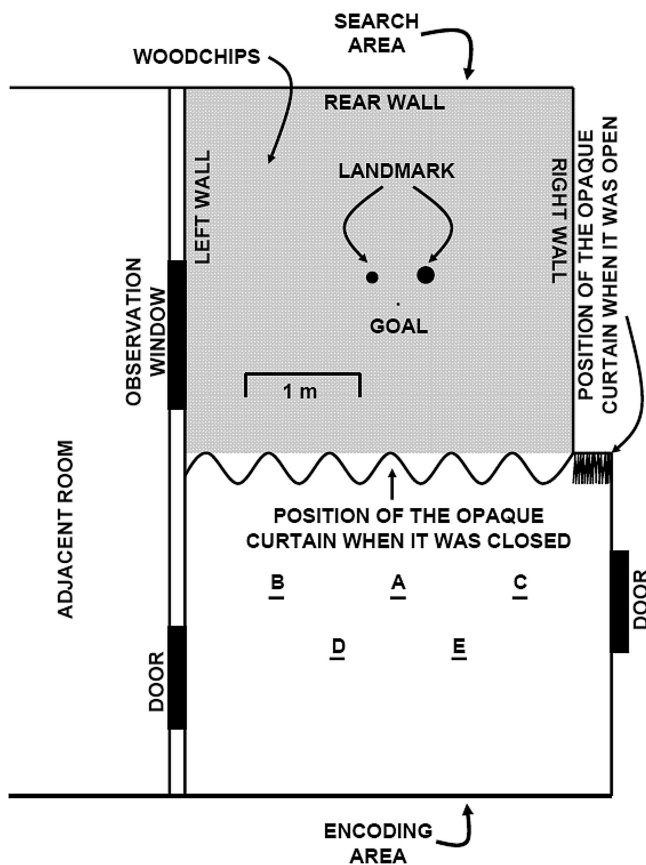


Figure 1. Schematic representation of the experimental room. The drawing is not at scale.

ing area from the search area was opened. First, E1 captured the dog's attention by moving the target object with his hand. Meanwhile, the second experimenter (E2) restrained the dog by holding its collar with one hand and made sure that the dog visually followed the displacement of the object. Once the dog looked at the object, E1 placed the object directly in a hole (approximately 10 cm × 10 cm) buried in the woodchips at the goal location and he made sure the object was visible to the dog. After the object was put down, with her free hand, E2 introduced the opaque screen in front of the dog and immediately removed it. The purpose of this manipulation was to habituate the dog to the manipulation that was used later in the training and testing sessions. Then, the dog was released by E2 and was reinforced if it touched the ball with one paw. A piece of commercial dry food (Diet NutriScience) and social rewards (strokes; verbal rewards, such as "Good dog") were used as reinforcements. The shaping phase was completed when the dog had touched the target object located at the goal for 10 consecutive trials. All dogs reached this criterion in 10 trials.

Training. The dogs were trained to find the target object buried in a layer of woodchips. As in the shaping phase, the position of the two landmarks and the goal remained the same in the search area from trial to trial.

Each training session began with three shaping trials described above which were followed by 30 training trials. At the beginning of a training trial, E2 positioned the dog at one of the five positions in the encoding area. Then, E1 opened the curtain separating the encoding and the search areas and took position 25 cm behind the array of landmarks. E1 showed the ball to the dog and put it down to the goal. Then, E2 placed the opaque screen in front of the dog and E1 immediately slid the opaque curtain between the encoding and the search area for a 30 s retention interval. This interval was aimed at habituating the dog to the delay required to complete the experimental manipulation in the test trials. Then, E2 removed the opaque screen and rotated the dog 360 degrees. After the rotation, the dog was randomly positioned to a new position in the encoding area. This manipulation served to prevent the use of linear egocentric spatial information by the dog to locate the goal (see Fiset et al., 2000). Once the dog was repositioned, E2 reintroduced the opaque screen in front of the dog. Meanwhile, E1 uniformly spread out the woodchips surrounding the target object and the landmarks. The goal was uniformly covered by a layer of woodchips if necessary (see below). At the end of the retention interval, E1 opened the opaque curtain and partially wrapped himself in the curtain, out of the dog's view. Then, E2 removed the opaque screen and released the dog. The dog was reinforced if it dug out the ball after its first touch with one of its forelegs. If the dog did not dig out the target object after its first touch, it was not reinforced and was brought back to an encoding position by E1 for the beginning of a new trial. At the end of the trial, E1 closed the opaque curtain, cleared off the goal, and replaced the woodchips appropriately for the beginning of a new trial.

At the beginning of the training phase, E1 left the target object clearly exposed. Over trials, however, the ball was gradually and partially covered by woodchips. Training was relatively easy for the dog until the ball was totally covered by a thin layer of woodchips. Then, trials where the target object was partially or totally covered were informally mixed within the same session until the dog dug out the ball totally covered by woodchips. Training ended when the dog had dug out the target object com-

pletely covered by a deep layer of woodchips during two consecutive training sessions of 30 trials.

Testing. For each trial of the testing phase, the general procedure was as described in the training phase. At the beginning of a trial, E1 showed the target object to the dog and put it down at the target location. Then, he drew the opaque curtain in front of the dog for a 30 s interval and E2, who was restraining the dog by its collar, rotated the dog 360 degrees and brought it to a new location in the encoding area. Meanwhile, E2 set up a training or a testing trial (see below). At the end of the 30 s interval, E1 opened the curtain and E2 released the dog. Each testing session began with three shaping trials. These trials were followed by six systematically placed unrewarded testing trials (see below) that were interspersed with 24 training trials. The training trials were identical to those of the training phase.

Four types of testing trials were performed by E2: three experimental and one control trials. In the three types of experimental trials, the array of two landmarks was moved to a new position in the search area (see Figure 2). In the lateral trials, the array was moved 20 cm lateral to the left relative to the rear wall. In the perpendicular trials, the array was moved 20 cm perpendicular toward the rear wall. In the diagonal trials, the array was moved both 20 cm lateral and perpendicular to the rear wall. In the control trials, the two landmarks remained at their initial position, but to control for the noise made in the experimental trials, they were moved and put back in place before the end of the 30 sec interval. In the testing trials, E1 removed the object from the goal and replaced uniformly the woodchips over the goal and around the landmarks before opening the curtain.

In each testing session, the six testing trials were randomly administered on Trial 3, 4, or 5; on Trial 8, 9, or 10; on Trial 13, 14, or 15; on Trial 18, 19, or 20; on Trial 23, 24, or 25; and on Trial 28, 29, or 30. Each of the four types of testing trials was administered once or twice in each testing session and they were randomly distributed within a session. Each dog was tested for four consecutive sessions. Hence, at the end of testing, each dog had been exposed to six trials of each type of testing trials. All trials (training and testing) were videotaped.

Data recording and analysis. The video analysis was made by a computerized system. The videotape of each test trial was played back using an ATI TV-WONDER video card on a computer monitor. For each test trial, an analog video was acquired onto the computer and saved as a file. Then, each frame (640 × 480 pixels) was extracted at a current rate of 18 images per second. Each image was viewed and only images from the first sequence of searching were kept. For each image, the location of search was defined as the middle point of the dog's paw. The start of searching was defined as the first time the dog dug into the woodchips with one of its forelegs. The search was judged terminated when the paw of the dog stopped moving at the end of the first touch. As a consequence, the duration of searching changed from trial to trial and the number of frames viewed for each test trial varied between 3 and 5.

Each frame was viewed with the help of a computer drawing program to determine the location of search on the floor. Each location of search was given an X and Y coordinates based on the coordinate system of the program. The X axis was parallel to the rear wall of the search area and the Y axis was perpendicular to it. The calibration of the search area revealed that each pixel of a frame represented 0.250 cm of real search space on both axes in

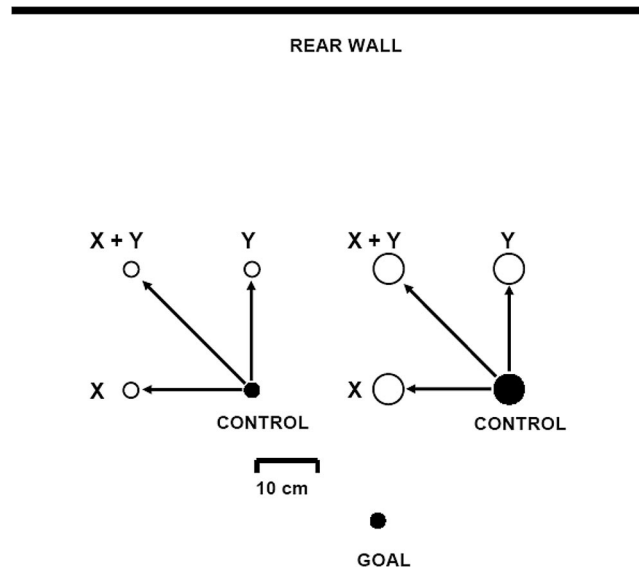


Figure 2. The positions of the two landmarks on tests relative to the rear wall and the goal. Closed circles represent the position of the array of two landmarks on control tests and training trials. Open circles represent the position of landmarks on translation tests; X = lateral test, Y = perpendicular test, X + Y = diagonal test; the drawing is not at scale.

the experimental room. By extrapolation, the distance from the goal was calculated for each axis. For each test trial, the location of search was determined by averaging independently the X and Y coordinates of each image for each dog. For all statistical analyses, a criterion of $p < .05$ was used for rejection of the null hypothesis.

Results

In the training phase, the dogs took a mean number of 5.50 sessions (range = 4 to 7 sessions) to reach the training criterion. In the testing phase, three test trials (one control and two perpendicular trials) were discarded from the statistical analyses because it was impossible to determine the position of the dog's paw from the overhead view provided by the camera.

Table 1 shows the mean search location of each dog for each condition and axis. As one can see, there was a lot of variation among the dogs. Nevertheless, the overall search pattern of dogs was consistent from condition to condition. Moreover, a closer examination of the data did not reveal any significant correlations between X and Y axes for all conditions, supporting the conclusion

that the variations observed within each condition were not attributable to one or several particular dogs. Consequently, the data collected from all dogs were grouped by condition. As one can see in Figure 3, the mean search location of dogs was not centered at the goal location (coordinates 0,0) in the control trials. By consequence, the predicted positions for the three translation tests were plotted relative to the search position on control tests. These prediction points strongly suggest that shifting of the array of landmarks seemed to have a significant, but moderate effect on the search location of dogs. To confirm these impressions, a series of statistic analyses were performed.

To determine whether dogs were sensitive to the displacement of the array of landmarks, factorial repeated-measures ANOVAs on the mean search locations of each dog were conducted separately for each axis (X and Y). For each test condition, two factors were identified: lateral and perpendicular shift of the array of landmarks. On the X axis, the lateral shift of the array produced a significant shift of the search location, $F(1, 4) = 47.01$, effect size = 0.92, $p = .002$, but no effect of perpendicular shift, $F(1,$

Table 1
Mean Search Locations of Each Dog for the Four Test Conditions for Each Axis (X and Y). Each Search Location is Defined in Centimetres Away From the Training Position of the Goal (Coordinates 0, 0)

Dog	Control		Lateral (X)		Perpendicular (Y)		Diagonal (X and Y)	
	X	Y	X	Y	X	Y	X	Y
1	-0.62	-2.21	-1.56	-3.33	-1.55	8.38	-15.20	9.48
2	7.02	-9.33	-11.42	-11.24	-2.40	0.76	-11.29	3.80
3	8.98	-7.09	-8.98	-6.63	6.75	6.67	-13.85	3.13
4	-2.63	-6.01	-17.67	-4.85	-6.93	10.85	-15.64	7.20
5	-0.44	-6.39	-15.73	-2.75	0.54	9.92	-13.95	15.83

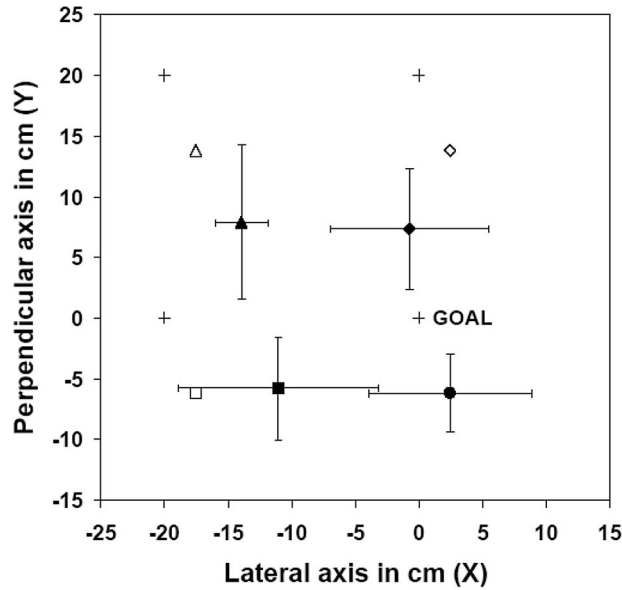


Figure 3. Mean search locations for both X and Y axes for each test condition. Horizontal and vertical bars show 95% confidence intervals. The crosses show the target location in relation to the position of the landmarks on tests. Closed symbols represent the actual mean search location of dogs for each condition. Open symbols represent the predicted coordinates of the goal for the translation tests, relative to the mean search position on control tests. The circle represents the control condition, the squares represent the lateral condition, the diamonds represent the perpendicular condition, and the triangles represent the diagonal condition.

4) = 4.10, effect size = 0.51, $p = .11$, nor interaction, $F < 1$, effect size = 0.001. Therefore, shifting of the array of two landmarks lateral to the rear wall of the search area (lateral and diagonal conditions) provoked a lateral shift of the mean search location of dogs on the X axis. On the Y axis, the perpendicular shift of the array produced a significant shift of the search location, $F(1, 4) = 160.83$, effect size = 0.98, $p < .001$, but no lateral shift, $F(1, 4) < 1$, effect size = 0.042, nor interaction, $F(1, 4) < 1$, effect size = 0.002. Thus, shifting of the array of two landmarks perpendicular to the rear wall (perpendicular and diagonal conditions) provoked a significant shift of the mean search location of dogs on the Y axis. In summary, these analyses support the conclusion that the dogs shifted their search in the direction of the shift of the array of two landmarks.

Next, I examined whether the dogs shifted their search by the same extent on both axes and whether they shifted their search by the same extent as the one expected on the basis of the shift of the two landmarks (i.e., 20 cm). Because the above ANOVAs performed on the mean search locations did not reveal any interaction between the lateral and perpendicular shifts of the array of landmarks (i.e., the perpendicular displacements of the array had the same effect whether or not there were lateral displacements and the lateral displacements of the array had the same effect whether or not there were perpendicular displacements), extent of lateral and perpendicular shifting were estimated by using pooled data for each axis. On the X axis, the control and perpendicular conditions were pooled and the lateral and diagonal conditions were pooled. Then, lateral shifting was estimated by subtracting the control and perpendicular conditions from the lateral and diagonal conditions. The mean extent of lateral shifting was 13.38 cm (95% CI = 7.97, 18.80). Similarly, on the Y axis, the perpendicular and diagonal

conditions were pooled and the control and lateral conditions were pooled. Perpendicular shifting was estimated by subtracting the control and lateral conditions from the perpendicular and diagonal conditions. The mean extent of perpendicular shifting was 13.62 cm (95% CI = 10.64, 16.59). A within-subject ANOVA did not reveal any significant difference between the mean extent of lateral and perpendicular shifting, $F(1, 4) < 1$, effect size = 0.003, revealing that the dogs shifted their search by the same extent on both axes. However, because the upper limits of the 95% confidence intervals were less than 20 cm for both axes of the pooled conditions, the dogs did not shift their search by the same extent as the one expected on the basis of the shift of the two landmarks. Search of dogs was, therefore, not totally under the control of the array of landmarks.

Finally, as one can see in Figure 3, the 95% confidence intervals for the control condition were less than the goal coordinates (0, 0) on the Y axis (95% CI = -9.41, -3.01), but not on the X axis (95% CI = -3.96, 8.89), suggesting that dogs' accuracy to locate the target position was better for the X axis than for the Y axis. This conclusion seems also be true for the lateral condition because the 95% confidence intervals were less than 0 on the Y axis (95% CI = -10.08, -1.56). It is interesting to note that the 95% confidence intervals for the perpendicular condition did not differ from 0 on the X axis (95% CI = -6.91, 5.47), providing additional support to the conclusion that dogs were more accurate on the X axis than on the Y axis.

General Discussion

The present study reveals that the domestic dog, similar to several mammalian species tested so far (e.g., humans and monkeys), dem-

onstrates the ability to encode and use metric properties from nearby landmarks. More specifically, when an array of two distinctive landmarks was shifted in one direction, the dogs shifted their search toward that same direction. However, the dogs did not shift their search by the same extent as the one expected by the shift of the array. They rather searched at an intermediate position, that is, somewhere between the target location and the predicted coordinates of the shift of the landmarks. This last observation therefore suggests that domestic dogs not only encode distance and direction from local landmarks, but also encode and use spatial information provided by some global cues to determine where to search.

The current results are, therefore, consistent with the predictions of the vector sum model (Cheng, 1988, 1989; Collett et al., 1986). Lateral shifts of the array of landmarks led to lateral, but not perpendicular shifts of searching. Perpendicular shifts of landmarks led to perpendicular, but not lateral shifts of searching. Similarly, diagonal shifts of the array provoked diagonal shifts of searching. In addition, the dogs seemed to average the dictates of some unshifted landmarks (global cues) and the shifted local landmarks (cylinders) because they did not shift their search by the same extent as the one expected on the basis of the shift of the array of landmarks. But why previous studies (Cheng, 1988, 1989; Cheng & Sherry, 1992; Gould-Beierle & Kamil, 1996, 1998; Spetch et al., 1996) have consistently failed to support the prediction of the vector sum model when the landmarks were moved in the orthogonal direction is unclear. One plausible explanation for this failure is that, in these later studies, the goal was systematically placed near one of the walls of a square arena, favoring the encoding of perpendicular vectors from a nearby edge. In the present study, the perpendicular distances to the three walls were similar and dogs might have weighted these perpendicular distances similarly. However, given that the walls were relatively far away from the goal (about 150 cm), it is reasonable to believe that perpendicular distances to the walls have played a minimal role in determining where to search. Comparative studies are, therefore, called for investigating whether domestic dogs encode perpendicular distances from nearby edges and whether the predictions of the vector sum model hold for species other than dogs when the target location is centered an equal distance from the edges of an arena.

How domestic dogs encode metric properties from an array of two local landmarks is, however, unclear. Do dogs encode distance and direction for each individual landmark or do they encode both distance and direction from the whole configuration of landmarks? Several studies have shown various encoding strategies about landmark-based memory in nonhuman animals (for a summary, see Cheng & Spetch, 1998; Cheng et al., 2006; Spetch & Kelly, 2006). In mammals, the results are contradictory. Gerbils (Collett et al., 1986) and marmoset monkeys (MacDonald et al., 2004) encode distance and direction from one particular landmark in an array of identical landmarks. On the contrary, humans tend to use the entire configuration of landmarks to extract an abstract geometric rule (Spetch et al., 1996; Spetch et al., 1997). In the present study, the two local landmarks had a similar cylinder shape, but differed in diameter. Consequently, it is probable that the distinctiveness of landmarks favored the encoding of distance and direction from one single landmark. Experiments are currently being conducted in my laboratory to investigate this hypothesis.

The present study also provides empirical support for the influence of global cues on landmark-based memory in animals (e.g., Goodyear & Kamil, 2004; Gould-Beierle & Kamil, 1996, 1998). But what were

those cues in the present study? They could be the geometry of the room, defined by its rectangular shape, or the nongeometric information (e.g., visual cues) available in the room, such as the observation window or any visual information fixed on the walls of the room. The encoding of geometric information as global cues has been first demonstrated in rats by Cheng (1986) and later in human children by Hermer and Spelke (1994, 1996). Other studies have also revealed that diverse species are able to conjoin geometric and nongeometric information, for example, in fish (Sovrano, Bisazza, & Vallortigara, 2002, 2003), in birds (Kelly, Spetch, & Heth, 1998; Vallortigara, Zanforlin, & Pasti, 1990), and in monkeys (Gouteux, Thinus-Blanc, & Vauclair, 2001). For a review, see Cheng and Newcombe (2005). To my knowledge, encoding of geometric information has not been investigated yet in the domestic dog. Consequently, more studies are needed to determine whether dogs' encoding of metric information from local landmarks uses geometric and/or nongeometric information.

In the current study, even though the global cues were far from the goal, they slightly interfered with the encoding of the metric information provided by the local landmarks. This observation contrasts with previous studies showing that global cues do not obstruct the use of local cues when the distance between the global cues and the goal is relatively large (Gould-Beierle & Kamil, 1998). One possible explanation is that the dogs tested in the present study (Labrador retrievers) were relatively large animals. Given their body size (approximately 1 m long), the dogs could perceive the distance between the target position and the global cues as relatively close to the goal and by consequence, encoding of vectors (e.g., perpendicular distances) from global cues, therefore, might be possible. Besides, recent evidence supports the assumption that the size of the testing space interferes with the nature of the encoded information. For example, Sovrano, Bisazza, and Vallortigara (2007) showed that the use of metric properties of a rectangular enclosure occurs in small spaces, whereas the use of landmark information occurs in large spaces. Further studies should investigate whether dogs' landmark-based memory is controlled by the size of the testing room.

Finally, even though the domestic dogs searched as a function of the displacement of the array of landmarks, as a group, they searched farther away from the goal on the Y axis than on the X axis. But why did dogs overestimate the distance between the landmarks and the goal on the Y axis? In humans, depth perception of nearby objects depends for the most part upon binocular disparity (Matlin & Foley, 1997). In the average dog, the eyes usually deviate approximately 20 degrees lateral to the midline (Miller & Murphy, 1995). By consequence, it is estimated that the area of binocular overlap varies 30 to 60 degrees between breeds, which is much less than in humans (who have about 140 degrees of binocular overlap). In the current study, since dogs have a relatively small binocular overlap, it could therefore be possible that they estimated nearby objects as being farther away from the goal than they really were. Nevertheless, it should be noted that several monocular cues (e.g., brightness, area of light and shadow) were also available to the dogs for estimating the distance between the goal and the landmarks. One could also suggest that the errors of dogs on the Y axis are due to a search strategy such as searching too far from the landmarks at the beginning of the search and then zeroing in on the landmarks. However, a posteriori examination of the search behavior of dogs after their first touch into the wood-

chips clearly revealed that the dogs systematically searched backward, walking away from the landmarks and the goal and they did not zero in on the landmarks.

The present study represents the first attempt to study landmark-based search memory in the domestic dog. In summary, domestic dogs average the direction and distance from nearby landmarks and some global cues to determine where to search, supporting the predictions of the vector sum model when the landmarks and goal are centered in a rectangular search arena. Investigation of landmark-based memory in domestic dogs is just beginning and more work is needed to determine the mechanisms underlying the spatial memory of dogs.

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Received December 6, 2006
 Revision received July 27, 2007
 Accepted August 3, 2007 ■

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