



# 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.

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## 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 ani-

mal 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,

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