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Evidence for averaging of distance from landmarks in the domestic dog

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ABSTRACT

Several studies in landmark use have shown that animals locate spatial positions by predominantly using perpendicular distance from extended surfaces over distance from individual landmarks. In the current study, I investigated whether the domestic dog encodes perpendicular distance from surfaces and whether they estimate distances from multiple cues. Dogs were first trained to locate a ball hidden at an equal and constant distance between an individual landmark and one wall (Experiment 1) or two walls (Experiment 2). On occasional unrewarded tests, the landmark was shifted laterally, perpendicularly or diagonally relative to one wall. Data revealed that the dogs largely determined where to search by averaging the distance from the walls of the room and the distance from the individual landmark. This study provides additional evidence that domestic dogs use metric properties of space to find a spatial location by use of landmarks. Although the present results are in accordance with the vector sum model, they are also consistent with current theories of spatial memory.

1. Introduction

Finding a way back to a specific location, such as a home or a food cache, is vital for many species. Among the diverse strategies available to animals to navigate back to a location, the use of visual landmarks is well spread in the animal kingdom (for an extensive review, see Shettleworth, 1998; Roberts, 1998). Pioneered by Tinbergen (1972), the transformational approach is typically used to demonstrate that animals rely on landmarks to locate a spatial position. This procedure consists in training an animal to find a piece of food hidden in proximity to a configuration of distinct landmarks. After training, without the subject's knowledge, one or several landmarks are systematically shifted *x* cm in a specific direction. Of particular interest is whether the animal shifts its search in regards to the distance and direction of the shift of the landmark(s).

This particular approach has been extensively used in recent contemporary studies of landmark use to investigate whether animals encode and combine the metric properties (distance and direction) of space (for a review, see Cheng and Spetch, 1998; Cheng et al., 2006; Spetch and Kelly, 2006). The vector sum model, proposed by Collett et al. (1986), and later extensively developed by Cheng (1988, 1989, 1990), has been advanced at first to explain how animals use distance and direction from multiple landmarks to navigate. This model assumes that during training, the animal encodes and combines in reference memory the components (distance and direction) of a single vector between the goal location and each landmark located in the vicinity of the goal (landmark-to-goal vectors). The model also presumes that when navigating towards the goal the animal perceives vectors from its current position and each landmark (self-to-landmark vectors). By averaging the landmark-to-goal and self-to-goal vectors, the animal computes a self-to-goal vector that points directly towards the goal location. By consequence, the vector sum model predicts that if a landmark is shifted by *x* cm in one direction, the self-to-goal vector is also shifted between 0 and *x* cm in the same direction as the landmark shift and not in the orthogonal direction.

The predictions of the vector sum model have been empirically tested in several avian species. In one specific study, Cheng and Sherry (1992) trained pigeons and black-capped chickadees to find food that was constantly hidden at an equal distance between a cylinder, that served as landmark, and the nearby edge of a square tray. On test, the landmark was occasionally shifted laterally, perpendicularly and diagonally relative to the edge of the tray. Cheng and Sherry found that the birds shifted their search when the landmark was shifted laterally to the edge but did not when the landmark was shifted perpendicularly, partially contradicting the predictions of the vector sum model. These results supported those initially observed by Cheng (1989, 1990) in pigeons and suggested that birds encode two kinds of vectors from nearby landmarks to navigate: they encode and use distance and direction from individual landmarks but predominantly encode and use the perpendicular distance from extended surfaces. This observation was later replicated in other avian species (Gould-Beierle and Kamil, 1996, 1998, 1999) and in a computerized version of this task as well (Spetch et al., 1992).

An additional problem with the initial formulation of the vector sum model was that the encoding of vectors was restricted to the landmarks located in the vicinity of the goal. Gould-Beierle

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and Kamil (1996) judiciously pointed out that animals do not solely encode distance and direction from nearby landmarks, such as those emanating from individual landmarks or extended surfaces, but possibly encode distance and direction from distal landmarks (also called global cues) to determine where to search. To prove their claim, Gould-Beierle and Kamil (1999) trained Clark's nutcrackers to use two individual landmarks to find food. On test, the landmarks were occasionally removed from the search area. The birds still accurately searched at the target location, revealing that they had also encoded some distal cues available in the room to pinpoint their search. Although it is generally recognized that global cues are simultaneously encoded by animals to determine a spatial position (e.g. Della Chiesa et al., 2006; Sturz and Katz, 2009; Spetch and Edwards, 1988), animals normally attribute more weight to the closest landmarks relative to the goal. For example, by systematically manipulating the distance between the landmarks and the goal, Gould-Beierle and Kamil (1999) were able to demonstrate that Clark's nutcrackers were more sensitive to the shift of the closest landmarks to the goal than to the shift of the landmarks that were further away. This observation is also supported by several other studies conducted in different avian species (Bennett, 1993; Cheng, 1989; Goodyear and Kamil, 2004; Lechelt and Spetch, 1997; Spetch, 1995; Spetch and Wilkie, 1994).

There is also evidence (Kamil and Jones, 1997, 2000; Cheng, 1994; Sturz and Katz, 2009) that birds do not combine the two components of a vector (direction and distance) as initially predicted by the vector sum model. In a series of elegant experiments, Cheng (1994) systematically put in conflict the relative weights given to the distance and direction components by rotating the landmarks. His results clearly revealed that pigeons encode both components separately. Kamil and Jones (1997, 2000) used an alternative approach to determine the role of direction when birds encode a food site. After training birds to locate a piece of food located along a line separating two landmarks, they rotated the array of landmarks relative to a target location. Birds' search errors were much less scattered along the directional than the distance component, supporting the conclusion that birds encode distinct components of vectors. Moreover, Kamil and Jones (2000) found that birds trained to use a constant bearing from an array of two landmarks learned much faster to locate hidden seeds than birds trained to use a constant distance from the array. These results, in line with Cheng's (1994) observations, therefore suggest that birds encode separately the distance and the direction to find a spatial position and that they primarily encode the directional information. To explain the predominance of direction over distance, Kamil and Cheng (2001) formulated a landmark piloting proposal, the Multiple Bearings Hypothesis. This model puts more emphasis on the compass direction between the landmarks and the goal than on the distance. Most specifically, the Multiple Bearings Hypothesis proposes that birds compute separated bearings from multiple landmarks. In addition, because of their stability, more weights are attributed to distant landmarks than proximal ones for orientation (for a review, see Sutton, 2009). Interestingly, the predictions of the Multiple Bearings Hypothesis have received some empirical supports (see Kamil et al., 2001).

Put together, these recent data therefore have led the way to the evidence that landmark based spatial memory in animals depends on the encoding of two independent spatial parameters (distance and direction) from multiple cues, which are hierarchically organized depending on the proximity of the landmarks or their attributes (Spetch and Kelly, 2006). As pointed out earlier, these data are also inconsistent with the predictions of the vector sum model and have paved the way to new theoretical developments. However, although the mechanisms underlying the use of landmarks have been subject of extensive research in the avian species, investigations in mammals are restricted to a few animal species, such as humans (Doeller and Burgess, 2008; Doeller et al., 2008; Hartley et al., 2004; Spetch, 1995; MacDonald et al., 2004; Spetch et al., 1996; Waller et al., 2000), gerbils (Collett et al., 1986), marmoset monkeys (MacDonald et al., 2004) and squirrel monkeys (Sutton et al., 2000). Overall, these studies revealed that when relying on landmarks to navigate and locate a spatial position, mammals seem to use the metric properties of space. Nevertheless, few systematic and extended investigations have been conducted on landmark based memory in mammals and whether or not the findings observed in birds can be generalized to mammals is still unclear.

To date, the most serious series of investigations in mammals has been performed in humans (Doeller and Burgess, 2008; Doeller et al., 2008; Hartley et al., 2004; Waller et al., 2000; for a review see Burgess, 2006, 2008). In these studies, the procedure required the participants to navigate within a virtual environment to return to a specific location they had visited before. Usually the target location is surrounded by a boundary and sometimes a landmark is placed near the goal. On tests, out of the subjects' knowledge, the arena is contracted or expanded (Hartley et al., 2004) or the landmark is shifted away from the goal (Doeller and Burgess, 2008). In one particular study (Hartley et al., 2004), when the target location was near the centre of the arena and far from the walls, the participants averaged the distances from the four boundaries of the arena to determine where to search. On the other hand, when the goal was close to one of the walls, the participants encoded the perpendicular distance from this nearby extended surface. Thus, depending on the distance between a target location and an extended surface, it seems that humans encode either the perpendicular distance or average the distance from all boundaries available. In another study, when an individual landmark and the boundaries of the enclosure were put in conflict (Doeller and Burgess, 2008), learning to local landmarks was reduced (overshadowed) by the presence of the nearby boundary while learning to the boundary was unaltered by the presence or absence of the nearby landmarks to the goal (blocking). Interestingly, both overshadowing and blocking of spatial information have also been demonstrated in several birds and mammals species (for a review, see Spetch and Kelly, 2006), although sometimes local features overshadow spatial information (see Gray et al., 2005). Put together, these studies strongly suggest similarities rather than differences in the way mammals and birds process spatial information. Nevertheless, more mammal species need to be tested under similar conditions before claiming that birds and mammals compute distance and direction from landmarks in a similar way.

Recently, I began a series of investigations aimed at determining the metric properties of landmark-based spatial memory in the domestic dog (Fiset, 2007), a mammal species. In this study, dogs were trained to find a ball hidden next to an array of two distinct landmarks that remained at a constant location in the middle of a large room covered by a layer of woodchips. After training, the array of landmarks was shifted on 20 cm laterally, perpendicularly or diagonally relative to the rear wall of the room. The dogs shifted their search as a function of the displacement of the array of landmarks and, by contrast to the avian species tested so far, the dogs did not shift their search in the orthogonal direction. These data, therefore, surprisingly supported the predictions of the vector sum model (Cheng, 1989, 1990). However, the dogs did not shift their search by the same extent as the shift of the landmark. It therefore appears that dogs encoded the distance and direction from the individual landmarks located in the vicinity of the goal and some distal cues available in the testing room as well, supporting the data observed by Gould-Beierle and Kamil (1996, 1998, 1999). However, given that the array of landmarks was centred in the testing room and that the three surrounding walls were almost at equal distance from the goal position, it is plausible that the dogs had also encoded, but to a lesser extent, the perpendicular distance from the walls, as observed by Hartley et al. (2004) in humans.

The purpose of the current study therefore was to investigate whether domestic dogs encode and use the perpendicular distance from a nearby extended surface (such as a wall) as initially demonstrated in birds (Cheng, 1989, 1990; Cheng and Sherry, 1992; Spetch et al., 1992) and humans (Doeller and Burgess, 2008; Hartley et al., 2004) and how they estimate distance from different landmarks. In order to do so, I replicated the general procedure used by Fiset (2007). However, only one landmark was present in the room and it was localized near one (Experiment 1) or two walls (Experiment 2), favouring the encoding of perpendicular distance. Moreover, in order to allow further comparison with the avian species, the distance between the landmark, the goal and the walls mostly replicated, but on a larger scale, the measurements used by Cheng and Sherry (1992).

2. Experiment 1

The objective of Experiment 1 was to determine whether domestic dogs predominantly encode and use perpendicular distance from an extended surface and whether they estimate distance from multiple cues. Dogs were first trained to find a ball hidden at equal distance between a wall and a landmark. Then, on occasional unrewarded trials, the landmark was shifted 25 cm laterally, perpendicularly or diagonally from the wall. Whether or not the dogs predominantly encoded the perpendicular distance from an extended surface (the wall), when the landmark was shifted along that surface, the dogs should have shifted their search in the direction of the landmark shift. However, when the landmark was moved away from the wall, if the dogs principally encoded the perpendicular distance from the wall, the dogs should not have shifted their search as a function of the displacement of the landmark. On the other hand, if the dogs encoded multiple cues simultaneously, when the landmark was shifted away from the wall, they should have searched somewhere between the position predicted by the distance from the individual landmark and the distance from the wall. Finally, if the dogs also encoded some distal and stable cues in the room, as shown by Fiset (2007), whatever the direction by which the landmark was shifted, they should not have shifted their search by the same extent as the landmark shift.

2.1. *Method*

2.1.1. *Participants*

The participants were five purebred Labrador retrievers (4 females and 1 male) and one mixed Labrador retriever/Husky dog (1 female) (mean age = 7 years and 6 months, range = 5 to 10 years) that belonged to private owners. To participate in the experiment, the dogs had to be motivated to play with a ball and interact with the experimenters.

2.1.2. *Apparatus*

The experimental room (362 cm wide × 604 cm long) was painted white and divided in two parts (see Fig. 1) by an opaque grey curtain (600 cm wide × 200 cm high). One part (362 cm wide × 320 cm high) served as the search area and its floor was covered with a layer (10 cm) of woodchips. The task of the dog was to find a fluorescent rubber ball (4.8 cm-diameter) buried at a specific location (labelled "the goal") in the search area. The goal, which remained at the same location in the search area throughout the experiment, was marked on the floor by a plus-shaped cross and it was located 25 cm from the rear wall, 177 cm from the right wall and 185 cm from the left wall. The left wall had a smoked glass observation window (90 cm high × 120 cm large) mounted in it. One PVC cylinder (10 cm diameter × 35.5 cm high) served as landmark and its bottom was filled with dry sand to increase inertia. The landmark was located 50 cm from the rear wall, 202 cm from the right wall and 160 cm from the left wall. The distance between the goal and the nearest edge of the landmark was 35.36 cm. From the encoding position of the dog, the landmark therefore was 25 cm on the left side of the goal and 25 cm in front of it. The search behaviour of the dog 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. The search area was lit by overhead fluorescent lights.

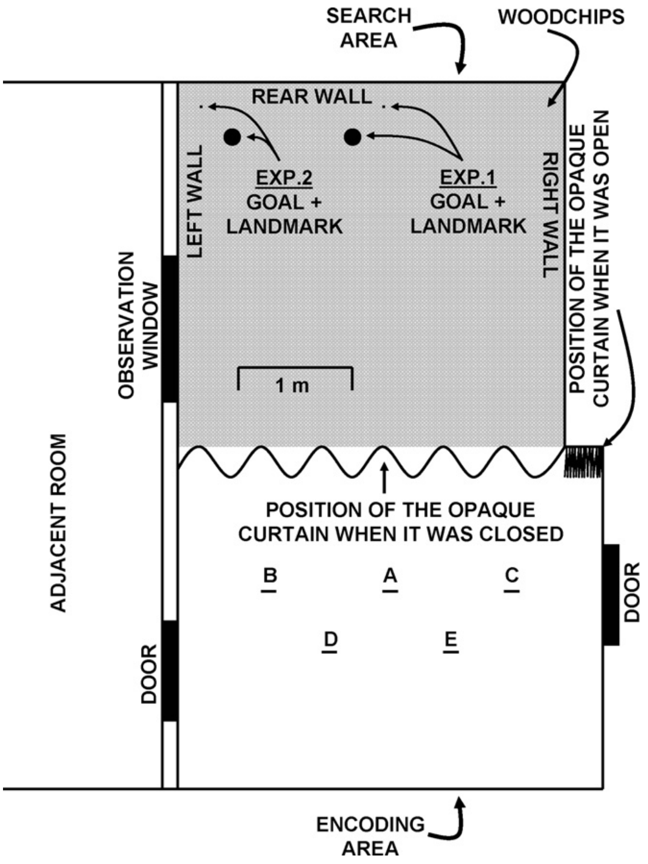

Fig. 1. Schematic representation of the experimental room.

At the beginning of each trial, the dog was positioned in the second part of the room (362 cm wide × 284 cm high), which served as encoding area (see Fig. 1). The dog could be positioned at five potential positions: One position (A) was 423 cm from the goal; two positions (B and C) were 445 cm from the goal and two positions (D and E) were 468 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 of the right side of the goal.

An opaque screen (150 cm wide × 156 cm high) made of Masonite was used to prevent the dog from seeing the manipulation of the curtain that separated the room in two parts. The screen was manipulated by a plastic L-shaped handle screwed to its top edge. Two experimenters, unfamiliar with the dogs, interacted with the animal during the testing. One experimenter (E1) performed the manipulations and a second one (E2) restrained the dog during the manipulations.

2.1.3. *Procedure*

The dogs were brought to the laboratory by the experimenters with one of the university vehicles, and after each session, which lasted about 60 min, they were brought back to their owner's house. The experiment was divided into three successive steps: shaping, training, and testing. Shaping was administered during the first visit along with the first training session. The remaining training sessions and all testing sessions were administered on separate and successive days (except on weekends). Dogs were tested approximatively at the same hour (morning or afternoon) every day. However, one dog was tested twice a day (morning and afternoon) during all the experiment. In each phase of the experiment, to prevent the use of olfaction by the dogs, every four trials, rose water (diluted 1/10 in water) was uniformly sprayed over the woodchips and the landmark.

2.1.3.1. Shaping. During shaping, the dogs were trained to touch the ball, which was visibly exposed at the goal. Although all dogs seemed to be highly motivated by the opportunity to play with the target object and interact with the experimenters, a food reinforcement procedure was introduced to prevent any motivation decline during the experiment.

Before each shaping trial, while E2 restrained the dog by holding its collar (or leash) with her left hand, E1 closed the opaque curtain separating the encoding area from the search area. Next, E2 randomly positioned the dog at one of the five positions in the encoding area. Meanwhile, E1 exposed the goal by burying a hole (approximatively 10 cm × 10 cm) in the woodchips. After that, E1 opened the opaque curtain and took position about 50 cm on the right side of the goal. Then, E1 attracted the dog's attention by moving the target object with her right hand, and while E2 made sure the dog was watching the manipulation, put down the object at the goal. Afterward, with her free hand, E2 introduced the opaque panel in front of the dog and immediately removed it. The manipulation was aimed at habituating the dog to the manipulation of the opaque screen that was used later in training and testing. The dog was subsequently released by E2 and was reinforced if it touched the ball with one paw or its mouth. A piece of commercial dry food (Diet NutriScience) and social rewards (strokes; verbal rewards) were used as reinforcements. The shaping phase was completed when the dog had touched the target object at the goal location for 5 consecutive trials.

2.1.3.2. Training. During this phase, the dogs were trained to find the target object buried at the goal location in the woodchips. As in shaping, from trial to trial, the position of the goal and the landmark remained the same in the search area.

Each training session began with three shaping trials followed by 24 training trials. In the training trials, the general procedure was similar to that used during the shaping phase. However, once the object was put down at the goal location, E2 held the opaque screen in front of the dog while E1 closed the opaque curtain between the encoding and the search area for a 30 s retention interval. The purpose of this interval was to habituate the dog to the delay required to complete the experimental manipulations used in the test trials. During the interval, E2 removed the opaque screen and rotated the dog 360 degrees. Next, E2 randomly moved the dog from its current position to one of the four remaining positions in the encoding area. This manipulation served to prevent the dogs from using linear egocentric spatial information to locate the goal (see Fiset et al., 2000, 2006). 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 landmark. If necessary (see below), the goal was uniformly covered by woodchips. At the end of the 30 s retention interval, E1 opened the opaque curtain and partially wrapped herself 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 (success). If the dog did not dig out the ball after its first touch (error), it was immediately brought back to the encoding area by E2 for the beginning of a new trial.

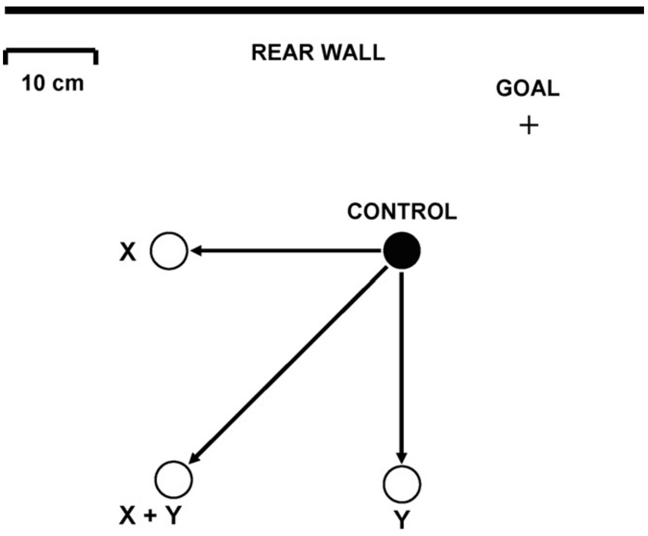

Fig. 2. The positions of the landmark on tests relative to the rear wall and the goal in Experiment 1. Closed circles represent the position of the landmark on control test and training trials. Open circles represent the position of the landmark on translation tests; X = lateral test, Y = perpendicular test, $X + Y$ = diagonal test; the drawing is not at scale.

At the beginning of the training phase, the goal was clearly exposed in the search area. However, over trials, the goal was gradually and partially covered by woodchips. Training was relatively easy for the dogs until the goal was totally covered by a thin layer of woodchips. Then, trials in which the target object was partially or totally covered were informally mixed within the same training session until the dog dug out the ball totally covered by woodchips. Training ended when the dog had successfully dug out the ball completely covered by a deep layer of woodchips (about 5 cm) in every trial of two consecutive training sessions.

2.1.3.3. Testing. Each training session began with three shaping trials, followed by 24 trials, which included four unrewarded test trials systematically interspersed with 20 training trials (see below). In the test trials, the general procedure was similar to that used in the training trials. However, E1 moved the landmark, removed the ball from the goal and replaced uniformly the woodchips over the goal and around the landmark before opening the curtain.

In each testing session, four types of test trials were administered to the dogs: three experimental trials and one control trial. In each type of experimental trial, the landmark was moved to a new position in the search area (see Fig. 2). In the lateral tests, the landmark was moved 25 cm lateral to the left relative to the rear wall. In the perpendicular trials, the landmark was moved 25 cm perpendicular away from the rear wall. In the diagonal trials, the landmark was moved both 25 cm lateral and perpendicular to the rear wall. In the control trials, the landmark was moved and put back in place before the end of the 30 s interval.

In each testing session, each of the four types of testing trials was randomly distributed on Trial 4, 5, or 6; on Trial 10, 11 or 12, on Trial 16, 17 or 18 or on Trial 22, 23 or 24. Eight consecutive testing sessions were administered. Consequently, over testing, eight testing trials of each type were given to each dog. All trials (training and testing) of a session were monitored and videotaped.

2.1.4. Data recording and analysis

The videotape of each test trial was played back on a computer monitor via an ATI TV-WONDER video card. For each test trial, an

Table 1
Mean search locations of each dog for the four test conditions for each axis (*X* and *Y*) of Experiment 1. 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	−2.45	1.85	−21.42	5.01	0.92	−1.91	−18.01	−3.90
2	0.14	−1.56	−19.81	−2.24	1.12	−7.60	−22.56	−10.30
3	−0.08	−0.03	−17.70	−0.52	2.00	−10.64	−12.38	−9.57
4	0.75	0.52	−19.85	−1.46	3.37	−7.80	−16.82	−9.24
5	−3.80	1.82	−19.30	1.74	2.74	−4.82	−21.48	−6.97
6	−1.40	1.67	−14.05	2.64	3.62	−8.21	−7.98	−10.30

analog video was acquired onto the computer and saved as a file. Next, each frame (640 × 480 pixels) was extracted at a current rate of 18 images per second. For each test trial, the start of searching was defined as the first time the dog dug into the woodchips with the paw of one of its forelegs. The search was judged terminated when the paw of the dog stopped moving at the end of the first touch. Consequently, the duration of searching changed from trial to trial and the number of frames viewed for each trial varied between 1 and 6.

Each frame was viewed with a computer drawing program and the *X* and *Y* pixel coordinates of the location of search were recorded. The location of search was defined as the central position between the second and third phalange of the dog's paw. The *X*-axis was parallel to the rear wall of the search area and the *Y*-axis was perpendicular to it. For each test trial, the location of search was determined by averaging independently the *X* and *Y* coordinates of each image for each dog. The calibration of the search area revealed that each pixel of a frame represented 0.37 cm of real search space on both axes in the search area. By extrapolation, the distance from the search location to the goal was calculated for each trial. For each dog, a mean search location was calculated for each axis by averaging the location of search of all trials of the same type of test. For all statistical analyses, the criterion of $p < 0.05$ was used to reject the null hypothesis.

2.2. Results and discussion

The dogs took a mean number of 5.00 ($SE = 0.00$) trials to reach the shaping criterion and a mean number of 12.17 ($SE = 0.42$) sessions to attain the training criteria.

In Testing, two perpendicular trials (two different dogs) were not recorded due to technical difficulties and were discarded from the final statistical analyses. Table 1 shows the mean search location of each dog for each condition and axis. Although there were some variations among the dogs as a function of conditions and axes, the matrix of variances–covariances was uniform and therefore the raw data were kept and used in the statistical tests.

Fig. 3 illustrates the mean search location (and 95% CI) of dogs as well as the predicted positions for each condition. First, as one can see, the 95% confidence intervals for the control condition on the *X* (95% CI = −2.97, 0.69) and the *Y* (95% CI = −0.71, 2.13) axis did not differ from the goal (0, 0). Thus, as a group, the dogs were very good at locating the goal. Secondly, shifting the landmark along the rear wall seemed to have a stronger impact on dogs' search behaviour than shifting the landmark perpendicular away from the wall. To confirm these impressions, a series of statistical analyses was performed.

A within subject ANOVA Lateral shift (shift, no shift) × Perpendicular shift (shift, no shift) × Axes (*X*, *Y*) was performed on the mean search locations. Lateral shift of the landmark (lateral and diagonal conditions) resulted in a significant shift of the search location, $F(1, 5) = 126.14$, partial eta squared = 0.962, $p < 0.001$. Therefore, the dogs shifted their search as a function of the displacement of the landmark to determine where to search on the *X*-axis. Perpendicular shift of the landmark (perpendicular and diagonal conditions) also provoked a significant shift of the search location, $F(1, 5) = 72.33$, partial eta squared = 0.935, $p < 0.001$, revealing that the dogs also followed the displacement of the landmark on the *Y*-axis. There was also a significant main effect of Axes, $F(1, 5) = 11.77$, partial eta squared = 0.702, $p = 0.019$, with the dogs shifting their search more along the *X*-axis than along the *Y*-axis. This indicates that the dogs were more sensitive to the displacement of the landmark along the *X* than along the *Y*-axis.

The ANOVA also revealed a significant interaction Lateral shift × Axes, $F(1, 5) = 181.12$, partial eta squared = 0.973, $p < 0.001$. When the landmark was shifted laterally, the dogs shifted their search significantly on the *X*-axis but not on the *Y*-axis. Similarly, there was a significant interaction Perpendicular shift × Axis, $F(1, 5) = 55.19$, partial eta squared = 0.917, $p = 0.001$. When the landmark was shifted perpendicularly, the dogs significantly shifted their search on the *Y*-axis but did not on the *X*-axis. Finally, there was no Lateral shift × Perpendicular shift interaction, $F(1, 5) = 1.78$, partial eta squared = 0.24, $p = 0.263$, nor Lateral shift × Perpendicular shift × Axes interaction, $F(1, 5) < 1$, partial eta squared = 0.011,

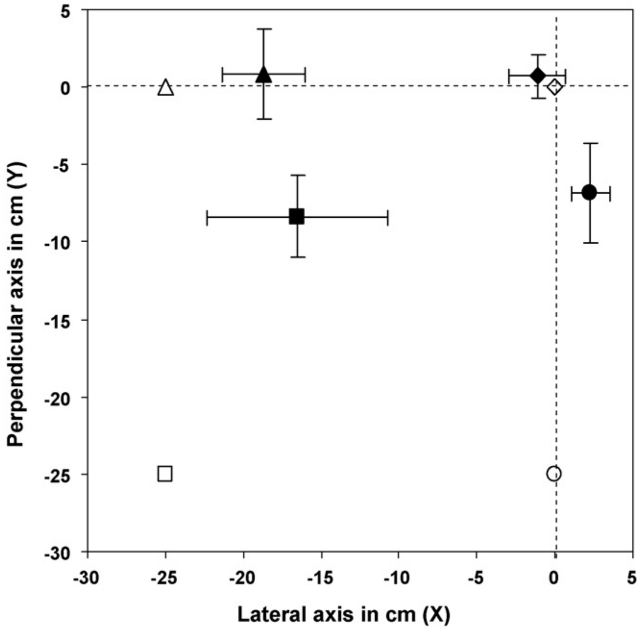

Fig. 3. Mean search locations for both *X* and *Y* axes for each test condition of Experiment 1. Horizontal and vertical bars illustrate 95% confidence intervals. The dashed lines indicate the *X* and *Y* axes from the origin (0, 0), which is defined as the position of the hidden object in training and control test trials. Closed symbols represent the mean search location of dogs for each condition. Open circles represent the predicted coordinates of the goal for the translation tests relative to the control position. The diamonds represent the control condition, the triangles represent the lateral condition, the circles represent the perpendicular condition, and the squares represent the diagonal condition.

$p = 0.823$. By consequence, the displacement of the landmark on one axis did not influence the dogs' search on the other axis.

Next, I estimated the extent by which the dogs shifted their search along both axes. On the *X*-axis, only one cue (the individual landmark) was located close by the goal during training whereas on the *Y*-axis, there were two nearby cues: the landmark and the wall, which were at equal distance from the goal. Therefore, if the dogs averaged the distance from both cues on the *Y*-axis, they should have searched about the half of the extent of shifting observed on the *X*-axis. Because there was no Lateral shift × Perpendicular shift interaction, data were pooled for both conditions. On the *X*-axis, the control and perpendicular conditions were averaged and the lateral and diagonal conditions were averaged for each dog. Then, lateral shifting was estimated by subtracting the mean extent of shifting for the control and perpendicular conditions from the mean extent of shifting for the lateral and diagonal conditions. On the *X*-axis, the mean extent of lateral shifting was 18.19 cm (95% CI = 14.47, 21.91). In a similar way, on the *Y*-axis, the perpendicular and diagonal conditions were averaged and the control and lateral conditions were averaged. Perpendicular shifting was estimated by subtracting the mean extent of shifting for the control and lateral conditions from the mean extent of shifting for the perpendicular and diagonal conditions. On the *Y*-axis, the mean extent of perpendicular shifting was 8.39 cm (95% CI = 6.41, 10.37). Therefore, lateral shifting on the *X*-axis was about the double of the extent observed on the *Y*-axis.

Then, the mean extent of perpendicular shifting on the *Y*-axis was compared to an hypothetical mean of 9.10 cm, which was the half of the mean extent of lateral shifting observed on the *X*-axis. A one sample *t*-test revealed no significant difference, $t(5) = -0.919$, $p = 0.400$, supporting the conclusion that on the *Y*-axis the dogs did average the distance from the landmark and the distance from the wall to determine where to search. Finally, the upper limits of the 95% confidence intervals of the mean extent of shifting were less than 25 cm for both axes of the averaged conditions, and therefore, on neither axis, did the dogs shift their search by the same extent expected on the basis of the shift of the landmark. This last observation confirms that the search of dog was not totally under the control of the individual landmark and/or the perpendicular wall.

In summary, Experiment 1 revealed that the dogs shifted their search in the direction of the landmark shift and did not search in the orthogonal direction. However, when the landmark was shifted perpendicularly to the wall, although the dogs shifted significantly away from the wall they did not shift to the same extent as when the landmark was shifted laterally to the wall. In fact, the extent of lateral shifting was twice the extent of perpendicular shifting, suggesting that the dogs averaged the distance from the wall and the distance from the individual landmark to determine where to search on the *Y*-axis. Finally, on both axes, the dogs did not shift their search by the same extent as the shift of the landmark. It therefore appears that the dogs have also encoded the position of the goal relative to other cues, such as the two lateral walls of the testing room or the opaque window mounted on the left wall of the room.

3. Experiment 2

In Experiment 1, the dogs simultaneously encoded the distance from an extended surface (the wall) and the distance from an individual landmark. It also seems that they used some undetermined cues available in the room. Put together, these results suggest that the domestic dog averages the distance from multiple cues to determine a spatial position and do not predominantly use the perpendicular distance from an extended surface. Experiment 2 therefore was designed to replicate findings observed in Experiment 1 by examining whether domestic dogs would encode distance from walls oriented in orthogonal directions. Dogs were trained to find a ball hidden at equal distance between a single landmark and two perpendicular walls, that is, the corner of the testing room. On tests, the landmark was shifted 25 cm laterally, perpendicularly or diagonally to one of the two walls. If the dogs encoded independently the distance from each wall, when the landmark was shifted away from one wall, they should have shifted their search in the same direction as the shift of the landmark and not in the orthogonal direction. Furthermore, given that both walls were located at the same distance from the goal and the landmark but in orthogonal directions, the dogs should have shifted their search by the same extent on both axes. Finally, if the dogs averaged the distance from the wall and the distance from the landmark, they should have shifted their search by about the same extent as the mean extent of perpendicular shifting observed in Experiment 1.

3.1. *Method*

3.1.1. *Participants*

The participants were two purebred Labrador retrievers (2 females), and 4 mixed dogs (1 female and 3 males), mean age = 6 years and 6 months, range = 1 to 10 years) that belonged to private owners. Three dogs had participated in Experiment 1 one year before and the three other dogs were naive to the task.

3.1.2. *Apparatus*

The testing room and apparatus were the same as those used in Experiment 1. However, the position of the goal and of the landmark differed (see Fig. 1). Both were now placed near a room corner. The goal was 25 cm from the rear wall, 25 cm from the left wall and 335 cm from the right wall. The landmark was 50 cm from the rear wall, 50 cm from the left wall and 310 cm from the right wall. Thus, the distances between the two walls and the goal and the distance between the goal and the landmark were all the same. The distance between the goal and each of the five potential positions of dogs in the encoding area was also altered. Position B was 432 cm from the goal, position A was 451 cm from the goal, position D was 473 cm from the goal and positions C and E were 511 cm from the goal. Finally, the camera was mounted over the new goal location.

3.1.3. *Procedure*

Shaping, training and testing were exactly the same as in Experiment 1. However, the four types of testing trials slightly differed (see Fig. 4). In the lateral tests, the landmark was moved 25 cm lateral to the right relative to the rear wall. In the perpendicular tests, the landmark was moved 25 cm perpendicular away from the rear wall. In the diagonal tests, the landmark was moved both 25 cm lateral and perpendicular to the rear wall. In the control trials, the landmark was moved and put back in place before the end of the 30 s retention interval. As in Experiment 1, within a session, each of the four types of testing trials was interspersed with 20 training trials and eight consecutive testing sessions were administered. Therefore, eight tests of each type were given to each dog.

3.1.4. *Data recording and analysis*

The extraction of frames and the analyses of images were performed as described in Experiment 1. However, due to focus adjustment resulting of the displacement of the camera over the new goal location, the calibration of the search area revealed that each pixel of a frame represented 0.30 cm of real search space on both axes in the search area.

3.2. *Results and discussion*

The dogs took a mean number of 5.33 (*SE* = 0.18) trials to attain the shaping criterion and a mean number of 11.33 (*SE* = 0.82) sessions to reach the training criteria.

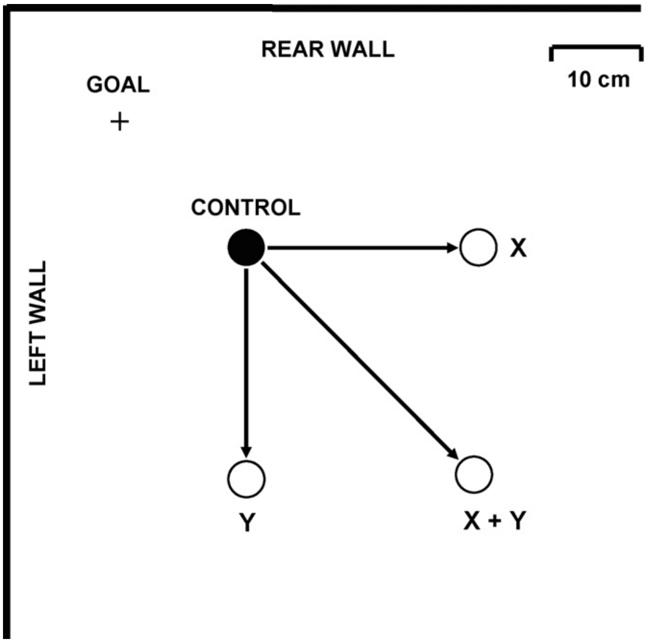

Fig. 4. The positions of the landmark on tests relative to the rear wall and the goal in Experiment 2. Closed circles represent the position of the landmark on control test and training trials. Open circles represent the position of the landmark on translation tests; X = lateral test, Y = perpendicular test, X + Y = diagonal test; the drawing is not at scale.

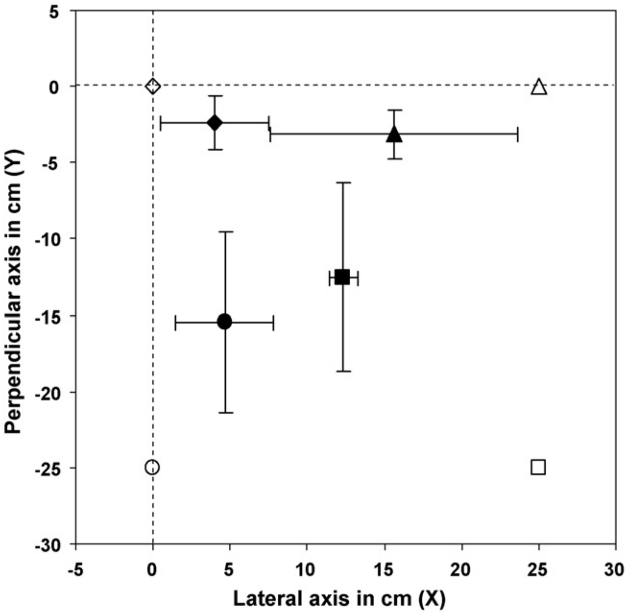

Fig. 5. Mean search locations for both *X* and *Y* axes for each test condition of Experiment 2. Horizontal and vertical bars illustrate 95% confidence intervals. The dashed lines indicate the *X* and *Y* axes from the origin (0, 0), which is defined as the position of the hidden object in training and control test trials. Closed symbols represent the mean search location of dogs for each condition. Open circles represent the predicted coordinates of the goal for the translation tests relative to the control position. The diamonds represent the control condition, the triangles represent the lateral condition, the circles represent the perpendicular condition, and the squares represent the diagonal condition.

In Testing, due to technical problems, two perpendicular and two lateral trials (distributed among three different dogs) were not recorded. In addition, one perpendicular trial was 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 2 shows the mean search location of each dog for each condition and axis. As one can see, there were some variations among the dogs for each condition and axis. However, the matrix of variances–covariances was uniform and the raw data were kept in the next statistical analyses.

Fig. 5 illustrates the mean search location of dogs as well as the predicted position for each type of test. First, it can be seen that in the control condition, the dogs' mean search location slightly differed from the goal location (coordinates 0, 0) on the *X* (95% CI = 0.487, 7.506) and *Y* (95% CI = 0.579, 4.131) axis. Similarly, the dogs' accuracy significantly differed from the goal coordinates on the *Y*-axis in the lateral condition (95% CI = 1.569) and on the *X*-axis in the perpendicular condition (95% CI = 1.458) as well. Consequently, although dogs were well trained to find the hidden object, they had some difficulties to accurately estimate position of the goal based on the distance between the landmark and the two perpendicular walls. Secondly, Fig. 5 strongly suggests that shifting the landmark along one of the two axes provoked a significant shift of search.

A within-subject ANOVA Lateral shift (shift, no shift) × Perpendicular shift (shift, no shift) × Axes (*X*, *Y*) performed on the mean search locations revealed a significant main effect of Lateral shift, $F(1, 5) = 29.87$, partial eta squared = 0.857, $p = 0.003$, and a significant main effect of Perpendicular shift, $F(1, 5) = 9.843$, partial eta squared = 0.663, $p = 0.026$, but no main effect of Axes, $F(1, 5) < 1$, partial eta squared = 0.025, $p = 0.736$. Thus, when the landmark was shifted perpendicularly (perpendicular and diagonal conditions) or laterally (lateral and diagonal conditions) relative to the rear wall, the dogs significantly shifted their search in the direction of the landmark shift. As predicted by the hypothesis, there were no differences between the two axes, revealing that the dogs shifted their search by the same extent on both axes.

The ANOVA also revealed a significant Lateral shift × Axes interaction, $F(1, 5) = 40.342$, partial eta squared = 0.890, $p = 0.001$, and a significant Perpendicular shift × Axes, $F(1, 5) = 37.884$, partial eta squared = 0.883, $p = 0.002$. Thus, when the landmark was shifted laterally, the dogs shifted their search on the *X*-axis but not on the *Y*-axis. In the same way, when the landmark was shifted perpendicularly, the dogs shifted their search on the *Y*-axis but not on the *X*-axis. Finally, there was no Lateral shift × Perpendicular shift interaction, $F(1, 5) = 3.922$, partial eta squared = 0.440, $p = 0.105$, nor

Table 2
Mean search locations of each dog for the four test conditions for each axis (*X* and *Y*) in Experiment 2. 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	−1.35	1.48	13.35	1.61	2.21	17.25	12.56	12.07
2	3.30	0.03	22.17	3.55	5.34	10.74	10.97	5.96
3	7.78	2.16	12.09	5.51	2.75	23.30	11.88	22.89
4	3.57	3.68	6.38	3.94	7.80	18.07	12.37	13.41
5	7.43	1.94	27.23	1.66	8.51	7.30	12.55	7.78
6	3.25	4.84	12.40	2.59	1.28	16.12	13.74	12.95

Lateral shift × Perpendicular shift × Axes interaction, $F(1, 5) < 1$, partial eta squared = 0.000, $p = 0.996$. Therefore, the displacement of the landmark on one axis did not influence the dogs' search on the other axis.

Then, I examined the extent by which the dogs shifted their search on each axis. Given that there was no interaction Lateral shift × Perpendicular shift, as in Experiment 1, pooled data were used to examine the extent of shifting for each axis. On the *X*-axis, the overall mean extent of lateral shifting was 9.65 cm (95% CI = 5.849, 13.454) and on the *Y*-axis, the overall mean extent of perpendicular shifting was 11.24 cm (95% CI = 6.083, 16.394). Thus, as confirmed by the previous ANOVA, there were no differences between the extent of shifting for both axes. In addition, because the upper limits of the 95% confidence intervals were well below 25 cm for both axes of the averaged conditions of Experiment 2, the dogs did not shift their search by the same extent than the one expected on the basis of the shift of the landmark.

Finally, the mean extent of lateral and perpendicular shifting was tentatively compared to the mean extent of perpendicular shifting observed in Experiment 1. To reduce the risk of making a type-I error, a corrected alpha level of 0.025 was used for each comparison. First, there were no significant differences between the mean perpendicular distance on the *Y*-axis of Experiment 1 ($M = 8.39$, 97.5% CI = 4.39, 12.93) and the mean perpendicular distance used in Experiment 2 ($M = 11.24$, 97.5% CI = 7.24, 15.24), $F(1, 10) = 1.755$, partial eta squared = 0.149, $p = 0.215$. Second, there were no significant differences between the mean perpendicular distance in Experiment 1 ($M = 8.39$, 97.5% CI = 5.29, 11.50) and the mean lateral distance on the *X*-axis of Experiment 2 ($M = 9.65$, 97.5% CI = 6.55, 12.76), $F(1, 10) < 1$, partial eta squared = 0.054, $p = 0.467$. As observed in Experiment 1, this pattern of results strongly suggests that the dogs averaged the distance from the landmark and the distance from the nearby wall to determine where to search.

In summary, Experiment 2 showed that the dogs shifted their search in the same direction than the shift of the landmark and not in the orthogonal direction. Moreover, the dogs shifted their search by the same extent on both axes, indicating that they independently encoded and used the distance from both walls, which were orientated in orthogonal directions. Furthermore, the extent of shifting was similar to the mean extent of perpendicular shifting observed in Experiment 1, suggesting that the dogs averaged the distance from the landmark and the distance from the nearby wall to determine where to search.

4. General discussion

The current study investigated whether domestic dogs primarily encode the perpendicular distance from an extended surface and whether they use distance from multiple cues to localize a spatial position. By contrast to the avian species tested so far (e.g. Gould-Beierle and Kamil, 1996, 1998, 1999; Cheng and Sherry, 1992; Spetch et al., 1992) and humans (e.g. Doeller and Burgess, 2008; Hartley et al., 2004), the present study clearly showed that domestic dogs do not predominantly use the perpendicular distance from a nearby extended surface. They rather simultaneously encode and use the distance from multiple cues to locate a spatial position. Most specifically, the dogs seemed to average the distance from a nearby wall and the distance from an individual landmark. Distances from some undetermined cues (e.g. walls, corners, window) appeared to be encoded and averaged as well.

Of particular interest is the support given by the present data to the predictions of the vector sum model, as initially observed in dogs by Fiset (2007). Whether the individual landmark was shifted 25 cm laterally, perpendicularly or diagonally relative to an extended surface (a wall), the dogs significantly shifted their search between 0 and 25 cm in the direction of the landmark shift and did not in the orthogonal direction. Thus, it seems that the dogs encode and use vectors from landmarks to find a spatial location. Nevertheless, one should be very careful before claiming that the spatial cognition of dogs for landmark use fully supports the predictions of the vector sum model. For example, there is evidence (Kamil and Jones, 1997, 2000; Cheng, 1994; Sturz and Katz, 2009) that birds encode direction and distance separately rather than combining them into a vector. Furthermore, whether or not domestic dogs use direction (bearings) from landmarks also remains to be empirically tested (for an example in birds, see Jones and Kamil, 2001; Kamil and Jones, 1997, 2000; Spetch et al., 2003). Interestingly, the Multiple Bearing Hypothesis (Kamil and Cheng, 2001) seems to be a viable approach to explain how dogs orient in the present experimental task. Indeed, the dogs could have remembered the goal's location by calculating separated bearings to a number of landmarks available in the room (e.g. walls, corners, window) and used them primarily for global orientation. The Multiple Bearing Hypothesis also assumes that distal cues are the primarily source of orientation for birds. However, given that the dogs tested in the present study were relatively large (their body length varied between 1.0 and 1.5 m long), it might be overstated to identify the walls or the corners of the room as distal cues. Indeed, the lateral walls and the corners were within 2 m from the goal and they possibly appeared relatively close to the dogs. This would also explain why dogs seemed to be sensitive to the distances from these cues and the goal when the landmark was shifted along a nearby wall.

The present results are also consistent with some current theories in the spatial domain. In an attempt to explain how the use of landmarks is controlled by cue-competition, Miller and Shettleworth (2007, 2008) have recently adapted Rescorla and Wagner's (1972) classical model of associative learning for geometry learning. Basically, their model assumes that different weights are attributed to different cues and predicts how these cues interact with each other to gain associative strength with the goal location. Although the current study was not aimed at testing Miller and Shettleworth's predictions, the present data clearly support the general idea that the distance from the walls and the distance from the landmark were subject to competition in order to be associated with the goal's location. For example, in the two experiments reported here, one wall and one landmark were at equal distance from the goal and the dogs searched precisely at midpoint along the line connecting the positions predicted by the wall and the individual landmark. Intriguingly, even if the wall was more salient than the individual landmark, it seems that the dogs attributed the same weight to both cues. This last observation therefore contrasts with the view that animals allocate more weight to prominent cues (Bennett, 1993) and raises several questions in regards to how dogs are sensitive to cue-competition. For example, do dogs allocate twice the weight to a landmark that is twice as close to the goal? Does dogs' averaging process of distance occur whatever the number of landmarks? In a similar vein, Cheng et al. (2007) lately used a Bayesian approach to evaluate how animals combine multiple cues to navigate. They suggested that when cues are too discrepant from each other, it is more appropriate for animals to use only one cue. However, when cues are not discrepant, combining cues seems to be a more appropriate way. In the present study, given that all visual cues (walls, landmarks, corners) pointed to the same target location and were within a reasonable distance from the dog, it may be argued that the cues were all similar, facilitating the averaging of multiple distances from landmarks to the goal.

Finally, how to explain that dogs average the distance from multiple cues whereas birds and humans principally use perpendicular distance from a nearby extended surface when available?

One plausible hypothesis could be that mammals and birds differ in the way distances from landmarks are weighted. However, given that both birds' and mammals' basic brain structures for spatial cognition are thought to be highly comparable and have possibly evolved from the same common ancestors (Rodriguez et al., 2002; Salas et al., 2003), the reasons underlying this possible difference in terms of landmark use remain unclear. Moreover, similar cue-competition phenomena (e.g. overshadowing and blocking) in the spatial domain have been observed in mammals (Doeller and Burgess, 2008; Spetch, 1995) and birds (e.g. Goodyear and Kamil, 2004; Spetch, 1995). Nevertheless, it should be pointed out that although previous studies strongly suggest comparable processes of spatial information in mammals and birds, it still remains to determine how humans weight distance from landmarks and extended surfaces when they are put into conflict in the real world (instead of a virtual environment as used by Burgess and his colleagues). To shed some light on this later question, experiments on landmark use, identical to those presented in the present article, are currently conducted in my laboratory with human adults as subjects.

In conclusion, the present study supports the interpretation that landmark-based spatial memory of domestic dogs is based on the metric properties of space. Most specifically, dogs accurately averaged the distance from multiple cues to find a spatial position. In conjunction with previous studies using an object permanence paradigm (Fiset et al., 2000, 2007), the present study also provides additional evidence that the domestic dogs encode and use divers cues when searching for a spatial location. Nevertheless, the present study also raises several questions in regards to the use of landmarks by dogs, mostly in terms of how they process cue-competition, and more studies are therefore needed to draw a more comprehensive picture of the spatial cognition in dogs.

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