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ORIGINAL ARTICLE

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Egocentric search for disappearing objects in domestic dogs: evidence for a geometric hypothesis of direction

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Abstract In several species, the ability to locate a disappearing object is an adaptive component of predatory and social behaviour. In domestic dogs, spatial memory for hidden objects is primarily based on an egocentric frame of reference. We investigated the geometric components of egocentric spatial information used by domestic dogs to locate an object they saw move and disappear. In experiment 1, the distance and the direction between the position of the animal and the hiding location were put in conflict. Results showed that the dogs primarily used the directional information between their own spatial coordinates and the target position. In experiment 2, the accuracy of the dogs in finding a hidden object by using directional information was estimated by manipulating the angular deviation between adjacent hiding locations and the position of the animal. Four angular deviations were tested: 5, 7.5, 10 and 15°. Results showed that the performance of the dogs decreased as a function of the angular deviations but it clearly remained well above chance, revealing that the representation of the dogs for direction is precise. In the discussion, we examine how and why domestic dogs determine the direction in which they saw an object disappear.

Keywords Egocentric spatial information · Search behaviour · Domestic dogs · Direction · Distance

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Introduction

Recent animal studies on object permanence—the cognitive capability to mentally represent an object and its displacements through space—have focused on determining the spatial memory mechanisms underlying spontaneous search behaviour for a disappearing object (Fiset and Doré 1996; Fiset et al. 2000, 2003). The ability to find a hidden object is an adaptive component of predatory and social behaviour and it has been empirically demonstrated in several species (for a recent summary, see Neiworth et al. 2003). To successfully locate a hiding location, animals must encode and use different sources of spatial information. Literature on search behaviour and object permanence suggests that two kinds of spatial information can be used for this purpose: egocentric and allocentric spatial information (e.g. Bremner 1978a, b; Pick and Lockman 1981; Thinus-Blanc 1996; Tomlinson and Johnson 1991).

Allocentric spatial information refers to the relationships between an external spatial position and its surrounding objects (Fiset and Doré 1996; Nadel 1990; Pick and Lockman 1981; Tomlinson and Johnson 1991). There is evidence to suggest that animals mainly use two sources of allocentric spatial information to navigate: (1) the relationship between a spatial location and distinctive surrounding landmarks and (2), the relationship between a spatial location and the global spatial organisation (e.g. the shape) of its immediate environment (for an extensive review, see Gallistel 1990; Thinus-Blanc 1996). Allocentric spatial information provides flexibility because the animal can reach a spatial position by following different routes or trajectories and reorient itself according to the spatial relationships between the objects or the shape of the environment. However, an animal that relies on allocentric information is vulnerable to changes in the environmental conditions: if the position of the landmarks or the shape of the environment is modified, the animal may fail to locate the target position.

Egocentric spatial information refers to the directional information derived from the coordinates of the animal in space (Fiset and Doré 1996; Nadel 1990; Pick and

Lockman 1981; Tomlinson and Johnson 1991). For instance, dead reckoning (also known as path integration) is a sophisticated form of egocentric spatial information that is used by animals to keep track of their displacements and reorientations through space by encoding inertial information such as direction, distance, and speed in order to return to a desired location (for a summary, see Étienne et al. 1998). A simpler form of egocentric spatial information is known as linear egocentric information (Fiset and Doré 1996; Fiset et al. 2000) and it is used by animals to plan and maintain a single direct trajectory towards a location. From a Cartesian plan, linear egocentric information is defined as a linear relationship between two points in space where one point is the spatial coordinates of the animal and the second point is the target. Both forms of egocentric spatial information, however, are inflexible: if the relationship between the position of the animal and the target location is modified by environmental changes, such as a strong wind that shifts the animal to a new position, egocentric spatial information would orient the animal towards a wrong location. Nevertheless, when changes in the environmental conditions are improbable and the desired goal is close to the position of the animal, the use of egocentric spatial information is well adapted and suitable.

Fiset et al. (2000) performed a series of experiments to investigate which of these two sources of spatial information are used by domestic dogs to locate a disappearing object. In these experiments, the dog faced a row of three identical opaque boxes and saw an attractive object moving and disappearing behind one of the boxes placed in front of it. Then, an opaque barrier was introduced in front of the animal for a retention interval of 10 s. During this interval, all visual sources of allocentric spatial information (boxes, experimenter, walls) were systematically and drastically shifted to a new position in the experimental room. The results indicated that the dogs did not use any of these sources of allocentric information. Instead, they primarily searched for the hidden object straight ahead at the spatial position where they had seen the object disappear. Detailed video analyses revealed that the dogs did not rely on body or head orientation to find the object. Fiset et al. (2000) concluded that the dogs used a linear egocentric frame of reference to locate the hiding location. Furthermore, the data also revealed that the spatial encoding process of dogs is flexible and adapted to the circumstances: the dogs encoded allocentric information to locate the hidden object but did not base their search behaviour on it unless the spatial position determined by linear egocentric information was not available. This last observation supports recent studies that have demonstrated that animals simultaneously encode egocentric and allocentric spatial information to determine a route (Étienne et al. 1990, 1995a, b; Wehner et al. 1996). Finally, Fiset et al. (2000) concluded that the spatial encoding of the dogs is primarily based on linear egocentric information rather than on allocentric information when the environmental conditions of the search behaviour of a hidden object meet three criteria: (1) The goal to be attained must be visible from the encoding and starting position of the animal, (2) for a given trial, the encoding and starting position of the animal should be the same, and (3) no obstacle should be placed between the position of the animal and the goal so that the animal must be able to follow a direct and stable route in the direction of the goal. Consequently, if the environmental circumstances encounter those criteria when the animal encodes the position of the disappearing object, the use of linear egocentric spatial information is favoured.

Linear egocentric spatial information is regularly defined as a simple left and right distinction based on the body axis of the animal (Nadel 1990; O'Keefe and Nadel 1978; Thinus-Blanc 1996; Tomlinson and Johnson 1991). However, in Fiset et al.'s (2000) experiments, the localization of the hidden object necessitated a finer estimation of egocentric information because the smallest angular difference between two adjacent boxes and the position of the dog was approximately 13°. This led us (Fiset et al. 2000) to postulate that in a search of a hiding location, the dog must determine its route towards a target location by establishing its current position according to its own spatial position. Then, the dog must mentally represent an algebraic vector that starts from its current position and points towards the location of the disappearing object. A vector is a directed line segment between two points in space; its length represents the distance and its orientation represents the direction. In the present paper, we investigated the hypothesis that the vector components of distance and direction are both used by the domestic dogs to egocentrically locate an object they saw move and disappear.

There is a lot of evidence that a variety of animal species use an allocentric spatial strategy to navigate through the environment by computing, on different levels, the vector components of distance and direction between one external spatial position and the surrounding landmarks or the global geometry of its immediate environment. This can be observed in mammals (Cheng 1986; Collett et al. 1986; Étienne et al. 1990; 1995a, b; Margules and Gallistel 1988), birds (Bennett 1993; Cheng and Sherry 1992; Cheng 1988, 1989, 1990, 1994; Cheng and Spetch 1998; Gould-Beierle and Kamil 1996, 1998; Jones and Kamil 2001; Jones et al. 2002; Kamil and Jones 1997, 2000; Kelly et al. 1998; Spetch 1995; Spetch and Mondlock 1993; Spetch et al. 1992, 1996, 1997; Vallortigara et al. 1990), fishes (Sovrano et al. 2002, 2003; Vargas et al. 2004) and arthropods (Cheng 1998; Cartwright and Collett 1982, 1983). However, there is little evidence that animals egocentrically encode the vector components of distance and direction between their own spatial coordinates and a desired goal. Nevertheless, Brownell (1984) demonstrated that the sand scorpion locates a prey moving into the sand by estimating the distance and the direction between its own position and the prey. Interestingly, the sand scorpion does not rely on visual information to estimate these geometric components, but rather uses tactile information such as the vibrations produced by the prey moving into the sand. Other species, such as locusts (Wallace 1959) and gerbils (Ellard et al. 1984), are known to visually estimate with accuracy the distance between their own spatial position and a goal before initiating a jump.

To our knowledge, however, no study has yet investigated the geometric features of linear egocentric spatial information for search of a hidden object. In experiment 1 we investigated whether domestic dogs use the vector components of distance and direction between their own spatial coordinates and the hiding location. In experiment 2, we investigated the accuracy of the vector component of direction to locate a hiding position egocentrically. We designed these two experiments around the three criteria enumerated by Fiset et al. (2000) for the use of linear egocentric information in animals. Consequently, the current experimental setting is similar to the one used by Fiset et al. (2000) which ensured that the dogs did rely on linear egocentric spatial information to find the hidden object.

Experiment 1

In order to determine whether domestic dogs use geometric information to egocentrically locate a disappearing object, the vector components of distance and direction between the spatial coordinates of the animal and the hiding location were put in conflict.

Materials and methods

Subjects

Subjects were ten purebred adult dogs (*Canis familiaris*; three females and seven males, mean age of 2 years and 3 months, range 1–5 years) that belonged to private owners. They came from breeds classified as sporting dogs by the American Kennel Club (AKC 1992); (five Labrador retrievers, two golden retrievers, one German shorthaired pointer), non-sporting dogs (one Dalmatian) and terriers (one Border terrier). Five dogs had participated in an unrelated experiment 12 months before with different experimenters. The other five dogs were experimentally naive. The dogs were recruited through acquaintance of the researchers, and each owner received $5.00 for each visit made at their house by the experimenters.

The dogs were selected on the basis of two criteria. Firstly, they had to appear highly motivated by the opportunity to interact with the experimenters and to play with a ball or a rubber toy. Secondly, the dogs had to rely on visual information to search for the target object. Dogs that seemed to rely on smell by putting their muzzle on the floor surrounding the boxes and/or by intensively smelling the boxes when they searched for the target object were excluded from the study (n=1).

Apparatus

The target object was either a tennis ball or a rubber squeezable toy (several different rubber toys of various shapes and colours were used), depending on the preference of the dog. Each object was handled by a translucent nylon thread (125 cm) tied to it. One wooden box (16.5 cm wide×29.5 cm high×11.6 cm deep) without a back panel served to hide the target object. The box was painted white and its bottom was filled with lead bars to increase inertia. A rubber sheet (16.5 cm wide×29.5 cm high) cut into 1-cm strips was vertically fixed to the top of the open back of the box; it served to prevent dogs from viewing inside the box when they moved behind the box and forced the animals to insert their paw or muzzle inside the box to search for the target object. A second identical wooden box was also used in the testing phase.

A grey rubber carpet (210 cm wide×90 cm long) was placed in front of the animal (see Fig. 1). On the surface of the carpet were three front positions and three back positions where the box could be placed. All positions (16.5 cm wide) were marked on the carpet with adhesive grey tape and were not discernable from the position of the dog. The three front positions (A, B, C) were equidistant (1 m) from the position of the dog and the adjacent front positions were separated by 42 cm (from inner edge to inner edge). The three back positions (D, E, F) were equidistant (1.42 m) from the position of the dog (and consequently they were at 42 cm from the front positions) and the adjacent back positions were separated by 66 cm (from inner edge to inner edge). From the position of the dog, all adjacent positions (both front and back) were separated from each other by an angle of 30°. An opaque screen made of masonite (150 cm wide×156 cm high) was used to prevent the dogs from seeing the wooden box between the trials and also, from seeing it after the disappearance of the object within a trial. The opaque screen was manipulated by a plastic L-shaped handle screwed to the top edge. The experimenter (E1), who performed the manipulations, stood 50 cm behind the carpet; another experimenter (E2) gently restrained the dog during the manipulations and stood to the side of the dog. All dogs were unfamiliar to both experimenters.

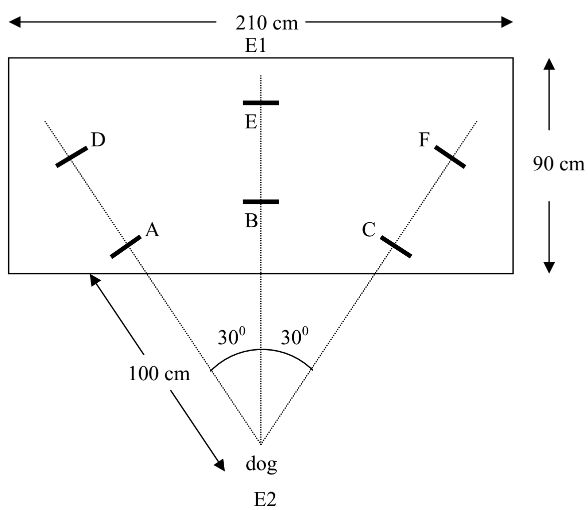

Fig. 1 Schematic representation of experimental setting used in experiment 1 (the drawing is not to scale). *E1* Experimenter 1; *E2* experimenter 2; *A, B, C* front positions; *D, E, F* back positions

The experiment was conducted in a large room (at least 4 m^2) in the house of the owner (or garage). The room was selected on the basis that we could conduct the experiment without being distracted. The experimental setting (boxes and carpet) was placed in the middle of the room in front of a bare wall and all prominent objects (chairs, tables, plants, etc.) were removed from the room or were moved behind the dog (out of sight). The door of the room (or garage) was closed to make sure that no noise disturbed the animal. All sessions were videotaped using a Panasonic camcorder (model PV-A208-K) which was perpendicularly placed at 150 cm to the left of the position of the dog.

Procedure

We divided the experiment into three successive steps: shaping, training, and testing. Shaping and training were administered during the first visit, whereas testing sessions were administered on 2 separate days within 7 days after the shaping and training sessions. The owner of the dog was allowed to watch the manipulations from behind the dog (at least 2 m) but did not interact with the dog.

Shaping

During shaping, the dogs were trained to touch the target object. Before each shaping trial, one box was randomly placed on one of the six positions on the carpet; it was never placed on the same location for two consecutive trials. To prevent the dog from seeing the displacement of the box from one position to another on the carpet between two trials, E2 introduced the opaque screen in front of the dog during the inter-trial interval of 30 s. At the end of the inter-trial interval, E2 removed the screen and E1 caught the attention of the dog. With the help of the nylon thread tied to the object, E1 moved the target object in front of the dog while E2 held the dog by its collar. Then, E1 randomly placed the object on the right or on the left of the box but not behind it. As soon as E1 put the object down, E2 released the dog. The dog was reinforced by E1 if one of the following behaviours was exhibited: grasping the object with its mouth, touching it with its paw or putting its muzzle on it. A piece of commercial dry food (Science Diet; Hill's Pet Nutrition, Topeka, Kan.) 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 near the target box for ten consecutive trials. All dogs met this criterion in ten trials.

Training

Five minutes after the end of shaping, the dogs were given a training phase where they learned that each position on the carpet had an equal probability of being a hiding location. At the beginning of each training trial, only one box was placed on the carpet. Within a training session, the object was hidden 4 times at each of the six potential spatial positions on the carpet. The hiding location (target box) changed from trial to trial so that the target object was never hidden at the same spatial location on two consecutive trials. Each trial was separated by a short inter-trial interval of 30 s. As in shaping, E2 introduced the opaque screen in front of the dog during the inter-trial interval to prevent the dog from seeing the displacement of the box from one position to another.

At the beginning of a training trial, E1 put down the target object in front of the dog while E2 gently restrained the animal by grasping its collar. Then, E1 lifted the object, caught the attention of the dog, moved the object visibly in front of the box and finally hid the object behind the target box where it remained hidden by the striped rubber sheet. Once the object had disappeared, E2 introduced the opaque screen in front of the dog for 5 s. The purpose of this manoeuvre was to habituate the dogs to the 5-s retention interval that was used later in testing. During this brief interval, E1 also made sure that the striped rubber sheet was uniformly replaced behind the box. At the end of the interval, E2 removed the screen and released the dog. To prevent cuing, E1 looked at E2 and remained immobile. If the dog introduced its paw or its muzzle through the striped rubber sheet at the back of the target box and found the object (success), it was reinforced. If the dog made no search attempt (no choice) or looked behind the box but did not insert its paw or its muzzle inside the box during the minute that followed its release (error), it was not reinforced.

Training ended when the dog met a criterion of 100% (24 out of 24 trials) during one training session. If the dog failed to meet the criterion, additional training sessions were administered over the next few days. Nine dogs took one session to meet the criterion and one dog needed an additional session, which was administered the next day.

Testing

Testing began the day after the end of training. Each testing session began following the administration of three shaping trials. On each testing trial, the general procedure was the same as in the training trials. E1 hid the target object behind the box. Then, the opaque screen was introduced by E2 in front of the dog for a 5-s interval. During this short retention interval, E1 performed the manipulations (experimental or control). During this brief interval, E1 also made sure that the striped rubber sheet was uniformly replaced behind the box. At the end of the retention interval, E2 removed the opaque screen and released the dog. To prevent cueing, E1 looked at E2 and remained immobile during the search behaviour of the dog.

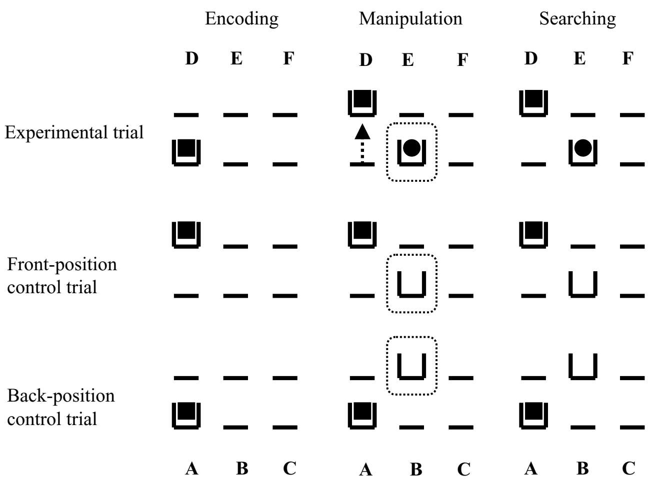

Fig. 2 Example of an experimental trial, a front-position control trial and a back-position control trial in the testing phase of experiment 1. The figure shows the positions of the target box (*open box*), the new box (*open box surrounded by a dotted line box*), the target object (*black square*) and the second target object (*black circle*) before (*Encoding*), during (*Manipulation*) and after (*Searching*) the test. The *dashed lines* show the displacement and the *arrows* show the direction and destination. For abbreviations, see Fig. 1

Experimental trials

In these trials, both directional and distance information were put in conflict. At the beginning of each trial, the target box was placed on one of the three front positions (A, B, or C) on the carpet (e.g. see Fig. 2). After the object was hidden inside the target box by E1, E2 introduced the opaque screen in front of the dog for a 5-s retention interval. During this interval, E1 moved the target box backwards to the same angular back position on the carpet. The target box was now 42 cm farther from the position of the dog but it was still in the same angle in relation to the encoding position of the dog. E1 also introduced a second box onto the carpet. This empty box was placed at a front position that was 30° to the left or right of the initial position of the target box. This second box was located at the same distance from the encoding position of the dog but it was located in a different direction (30°). The sequence of manipulation of the target box and of the second box within a single trial by E1 was randomly ordered from trial to trial. E1 also placed a second object, identical to the target object, inside the second box. Therefore, at the end of the manipulation, there was one target object inside both boxes. This procedure provided an equal probability of reinforcement for both directional and distance information. In the experimental trial illustrated in Fig. 2, dogs should have searched for the object at position D if they used the vector component of direction. If they used the vector component of distance, they should have searched for the object behind the box in position B. If they used both vector components of direction and distance, the dogs should have equally searched at both boxes or perhaps demonstrated behaviour interest at the spatial location of the target box at the time of encoding.

Control trials

Two types of control trials were used: front-position control trials and back-position control trials.

At the beginning of a front-position control trial, the target box was placed at one of the three back positions (D, E, or F) on the carpet (e.g. see Fig. 2). After the disappearance of the object inside the target box, E2 introduced the opaque screen in front of the animal. During the 5-s retention interval, E1 introduced an empty box, identical to the target box, at one of the front positions adjacent to the position of the target box. To control for the noise made in experimental trials, E1 lifted up the target box and put it back in its place. The sequence of manipulation of the target box and of the second box within a single trial by E1 was randomly ordered from trial to trial. At the end of the retention interval, the initial target location was still occupied by a box and the physical arrangement of both boxes on the carpet was similar to the one observed at the end of the experimental trials. If dogs used the vector components of distance and/or of direction to locate the hiding position in the front-position control trial as illustrated in Fig. 2, they should have searched successfully for the object at position D. If they were attracted to the new empty box located on a front position, they should have searched for the hidden object behind the box in position B and failed.

At the beginning of a back-position control trial, the target box was placed at one of the three front positions (A, B, or C) on the carpet (e.g. see Fig. 2). After the target object was hidden by E1 and E2 had introduced the opaque screen in front of the dog for a 5-s retention interval, E1 introduced an empty box at one of the back positions adjacent to the position of the target box. To control for the noise made in experimental trials, E1 lifted up the target box and put it back in its place. The sequence of manipulation of the target box and of the second box within a single trial by E1 was randomly ordered from trial to trial. At the end of the retention interval, the initial target position was still occupied by a box and the physical arrangement of both boxes on the carpet was identical to that observed at the end of the experimental trials. In the back-position control trial illustrated in Fig. 2, if dogs used the vector components of distance and/or of direction, they should have searched successfully for the object at position A. If they were attracted by the new empty box located on a back position, they should have searched for the hidden object behind the box in position E and failed.

We presented trials in sets; each set including one experimental trial, one front-position control trial, and one back-position control trial. Within a set, the three types of trials were randomly distributed. The spatial position of the target box at the beginning of each trial was randomly selected among the potential positions for each type of trials: positions A, B and C for the experimental and the back-position control trials and positions D, E and F for the front-position control trials. For example, the three trials in Fig. 2 could form a set. As in the shaping and the training phases, each trial was separated by a 30-s inter-trial interval where the opaque screen was introduced by E2 to prevent the dog from viewing the displacement of the box on the carpet between each trial. Each session was divided into ten randomly distributed sets of three trials each. Two testing sessions were administered to each dog on 2 separate days. Hence, at the end of testing, the dogs had been exposed to 20 experimental trials, 20 front-position control trials and 20 back-position control trials.

Video analysis

The search behaviour of the dogs in each experimental trial was analysed with the assistance of the video recording. The purpose of the video analysis was to detail the search behaviour of the dog while moving towards the boxes. Three types of search behaviour were considered: (1) direct search (from its starting position, the dog walked at constant speed and maintained the same course of direction towards the selected box), (2) indirect search (from its starting position, the dog directly walked towards a box but did not insert its paw or muzzle inside it; then, the dog moved towards a second box where it searched inside it for the hidden object), and (3) interrupted search (the dog temporary halted or hesitated when it crossed the empty spatial location where the target box was located at the beginning of the trial and then, selected one of the two boxes). Videotapes of the testing trials were viewed by E1 and by an independent judge. An inter-judge validity of 94.5% was observed. The judges solved disagreements by discussing and agreeing on the behaviours performed.

Results and discussion

Only two trials out of 600 did not result in a search attempt, revealing that the dogs were highly motivated to search for the hidden object.

Search behaviour

The objective of the analysis of search behaviour was to determine whether the vector components of distance and direction were individually or simultaneously used by the dog to egocentrically locate a disappearing object within a single trial. If they individually used one of the two vector components, the search behaviour of the dogs should have been direct toward the selected box. On the other hand, if the dogs simultaneously used both vector components, their search behaviour should have been indirect and/or interrupted.

In order to determine whether the dogs showed a specific pattern of search behaviour, the number of search attempts made as a function of each of the three types of search behaviour in the experimental trials was expressed as a percentage of the total number of search attempts made either to the box corresponding to the vector component of direction or to the box corresponding to the vector component of distance. For the box located as a function of directional information, the mean percentage of direct search (mean=89.47, SD=13.10) was high and the mean percentages of interrupted (mean=9.19, SD=13.40) and indirect search (mean=1.34, SD=2.83) were very low. For the box located as a function of distance information, the mean percentage of direct search (mean=92.90, SD=12.81) was high, the mean percentage of interrupted search (mean=7.10, SD=12.81) was low and there were no indirect searches (mean=0.00, SD=0.00). Because the percentages of search attempts made as a function of each of the three types of search behaviour were not independent, a non-parametric Friedman two-way ANOVA by ranks was used to verify whether the dogs showed a specific pattern of search behaviour for locating the hiding position. Therefore, the percentage of search attempts made as a function of each of the three types of search behaviour was transformed by ranks from 1 to 3 for each dog. Rank 1 was given to the lowest percentage and rank 3 was given to the highest percentage. Then, significant F-values were followed by multiple comparisons performed on the difference between the rank sums (Siegal and Castellan 1988). A first Friedman two-way ANOVA showed a significant difference between the three types of search behaviour made as a function of the vector component of direction, $Fr(2)=16.80$, $P<0.001$. Multiple comparisons tests ($P<0.05$) revealed that direct searches (mean rank=3.00) were higher than indirect (mean rank=1.33) and interrupted searches (mean rank=1.67), which did not differ. A second Friedman two-way ANOVA indicated a significant difference between the three types of search behaviour as a function of the vector component of distance, $Fr(2)=17.66$. Multiple comparisons tests ($P<0.05$) showed that direct searches (mean rank=3.00) were more frequent than indirect (mean rank=1.35) and interrupted searches (mean rank=1.65), which did not differ.

Put together, these results reveal that the dogs executed most of their search behaviours without any hesitation: they maintained their speed and direction towards the selected box and did not attempt to visit the other box. This observation indicates that within a single trial, the dogs did not simultaneously use the vector components of direction and of distance to locate the target object. They rather seemed to select only one vector component of linear egocentric spatial information, either the distance or the direction between their own spatial coordinates and the visited box. The analysis of the percentage of success was aimed at determining whether the dogs primarily used one of these two vector components of linear egocentric information throughout the entire experiment.

Analysis of success

In this experiment, the percentage of success expected by chance was 50% because if dogs searched randomly, they should have searched equally behind each of the two boxes.

In the testing trials, there were empirically no errors because the dogs were reinforced whether they searched for the hidden object behind one box or the other. Nevertheless, to simplify the analysis of results, we arbitrarily decided that the search attempts made at the box located as a function of the vector component of direction were quoted as success. For the same reason, the search attempts made at the box located as a function of the vector component of distance were quoted as errors.

Data screening revealed that one dog presented an abnormal search pattern by comparison to the other subjects. Overall, this dog showed a low percentage of success in the experimental trials (20%) and in the front-position control trials (25%) but it presented a very high percentage of success in the back-position control trials (95%). This pattern of results strongly suggests that this dog used a local rule to solve the problem: it systematically visited the nearest box from its starting position. None of the other dogs used this local rule. Since it did not rely on geometric information to locate a disappearing object, data for this dog were removed from the subsequent statistical analyses.

Figure 3 illustrates the mean percentage of success as a function of the three types of trials. A series of one-sample *t*-tests revealed that the mean percentage of success was higher than the chance level for back-position control [$t(8)=32.33, P<0.0001$], front-position control [$t(8)=3.45$, $P=0.0087$] and experimental trials [$t(8)=3.71$, $P=0.006$]. Therefore, the dogs succeeded in both types of control trials as well as in the experimental trials. Because success in experimental trials was associated with search attempts made as a function of directional information, it appears that in the conflicting task of experimental trials, the dogs significantly searched for the hidden object as a function of the direction by which they saw the object disappear. Inversely, the percentage of errors in experimental trials (mean=27.22, SD=16.22) was lower than chance level [$t(8)=-4{,}21$, $P=0.0056$] thus revealing that the dogs did not rely on the distance between their own spatial position and the target box to locate a hidden object.

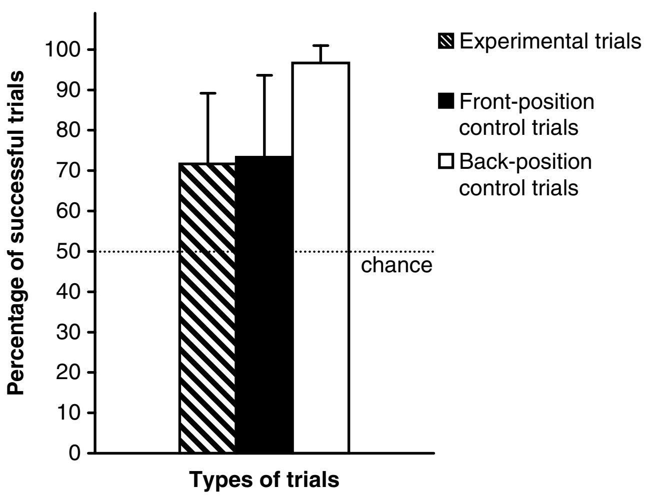

Fig. 3 Mean percentage of successful trials as a function of the types of trials (*error bars* represent SDs)

Analysis of errors

In order to determine why the dogs occasionally searched behind the box located as a function of the distance information in the experimental trials, we compared the percentage of errors in experimental trials with the percentage of errors in both types of control trials. The percentage of errors made at the second box (distance information) in the experimental trials was either due to the proximity of this box and the encoding position of the dogs or to the attraction of the dogs for this new object placed in the search area between encoding and searching. A within-subject ANOVA on the percentage of errors revealed a significant difference between the three types of trials, $F(2,16)=11.64$, $P=0.001$ [a factorial within-subject ANOVA (blocks of trials×sessions×types of trials) that is not shown here revealed that the percentage of errors was stable within and across sessions]. An a posteriori Newman-Keuls test ($P<0.05$) confirmed that the mean percentage of errors was lower in back-position control trials (mean=3.33, SD=4.33) than in experimental (mean=28.33, SD=17.5) and front-position control trials (mean=26.67, SD=20.31), which did not differ. The absence of significant differences between experimental and front-position control trials strongly suggests that the percentage of errors made at the box corresponding to the vector component of distance in the experimental trials was due to the close proximity between this box and the encoding position of the dog. This conclusion is supported by the fact that the percentage of errors in the back-position control trials was lower than in the front-position control trials. In these latter trials, when the dogs searched behind the second box, they did it because it was the nearest box from their starting position and not because they were attracted to the second box in the search area. Otherwise, the dogs would have failed a greater number of back-position control trials and the performance would have been similar in both types of control trials.

In summary, the statistical analyses indicate that in experiment 1, the dogs primarily searched as a function of only one vector component when they used linear egocentric spatial information to locate a hiding position, which was the direction in which they saw the object disappear.

Experiment 2

In experiment 2, we estimated the accuracy of dogs to egocentrically locate a disappearing object using the vector component of direction. In this experiment, we tested dogs in conditions where the angular deviation between two adjacent boxes and the position of the animal varied between 5 and 15°.

Two approaches for manipulating the angular deviation between two boxes and the position of the animal were possible. One was to increase the spatial separation between the adjacent boxes and to keep constant the distance between the animal and the boxes. Another approach was to increase the distance between the dog and the potential hiding boxes and to keep constant the spatial separation between two adjacent boxes. We used the second approach because the results of experiment 1 revealed that linear egocentric search for disappearing objects in dogs is not influenced by the distance between the spatial coordinates of the dogs and the hiding position. In experiment 1, when the target box was moved backward, the dogs still searched egocentrically by using exclusively directional information. In addition, Harrison and Nissen (1941) have demonstrated the influence of spatial separation of adjacent food containers in chimpanzees: the greater distances between containers were associated with better performance. Consequently, to avoid the rival hypothesis that the spatial separation between the adjacent potential hiding locations would have added distinctiveness to the boxes, we discarded this approach. Therefore, in experiment 2, we manipulated the angular deviation between the boxes by varying the distance between the animal and the hiding boxes.

Materials and methods

Subjects

Seven purebred adult dogs (*Canis familiaris*; two females and five males, mean age of 4 years, range 2–6 years), which belonged to private owners, participated in this experiment. They came from breeds classified by the American Kennel Club (AKC 1992) as sporting dogs (three Labrador retrievers and two golden retrievers), non-sporting dogs (one Dalmatian), working dogs (one boxer) and herding dogs (one German shepherd). Three dogs were naive and four dogs had participated in experiment 1. They were recruited and selected on the same basis as in the previous experiment.

Apparatus

The apparatus was the same as in experiment 1 except for the carpet dimensions, the number of boxes and their positions on the carpet. The grey rubber carpet was 552.45 cm long × 184.65 cm wide (Fig. 4). It included four rows that where located at 165 cm (R1), 247.50 cm (R2), 330 cm (R3) and 495 cm (R4) from the starting position of the dog. Each row included four positions (A, B, C, D) where it was possible to place the four boxes. The positions were in a semi-circle and were equidistant from the position of the dog. Adjacent positions were separated by 45 cm.

Procedure

Experiment 2 was conducted at the house of the respective dog's owner. Four dogs were tested in a room (basement or garage) and three dogs were tested in the backyard. When

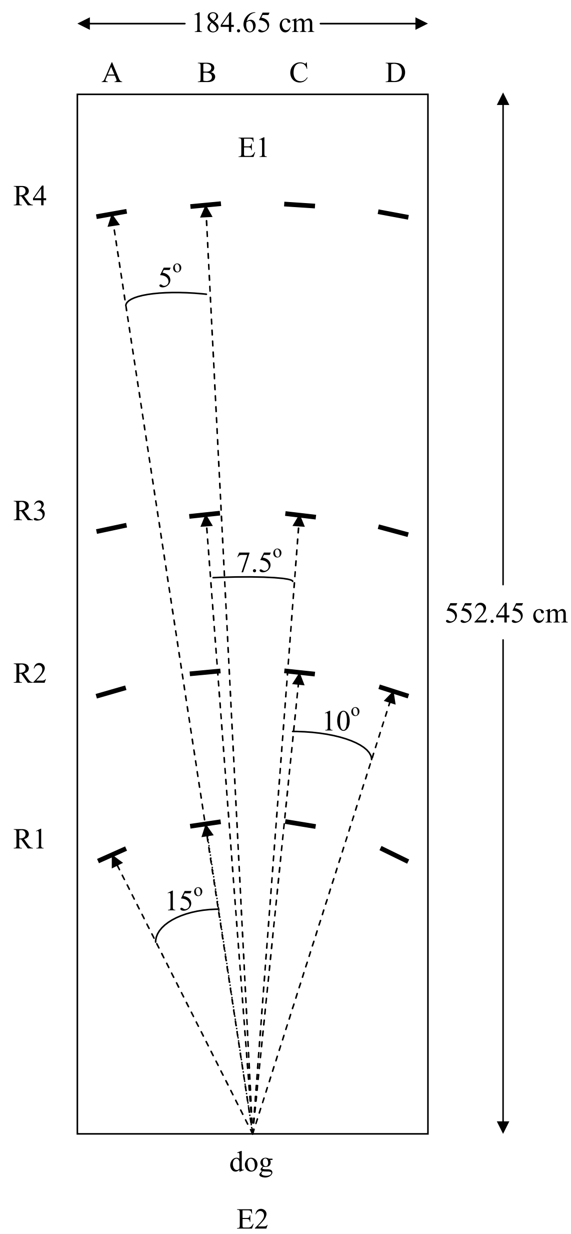

Fig. 4 Schematic representation of the experiment setting used in experiment 2. The drawing is not to scale. *A, B, C, D* Potential positions of boxes on the carpet; *R1, R2, R3, R4* potential rows on the carpet; *5°, 7.5°, 10°, 15°* angular deviation between two adjacent potential positions on the carpet and the position of the dog

the experiment was conducted in a room, the experimental environment was set up as in experiment 1. When the experiment was conducted in the backyard, we made sure that the dogs were not disturbed by distracting noises or visual stimuli. We divided the experiment into three successive steps: shaping, training, and testing.

Shaping

Shaping was identical to that of experiment 1 except that the box was randomly placed on one of the 16 potential positions on the carpet. All dogs met the shaping criterion in ten trials.

Training

Training began 5 min after the end of shaping. During this phase, the dogs learned that the boxes could be placed on different positions on the carpet and at different distances from their encoding position. In each training trial, two boxes were used. They were always placed on positions A and D on the carpet, and from trial to trial, they were randomly put on one of the four rows (R1, R2, R3, R4). For each row, the angular deviation between the two boxes (computed from centre to centre) and the dog's encoding position was 45° (R1), 30° (R2), 22.5° (R3) and 15° (R4). In a training session, each position (A and D) was used twice as target location for each row (R1, R2, R3, R4) for a total of 16 training trials. Each trial was separated by a 30-s inter-trial interval in which E2 introduced the opaque screen in front of the dog to prevent the dog from seeing the displacement of the two boxes from one position to another on the carpet.

At the beginning of a training trial, E1 put down the target object in front of the dog while E2 gently restrained the animal by grasping its collar. Then, E1 lifted the object, moved it visibly in front of the two boxes and finally hid the object inside the target box from behind which it remained hidden by the striped rubber sheet. Once the object had disappeared, to prevent cueing, E1 looked at E2 and remained immobile. Then, E2 introduced the opaque screen in front of the dog for 3 s. During this brief interval, E1 made sure that the striped rubber sheet was uniformly replaced behind the box. At the end of the interval, E2 removed the screen and released the dog. E1 still looked at E2 and remained immobile. Successes and errors were quoted according to the same criteria as those used in experiment 1.

Training ended when dogs met a criterion of 81.25% (13 successful trials out of 16) and no more than two errors where made at the same position (A or D). If the dog failed to meet this criterion, additional training sessions were administered over the next few days. All dogs took one session to meet the training criterion. There was only one error out of the 112 training trials and it occurred when the target object was hidden behind a box located on position D on row R1, that is, when the target location was close to the encoding position of the dog. This high level of performance in the training phase supports observations by Fiset et al. (2000) indicating that dogs can find a hidden object when the angular deviation between two adjacent boxes and the position of the dog is at least 15°.

Testing

Testing began the day following the end of training and each testing session began following three shaping trials. The general procedure was the same as in the training phase. E1 showed the object to the dog and hid it inside the target box. Then, E2 introduced the opaque panel for a 3-s interval and E1 made sure that the striped rubber sheet was uniformly placed behind the box. At the end of the interval, E2 removed the opaque panel and released the dog. To prevent cueing, E1 looked at E2 and remained immobile during the search behaviour of the dog.

In a testing session, the four boxes were used and they were placed on each position (A, B, C, D) on the carpet. From trial to trial, the boxes were randomly placed on one of the four rows (R1, R2, R3, R4) on the carpet. For each row, the angular deviation between adjacent boxes from the encoding position of the dog was 15° (R1), 10° (R2), 7.5° (R3) and 5° (R4).

The target object was hidden 5 times behind each of the four positions (A, B, C, D) for each of the four angular deviations, for a total of 80 trials that were distributed over four sessions. The order of the four sessions was counterbalanced among dogs and was administered within 7 days. A 30-s inter-trial interval was introduced between each testing trial.

Results and discussion

There was no test trial without a search attempt, indicating that the dogs were highly motivated to search to the target object. During testing, the percentage of success expected by chance was 25% because if the dogs searched randomly, they should have searched equally behind each of the four boxes.

Figure 5 illustrates the mean percentage of successful trials as a function of the four angular deviations. The performance of the dogs decreased as a function of the angular deviation as indicated by a within-subject ANOVA on the percentage of success, $F(3, 18)=4.70$, $P=0.0136$ [a factorial within-subject ANOVA (angle$\times$position$\times$session) not shown here revealed that for each angular deviation, the performance of the dogs was stable between sessions and

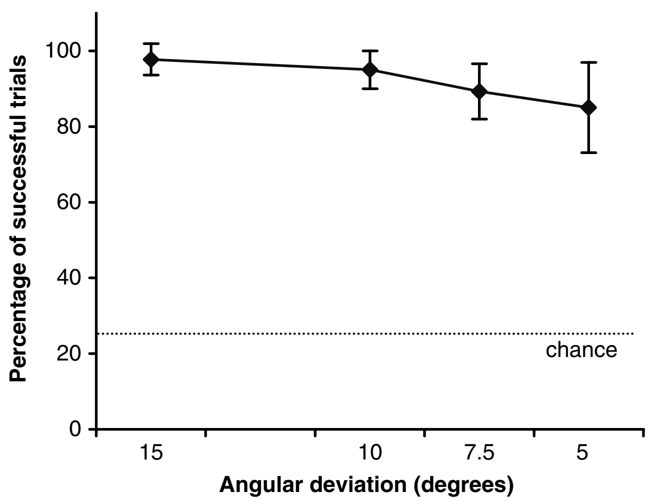

Fig. 5 Mean percentage of successful trials as a function of the four angular deviations between the boxes in the testing phase of experiment 2 (*error bars* represent SDs)

that the position of the target box within the row of the four boxes did not influence the dogs' performance]. An a posteriori Newman-Keuls test ($P<0.05$) revealed that the performance of the dogs was significantly higher when the angular deviation between the boxes was 15° (mean=97.74, SD=3.83) than when it was 5° (mean=85.03, SD=11.02).

Although the mean performance of the dogs decreased as a function of the angular deviation between the boxes, it remained very high (≥80%). A series of one-sample *t*-tests revealed that the mean percentage of success was greater than chance for each angular deviation [15°, $t(6)=46.49$, $P<0.0001$; 10°, $t(6)=37.04$, $P<0.0001$; 7.5°, $t(6)=23.24$, $P<0.0001$; 5°, $t(6)=13.35$, $P<0.0001$].

Put together, the results of experiment 2 clearly indicate that the vector component of direction used by the domestic dogs to egocentrically locate a hidden object was very accurate, even if the angular deviation between adjacent boxes from the encoding position was as low as 5°.

General discussion

The objective of the present study was to investigate the geometric components of linear egocentric spatial information used by domestic dogs for locating a disappearing object. To reach this goal, the experimental setting used in the present study met the three criteria enumerated by Fiset et al. (2003) which support the use of linear egocentric spatial information in dogs. Given these environmental conditions, the results of the present study suggest: (1) that domestic dogs primarily use the geometric component of direction when they use linear egocentric spatial information to locate a hidden object, and (2) that their egocentric estimation of the direction in which the object has disappeared is accurate.

Since our experimental paradigm involved a face to face interaction between the dog and the experimenter who manipulated the target object (E1), one could argue that the dogs did not use linear egocentric spatial information but rather solved the task by using involuntary perceptual cues provided by E1. However, it should be reminded that E1 made certain not to give any cues to the dog: she remained totally immobile and looked at E2 during the entire search by the dog. As a consequence, we did not see any behaviour (e.g. head raising, fixation) suggesting that the dogs were looking at E1. Similarly, one could also argue that the dogs used their sense of smell for finding the hidden object. However, we did not see any behaviour suggesting that the dogs were using odour cues. They neither lowered their muzzle to the ground nor sniffed the boxes. These observations were supported by the video analysis of experiment 1 which revealed that the dogs did not interrupt their search behaviour but rather walked at constant speed and maintained the same course of direction towards the selected box.

This study was based on the assumption that the domestic dogs compute vector components of direction and distance to egocentrically locate a disappearing object. Vector computations of distance and direction require a very precise evaluation and they are likely to be successful the closer the animals are to the objects (Thinus-Blanc 1996), or to the hiding location of an object, as in the present task. Although experiment 1 met this condition (the target box was located at 100 cm from the position of the animal), it appears that the dogs did not use the distance between their own spatial coordinates and the hiding box. Why did dogs only rely on the direction in which they saw the object disappear? We presume that the dogs used the direction because, during ontogeny, they might have learned through instrumental learning that in searching for a hidden object, it does not matter whether the spatial position of the disappearing object is close or far from their starting position because sooner or later they will inevitably encounter the target position if they maintain the right direction. Nevertheless, there is evidence that dogs can use the vector component of distance to egocentrically locate a position in space. Séguinot et al. (1998) have investigated how domestic dogs estimate distance and direction to return to a starting position after they have walked an L-shape path in the absence of visual and olfactory information. Although they overestimated the angle of deviation by about 6° and underestimated the distance of the return vector by about 6%, the dogs demonstrated the ability to egocentrically encode and use the vector components of distance and direction. Although the study by Séguinot et al. (1998) investigated a more complex form of egocentric information, that is, dead reckoning, we cannot reject the possibility that the dogs encode the distance when they use linear egocentric spatial information to locate a hidden object. Therefore, we suggest that the vector component of distance may play a secondary role in limiting the searching behaviour of dogs in the vicinity of the hiding location in relation to the taken route. After walking an approximate distance from its starting position, if it does not cross the target location, the dog possibly begins to search for the hidden object in another direction. These last hypotheses, however, are speculative and need to be empirically tested.

Our results also raise the question of how linear egocentric spatial information is represented in dogs to locate a disappearing object and how it is related to the other sources of spatial information. First, we propose that the dogs construct a cognitive map of their environment by encoding the allocentric spatial information available in the environment. The concept of a cognitive map, which was initially proposed by Tolman (1948) and extensively explored in several species in the last 25 years, assumes that animals create a spatial representation of the external world to navigate and find locations. Gallistel (1990) has extended this notion of cognitive map and has suggested that animals encode and use the geometric components of distance and direction among landmarks to navigate. Although the concept of a geometric cognitive map has not been yet explicitly investigated in domestic dogs, there are evidences that dogs construct an allocentric representation of their immediate environment by reference to some prominent landmarks. Several studies have shown that the dogs can solve detour (Chapuis et al. 1983), inverse trajectory (Chapuis 1982), shortcuts (Chapuis and Varlet 1987) and object permanence (Fiset et al. 2000) tasks by encoding and using allocentric spatial information. Therefore, in searching for a disappearing object, the dogs probably position themselves in this cognitive map by encoding the relationships between their own position and the prominent landmarks. Gallistel (1990) called "egocentric percepts" the segments of the world perceived from the viewpoint of the animal in relation to the objects in space. The dogs can only find an object they saw disappear behind an obstacle once they have established this cognitive map. Then, by reference to their cognitive map, the dogs determine the angular deviation between their own spatial coordinates and the location where they saw the object disappear. It is this last form of representation that corresponds to linear egocentric spatial information. Finally, if there is no obstacle between the animals and the desired location, the dogs can reach the hiding position of the object by maintaining the right direction from their starting point towards the target position.

In conclusion, the present study represents one of the first attempts to investigate the underlying mechanisms of linear egocentric spatial information in animals and it reveals that domestic dogs primarily use an accurate directional code to locate a disappearing object. Nevertheless, more studies are called for to determine whether dogs encode the distance between their own spatial position and the hiding location when they use linear egocentric spatial information to find a hidden object.

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