Anim Cogn (2007) 10:211–224
DOI 10.1007/s10071-006-0060-5

ORIGINAL ARTICLE

Invisible displacement understanding in domestic dogs (*Canis familiaris*): the role of visual cues in search behavior

Sylvain Fiset · Valérie LeBlanc

Received: 17 October 2005 / Revised: 2 November 2006 / Accepted: 3 November 2006 / Published online: 13 December 2006

Abstract Recently, (Collier-Baker E, Davis JM, Suddendorf T (2004) J Comp Psychol 118:421–433) suggested that domestic dogs do not understand invisible displacements. In the present study, we further investigated the hypothesis that the search behavior of domestic dogs in invisible displacements is guided by various visual cues inherent to the task rather than by mental representation of an object's past trajectory. Specifically, we examined the role of the experimenter as a function of the final position of the displacement device in the search behavior of domestic dogs. Visible and invisible displacement problems were administered to dogs ($N = 11$) under two conditions. In the Visible-experimenter condition, the experimenter was visible whereas in the Concealed-experimenter condition, the experimenter was visibly occluded behind a large rigid barrier. Our data supported the conclusion that dogs do not understand invisible displacements but primarily search as a function of the final position of the displacement device and, to a lesser extent, the position of the experimenter.

Keywords Object permanence · Experimenter cues · Invisible displacements · Visible displacement · Search behavior · Domestic dogs · Visual cues

S. Fiset (✉)
Secteur Sciences Humaines,
Université de Moncton,
Campus d'Edmundston,
Edmundston, New-Brunswick, E3V 2S8 Canada
e-mail: sfiset@umce.ca

V. LeBlanc
École de psychologie, Pavillon Félix-Antoine-Savard,
Université Laval,
Laval, Québec, G1K 7P4 Canada

Introduction

In several species, the knowledge that objects still exist when out of sight is of great adaptive value for survival. For instance, predators must be able to find prey that has suddenly disappeared behind a tree without having to learn its position by trial and error. In the last 25 years, the Piagetian framework of object permanence has provided a suitable approach (both methodologically and theoretically) to determine how animals spontaneously represent physical and/or social objects that are no longer visible (for a review, see Doré and Dumas 1987; Pepperberg 2002). This approach has been extensively used in the field of comparative cognition to identify and compare the upper limits of object representation in several avian and mammal species. Recently, however, Collier-Baker et al. (2004, 2006) pointed out that the testing and control procedures used to administer object permanence tasks have largely varied and they questioned the level of object representation attributed to diverse species. In the present study, we introduced further control procedures aimed at investigating the upper limits of object permanence in the domestic dog.

According to Piaget (1937), object permanence gradually develops during ontogeny through the interaction between an organism and its surrounding physical world. In human infants, object permanence progresses through a series of six distinctive stages within the first 2 years of life. In the first stages, search attempts to find a disappearing object are either absent or limited. Understanding of object permanence is fully functional when the child reaches Stage 5 (12 months of age). This stage is typically assessed with a visible displacement problem in which the subject faces an experimenter and a number (between 2 and 5) of identical hiding locations (e.g., boxes or wells). Then, the experimenter visibly moves and hides an attractive object inside one of the hiding locations. In Stage 5a, the subject is able to solve single visible displacement problems in which the object is hidden inside one of the locations. In Stage 5b, the subject can succeed on double visible displacement problems in which the object is first moved inside one of the hiding locations and then it reappears before disappearing inside a second one. Organisms that achieve Stage 5 are well adapted to interact with physical or social objects in their immediate environment. For example, they can spontaneously pursue and locate disappearing prey. They can also remember and predict the position of social partners that have moved and momentarily disappeared from view. Comparative cognition studies have shown that several species demonstrate the ability to solve single and double visible displacement problems, including dogs (Triana and Pasnak 1981; Gagnon and Doré 1992, 1993, 1994), cats (Gruber et al. 1971; Triana and Pasnak 1981; Thinus-Blanc et al. 1982; Doré 1986; Dumas and Doré 1989, 1991), chimpanzees (Mathieu et al. 1976; Spinozzi and Potí 1993; Call 2001), gorillas (Wood et al. 1980; Natale et al. 1986), orangutans (De Blois et al. 1998; Call 2001), several species of monkeys (Parker 1977; De Blois and Novak 1994; Neiworth et al. 2003; Mendes and Huber 2004), psittacine birds (Pepperberg and Kozak 1986; Pepperberg and Funk 1990; Funk 1996; Pepperberg et al. 1997), and magpies (Pollok et al. 2000).

In Stage 6, however, the task is more demanding and the organism must infer the displacement of an object from an indirect visual cue. Stage 6a is assessed with a task called the single invisible displacement problem in which the experimenter first inserts an object inside a displacement device, typically a small opaque container (e.g., a cup). Then, he moves the displacement device inside one of the boxes placed in front of the subject. There, he imperceptibly transfers the object from the displacement device to the target box. In double invisible displacement problems (Stage 6b), the experimenter moves the displacement device inside a first box and subsequently to a second box and the target object can be transferred from the device to either one of the two visited boxes. In double invisible displacements, because the target object can logically be at either location, the subject is given a second choice if he first chooses the visited box that is empty. To succeed on invisible displacement problems, an organism must encode a representation of the target object, ignore the initial hiding location (the displacement device), and infer the invisible displacement of the object by relying on the visual cue (empty displacement device) to deduce where the object is. Organisms that are able to solve invisible displacements are thought to be able to mentally manipulate their own representations to guide their behavior and actions (Suddendorf and Whiten 2001).

In human infants, the ability to solve invisible displacement problems occurs at 18–24 months of age (Piaget 1937). Besides humans, however, very few nonhuman species have shown the capacity to understand invisible displacements. Actually, only great apes (Mathieu et al. 1976; Redshaw 1978; Wood et al. 1980; Natale et al. 1986; De Blois et al. 1998; Call 2001; Barth and Call 2006; Collier-Baker et al. 2006) have shown convincing and persistent evidence that they have the ability to solve invisible displacement problems. Nevertheless, apes have difficulties with standard double invisible displacements in which the displacement device visits two nonadjacent boxes in a linear array (see De Blois et al. 1998; Call 2001; Collier-Baker and Suddendorf 2006). As for monkeys, the results are still controversial and more experiments are needed (Collier-Baker et al. 2006). For example, Mendes and Huber (2004) presented evidence that common marmosets are able to cope with single invisible displacements. However, large individual differences among the marmosets suggest that prior experimental testing instead of representational capability may explain the performance of the successful monkeys. Finally, although psittacine birds have consistently passed invisible displacement tests (Pepperberg and Kozak 1986; Pepperberg and Funk 1990), more rigorous control procedures are necessary before claiming they can represent an object's past trajectory (Collier-Baker et al. 2004).

Until recently, the domestic dog was labeled as one of the rare species that understood invisible displacement problems. Most of this credit was attributable to Gagnon and Doré (1992, 1993, 1994) who extensively investigated the upper limits of object permanence in dogs and its ontogenetic development. First, they revealed that object permanence in dogs follows the same developmental stages as in humans but at different developmental rates where Stages 4 and 5 are acquired more rapidly (Gagnon and Doré 1994). Second, they found that dogs partially solved invisible displacements because they performed above chance in this kind of problem. However, because the performance of dogs was lower in invisible than in visible displacement problems, they also investigated the possibility that dogs might have used olfaction, visual fixation, or a local rule learning, such as "Always pick the box that has contact with the container" or "Always pick the box that last had contact with the container," to solve invisible displacement problems. However, they found no alternative explanations. Consequently, Gagnon and Doré (1992, 1993) concluded that dogs were able to infer invisible displacements to some extent.

However, Collier-Baker et al. (2004) recently reported that dogs failed single invisible displacements when tested under more rigorous conditions. In their study, they compared the performance of dogs in standard invisible displacements with four control conditions: the head and upper body of the experimenter who performed the manipulations were hidden behind a curtain, the first or the last box visited by the displacement device was not the target box, and the final position of the displacement device relative to the target box was systematically controlled. Although the performance of dogs was similar to chance level when the last box visited by the displacement device was not the target box, it was apparent that the final position of the device mainly controlled the search behavior of dogs. Indeed, dogs succeeded on invisible displacements when the final position of the displacement device was adjacent to the target box but failed the tests when the device was nonadjacent. This effect was also observed in the three other control conditions in which adjacent and nonadjacent positions of the displacement device were randomly distributed. By consequence, Collier-Baker et al. concluded that domestic dogs are incapable of representing invisible displacements and they suggested that dogs succeed on standard invisible displacement problems by utilizing an associative rule such as “Search at the box adjacent to the final position of the displacement device”.

On the contrary, Collier-Baker et al. (2004) did not demonstrate that domestic dogs use social cues inadvertently provided by the experimenter to solve invisible displacements. To control for the presence of the experimenter who performed the manipulation, they suspended a 50 cm high opaque curtain above the hiding boxes. This curtain hid the experimenter’s head and upper body and it prevented the dog from using the experimenter’s gaze or head movement to locate the hidden object. In Experiment 2 of Collier-Baker et al., the performance of dogs was at chance when the curtain was present, suggesting that in the standard condition, the dogs might have used subtle cues involuntarily provided by the experimenter. This effect, however, was not replicated in Experiment 3 and the authors concluded that dogs do not use this kind of cue to locate the object in invisible displacements.

This last observation is surprising because recent investigations have indicated that domestic dogs are sensitive to a variety of human social cues. For instance, the domestic dog has shown considerable abilities to use human signals such as pointing, head and body orientation, eye gaze, and visual attention to locate hidden food (Miklósi et al. 1998, 2003; Hare and Tomasello 1999; Agnetta et al. 2000; McKinley and Sambrook 2000; Hare et al. 2002; Bräuer et al. 2006; Riedel et al. 2006). Nevertheless, although visible and invisible displacement problems of object permanence involve a face-to-face interaction between a subject and an experimenter, the possible influence of involuntarily cues provided by the experimenter (called “the Clever Hans effect”) has not received considerable attention in the field of comparative cognition. In support for this lack of interest, Pepperberg (2002) argued that (1) more direct perceptual cues are inherent in the task, (2) obvious pointing does not help the organism that does not understand the task, and (3) most experimenters control those cues by wearing smoke glasses or by looking straight ahead. In spite of these arguments, there is a possible explanation for why Collier-Baker et al. (2004) did not find an effect of the experimenter on dogs’ performance in invisible displacements. Indeed, although the opaque curtain hid the head and shoulders of the experimenter who performed the manipulations, the dogs could partially perceive the experimenter because her lower body was still visible. Therefore, it remains possible that dogs increased their level of success in invisible displacements by using indirect visual cues provided by the experimenter’s legs and/or hands while she was manipulating the object and the displacement device.

In the present study, we introduced further controls to investigate the hypothesis that the search behavior of domestic dogs in invisible displacements is guided by various visual cues inherent to the task rather than by representation of an object’s past trajectory. First, we reinvestigated whether the performance of dogs in invisible displacements is influenced by visual cues inadvertently provided by the experimenter. Contrary to Collier-Baker et al. (2004) who used a curtain to hide the upper body of the experimenter, we introduced a large rigid barrier that hid the entire head and body of the experimenter who performed the manipulations, therefore eliminating the possibility of experimenter cues. Two conditions were administered to dogs. In one condition, the experimenter was visibly occluded behind the opaque barrier whereas in the other condition, the experimenter was visible as in the standard procedure. In both conditions, visible and invisible displacement problems were given to dogs in order to determine if the influence of the experimenter depended on the complexity of the task.

Second, given that previous comparative studies have repetitively supported the conclusion that domestic dogs do understand invisible displacements (Triana and Pasnak 1981; Pasnak et al. 1988; Gagnon and Doré 1992, 1993, 1994), it was of particular interest to corroborate the influence of the displacement device on dogs’ search behavior in invisible displacements. As pointed out by Collier-Baker et al. (2004), methodological variations could explain to some extent why their data differ from those previously observed by Gagnon and Doré (1992, 1993). Among the various possibilities they explored, the number of boxes and the final position of the container on the search area appear to be the most probable. In Gagnon and Doré’s studies, there were four boxes and the final position of the container was always at either end of the array of boxes. In Collier-Baker et al.’s experiments, however, there were three boxes and the container was placed at either end of the array or between two adjacent boxes. Although it is not clear how these minor methodological variations could account for the large impact of the displacement device observed in Collier-Baker et al.’s study, the final position of the displacement device between adjacent boxes certainly added visual information to dogs. Therefore, to rule out those rival hypotheses, in the current study we replicated the experimental setup used by Gagnon and Doré (1992, 1993): four hiding boxes were equally distributed on the platform and the displacement device was always placed at either end of the array of boxes.

Method

Subjects

We used 11 purebred adult Labrador retrievers (*Canis familiaris*; 5 females and 6 males, mean age of 4 years and 10 months, range from 2 to 7 years) that belonged to private owners. The Labrador retriever is a breed classified as sporting dog by the American Kennel Club (AKC 1992).

The dogs were selected on the basis of two criteria. First, they had to be highly motivated by the opportunity to interact with the experimenters and to play with a ball or a rubber toy. All dogs showed a strong interest toward the target object. Second, 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. Only one dog out of 12 that were screened had to be rejected based on these criteria.

Apparatus

The target object was either a tennis ball or a rubber squeezable toy (several different rubber toys of various shapes [height varied between 7 and 12 cm] and colors were used), depending on the preference of the dog and its motivation to grab it. Each object was handled by a translucent nylon thread (125 cm) tied to it. A small wooden box (9 cm wide × 15 cm high × 9 cm deep) without top and front panels was used in the invisible displacement trials. The inside of this box (called *displacement device*) was painted black and its outside was painted white. The box played the same role as the container (hand or small cup) in human infant testing of invisible displacements. This box was fixed at the bottom of a 117 cm vertical plastic stick.

The experiment was conducted in a bare experimental room (362 cm wide × 604 cm deep). Four white wooden boxes (17.5 cm wide × 19.5 cm high × 11.5 cm deep) served to hide the target object. They were permanently fixed on a black plywood sheet (244 cm wide × 122 cm deep) to prevent the dog from moving them during searching. Each box could be opened by pulling down its front panel (called "*the front door*"). The front door was fixed on the bottom of the box by a metal strap hinge and its top was fastened to the box with a piece of Velcro. The front door also exceeded the top of the box by 4 cm for helping the dog to grab it with its paw. To reduce the noise when the front door was pulled down, a small piece of sponge was stuck on its front surface. The inside walls and floor of each hiding box were covered by pieces of sponge to reduce noise when the target object was placed inside it. The back panel had a small opening (12 cm wide × 15 cm high) by which the target object was put in. Four translucent nylon threads (125 cm) were fixed on the bottom of each box and were stretched behind the box. These threads served to control for the possibility that dogs could find the ball by using the translucent nylon thread tied to the target object, which could not be entirely inserted, into the target box at the end of the manipulation. The boxes were arrayed in a row at a distance of 32 cm from each other, and the center of the array was 200 cm from the starting position of dogs.

A white curtain hanging from the ceiling of the experimental room provided a uniform visual background behind the experimental setting. Two black speakers (Sony Model HST-313-2) (18 cm wide × 27 cm high × 22 cm deep) were placed 32 cm on each side of the array of boxes. They faced the position of the dog and the transmitter was located in an adjacent room. Finally, the gaze of the dog was monitored by a camera (Panasonic camcorder Model PV-A208-K), which was fixed on the top of the speaker placed on the right side of the array, and it was recorded on a VHS video recorder (Panasonic Model PV-8664-K) located in an adjacent room.

The material also included two large plywood barriers that served to hide the experimenter in the Concealed-experimenter condition (see Fig. 1). The back barrier (244 cm wide × 107 cm high) was vertically placed 25 cm behind the array of boxes. The front barrier (244 cm wide × 96.5 cm high) was suspended 91.5 cm above the floor by two vertical poles (200 cm high) and it was placed 38 cm in front of the array of boxes. The front and the back barriers were vertically supported by two wooden triangle-shape stands (60 cm × 60 cm × 60 cm), which were fixed on each end (left and right) of both barriers. On the vertical plane, the two barriers overlapped on 15.5 cm and on the horizontal plane, a space of 63 cm separated the two barriers. The disposition of the barriers assured that the dog could not view any body parts (e.g., hands, legs) of the experimenter who performed the manipulations.

The experimenter (E1) who performed the manipulations stood up 50 cm behind the two central boxes; the other experimenter (E2), who restricted the dog during the manipulations, stood up to the right side of the dog.

Procedure

We divided the experiment into three successive steps: shaping, training, and testing. The shaping and training phases were administered during the first session whereas the testing sessions were administered on the next four consecutive days. To prevent dogs from using olfaction, rose water (1/10

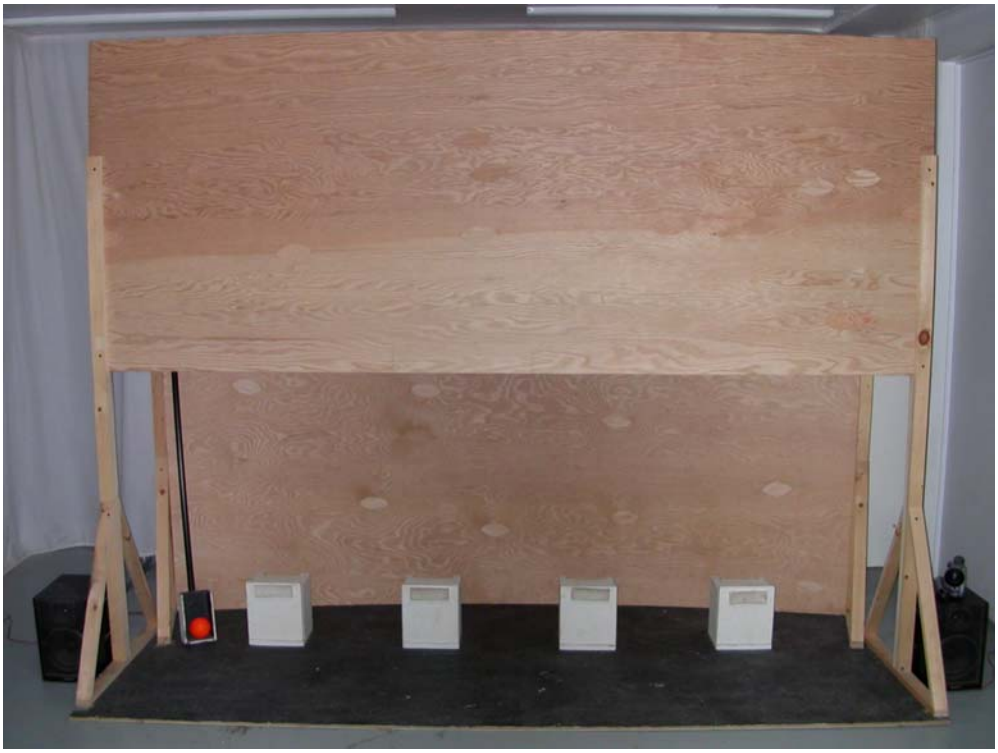

Fig. 1 Picture of the apparatus used in the Concealed-experimenter condition

dilated in water) was sprayed over the apparatus every four trials. Moreover, to avoid that dogs use auditory cues, white noise (78 dB) was played back by the speakers during the entire experiment.

Shaping

During shaping, a single box was used. It was centrally fixed on a black plywood sheet (81.5 cm wide × 122 cm deep) and faced a wall of the testing room. The testing setup described in the *Apparatus* section was absent in the room.

In shaping, the dogs were trained to touch the target object. Although all dogs demonstrated a strong motivation by the opportunity to grab the target object, we introduced a food reinforcement procedure to prevent motivation from declining during the experiment. At the beginning of a shaping trial, E1 put down the target object in front of the box while E2 restrained the animal by grasping its collar. With the help of the nylon thread tied to the target object, E1 lifted up the object, captured the dog's attention, moved the object visibly in front of the box, and finally placed the object on the right or the left side of the box (but never behind or inside). Once the object was put down, E1, to prevent cuing, looked at E2. Then, E2 released the dog. The dog was reinforced by E2 if one of the following behaviors was exhibited in the 15 s that followed its release: grasping the object with its mouth, touching it with its paw, or putting its muzzle on it. A piece of commercial dry food (Diet NutriScience) and social rewards (strokes, verbal rewards such as "Good dog!") were used as reinforcements. We ended shaping when the dog had touched the target object in five consecutive trials. The dogs needed a mean number of 5.27 trials (SD $=$ 0.90) to reach the criterion.

Training

Immediately after the end of shaping, the dogs were trained to open the front door of the box with their paw in order to retrieve the target object. We used the same single box as described in the shaping phase. Training included two phases. In the first phase, E1 caught the attention of the dog by calling its name and opened the front door of the box with her hand. Then, E1 took the object and moved it in front of the dog and finally introduced it inside the box from behind. After the manipulation, E1 closed the front door and E2 released the dog. The dog was reinforced if it retrieved the target object by pulling down the front door with its paw or muzzle. We ended this first step after five consecutive successes. All dogs reached the criterion in five trials (M $=$ 5.00, SD $=$ 0.00). In the second phase of training, the front door was closed at the beginning of the trial. E1 moved the object in front of the dog and hid the target object inside the box. The dog was reinforced if it pulled down the frontal door and touched the object. This second phase was completed when the dog had retrieved the target object in 10 consecutives trials. The dogs needed a mean number of 10.00 trials (SD $=$ 0.00) to reach the criterion.

Testing

In the testing phase, the four hiding boxes were present in the room as described in the *Apparatus* section. Two testing conditions were administered to the dogs. In the Visible-experimenter condition, E1 was visible from the encoding position of the dog, that is, the back and front barrier were behind E1 and all movements and manipulations performed by E1 were perceptible by the dog. Consequently, in each trial of this condition, the dog could observe E1 while she was manipulating the target object. In the Concealed-experimenter condition, E1 manipulated the object from behind the two opaque barriers. Therefore, it was impossible for the dog to observe any body parts of E1 when she was performing the manipulations. Each of the two conditions included two consecutive sessions and they were counterbalanced among the dogs.

Each session began with three warm-up trials where the object was placed between two boxes but never behind or inside. The warm-up trials were followed by two types of trials: visible and invisible displacement trials.

Visible displacement trials (VD) At the beginning of a trial, E1 stood up behind the two central boxes. The displacement device was placed at one end of the array of boxes, its open side facing the dog, and did not move during the trial. E1 put down the object between the two central boxes located in front of the dog while E2 gently restrained the animal by grasping its collar. Then, E1 lifted the object via the thread, captured the dog's attention, moved the object visibly in front of each of the four boxes, returned the object between the two central boxes, and finally hid the object behind the target box. In order to move the object in front of each box, E1 silently moved behind the boxes. At the end of the manipulation, E1 returned behind the two central boxes and E2 released the dog. If E2 noticed that the dog did not watch the manipulation throughout the entire sequence, the trial was interrupted and repeated. Repeated trials rarely occurred. In the Visible-experimenter condition, once the object had disappeared and during searching, to prevent cuing, E1 looked at E2 and remained immobile. If the dog made no search attempt during the minute that followed its release (no choice), it was called back by E2 for the beginning of the next trial. If the dog found the object inside the target box (success), it was reinforced by E2. However, if the dog chose a nontarget box (error), the trial was immediately interrupted, and the dog was not allowed to search for the object behind a second box.

Invisible displacement trials (ID) The procedure was the same as for the VD trials except for the following modifications. At the beginning of a trial, the displacement device was always placed at one end of the array of boxes, its open side facing the dog. Then, E1 inserted the target object into the displacement device, rotated it 180° on its vertical axis, its open side now facing the experimenter, and moved the device behind one of the boxes. There, the target object was invisibly transferred from the displacement device to the target box where it was left. E1 removed the displacement device from behind the target box by using the same side of the box by which it had been introduced. Finally, E1 rotated the displacement device 180° on its vertical axis, its open side now facing the dog, and she brought it back to its initial position. This manipulation served to show to the dog that the object was no longer in the displacement device. Performance was quoted as in the VD trials. However, if the dog first searched into the displacement device, the dog was allowed a second choice inside one of the four boxes.

Each of the four testing sessions included 16 VD and 16 ID trials. In a session, the target object was equally hidden four times behind each of the four boxes for each type of trial. Moreover, the hiding location changed from trial to trial so that the target object was never hidden at the same spatial location on two consecutive trials. In each session, the VD and ID trials were presented in eight blocks of four trials each. Each block included 2 VD and 2 ID trials that were randomly distributed. However, to avoid the negative effect that a long succession of ID trials might have on the performance, each block of trials were distributed in the session so that no more than two trials in a row were given the same type of trial. In each block of four trials, the initial and the final position of the displacement device were two times on the left end and two times on the right end of the array of boxes and they were equally distributed as a function of the VD and ID trials. For each of the four hiding positions, the target object (VD trials) or the displacement device (ID trials) bypassed the target box two times by its left side and two times by its right side. Finally, each trial was separated by a short intertrial interval of 30 s.

Video analysis

The gaze of dogs was analyzed with the assistance of the video recording. The purpose of this video analysis was to assure that the dogs watched the displacement of the object (or of the displacement device) during the whole manipulation in the VD and ID trials as a function of the visibility of the experimenter. Although E1 could look at the dog in the Visible-experimenter condition, given the complexity of the manipulation she had to perform, particularly in the ID trials, it was extremely difficult for her to observe the dog while performing the manipulations. In addition, in the Concealed-experimenter condition, E1 did not see the dog and could not verify whether the dog looked at the moving object. Consequently, E2 was responsible for determining whether the dog tracked the moving object. However, because E2 was standing on the right side of dog while restraining it, errors by E2 were probable because she did not efficiently see the dog's eyes. Therefore, we relied on the video recording for determining afterward whether dogs watched the displacement of the object in all trials of the four testing sessions. Given that dogs turn their head for tracking moving objects, we evaluated if the dogs' head movements correlated with the displacement of the target object (or of the displacement device) manipulated by E1. Videotapes of each testing trial were viewed by E1 and an independent judge. Both judges perfectly agreed on each trial.

Statistical analyses

For all statistical analyses, a criterion of $P < .05$ two-tailed was used for rejection of the null hypothesis. In the within-subject ANOVAs, the Mauchly's test of sphericity was used to determine the homogeneity of the covariance matrix. When the covariance matrix was heterogeneous, the Huynh–Feldt's index was used to adjust the degrees of freedom of the averaged test of significance. Significant main effects of within-subject ANOVAs were followed by a series of *a posteriori t* tests. Significant interactions of factorial within-subject ANOVAs were followed by analyses of the simple main effects and the degrees of freedom were adjusted according to the method proposed by Howell (1987).

Results

In the 1408 trials of testing, there were only two trials without a search attempt. This result indicates that dogs were highly motivated to search for the disappearing object.

Gaze of dogs

First, the video analysis revealed that one of the dogs did not watch the manipulation of the displacement device in 25 out of the 32 ID trials of the Visible-experimenter condition. Due to this high percentage of inattention, this dog was removed from all subsequent statistical analyses. Second, Table 1 presents the mean number of trials in which the 10 remaining dogs looked at the manipulations in the VD and ID trials as a function of the visibility of the experimenter. A factorial within-subjects ANOVA with types of trial (2) $\times$ visibility of the experimenter (2) revealed a significant effect of types of trial, $F(1, 9) = 14.89$, $P = 0.004$, of visibility of the experimenter, $F(1, 9) = 14.89$, $P = 0.004$, and of the interaction, $F(1, 9) = 14.89$, $P = 0.004$. All significant effects were due to the fact that the dogs watched the whole manipulation in all trials except for 80.94% of the ID trials of the Visible-experimenter condition.

Therefore, when the experimenter was visible, the dogs had difficulties in tracking the whole movement of the displacement device in the ID trials. A closer look at the behavior of the dogs also revealed that all dogs (including the dog that was removed from the analyses) systematically raised their head and stared at E1 while they did not watch the manipulation. When they did pay attention to the experimenter, the dogs failed 93.17% (SD = 8.59) of the trials. Put together, these observations strongly suggest that the presence of the experimenter behind the array of boxes influenced the search behavior of dogs in ID trials.

Analysis of success

In the next statistical analyses, only the trials in which the dogs watched the manipulation were kept. Consequently, the number of successful trials was transformed as a percentage of the total number of valid trials in which each dog watched the manipulation. Figure 2 illustrates the mean percentage of success in the VD and ID trials as a function of the visibility of the experimenter (previous factorial within-subject ANOVAs showed no significant effect of sessions or blocks

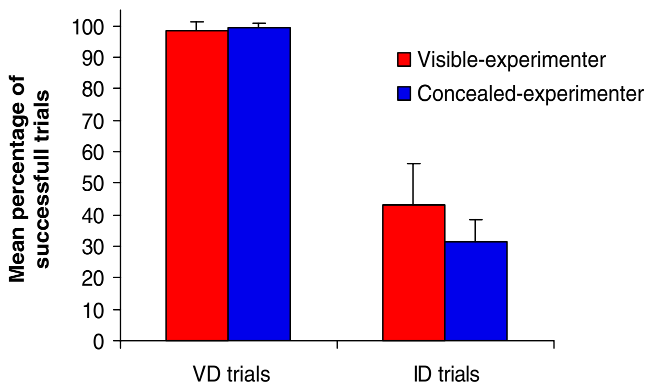

Fig. 2 Mean percentage of successful trials in the VD and ID trials as a function of the visibility of the experimenter. *Error bars* = Standard deviations

Table 1 Mean number of trials (out of 32) in which the dogs watched the whole displacement of the target object in VD and ID trials as a function of the visibility of the experimenter

	Conditions	
	Concealed-experimenter	Visible-experimenter
Type of trials	$M \pm$ SD	$M \pm$ SD
Visible displacement	32.0 ± 0.0	32.0 ± 0.0
Invisible displacement	32.0 ± 0.0	25.9 ± 5.0

of trials within a session). A factorial within-subject ANOVA with types of trial (2) × visibility of the experimenter (2) revealed a significant effect of types of trial, $F(1, 9) = 411.97$, $P < 0.0001$; VD trials being more successful than ID trials. The analysis also showed a significant effect of visibility of the experimenter, $F(1, 9) = 11.06$, $P = 0.009$; trials in which the experimenter was visible were more successful than trials in which the experimenter was visibly occluded behind the barriers. The analysis also revealed a significant interaction, $F(1, 9) = 8.78$, $P = 0.016$. In the ID trials, the analysis of simple effects showed that the percentage of success was higher in the Visible-experimenter condition than in the Concealed-experimenter condition, $F(1, 17) = 19.10$, $P = 0.0004$. In the VD trials, however, the performance of dogs was similar in both conditions. Finally, a series of one-sample t tests was computed to estimate whether the mean percentages of success in the VD and ID trials was significantly higher than that expected by chance. The mean percentage of success expected by chance was 25% because if the dogs searched randomly, they should have searched equally often behind each of the four boxes. The dogs performed above chance in the VD trials (Concealed-experimenter condition: $t(9) = 178.50, p < 0.0001$; Visible-experimenter condition: $t(9) = 87.44, P < 0.0001$) and the ID trials (Concealed-experimenter condition: $t(9) = 3.04$, $P = 0.014$; Visible-experimenter condition: $t(9) = 4.46$, $P = 0.002$).

These first analyses reveal that the dogs succeeded on VD and ID trials but the performance of dogs was much better in VD trials than in ID trials. On VD trials, the performance was almost perfect in both conditions, revealing that the presence of the experimenter did not influence the search behavior of dogs when the task was undemanding. On ID trials, the performance was over chance in both conditions but it was higher in the Visible-experimenter condition than in the Concealed-experimenter condition, suggesting that the dogs used cues inadvertently provided by the experimenter to locate the object.

In order to document the role of the visual cues inherent in the ID task on dogs' performance, we examined the influence of the visibility of the experimenter as a function of the final position of the displacement device relative to the target box. In the ID trials of both experimental conditions, each of the four boxes was the target box with an equal number of trials ($n = 8$) and the displacement device was always placed at either end of the array of four boxes. By consequence, the target box was either the first, second, third, or fourth box adjacent to the final position of the displacement device. The first position was adjacent to the displacement device whereas the three other positions were nonadjacent to the displacement device, resulting in a proportion of 25% of adjacent trials and 75% of nonadjacent trials. Figure 3 illustrates the mean percentage of successful trials in the ID trials in both experimental conditions as a function of the relationship between the target box and the displacement device. As one can see, whether the experimenter was visible or not, the mean percentage of successful trials was very high when the target box was adjacent to the displacement device and it was low when the target box was nonadjacent. Moreover, the percentage of success appears higher at the two central positions (2nd and 3rd adjacent boxes) when the experimenter was visible than when she was not.

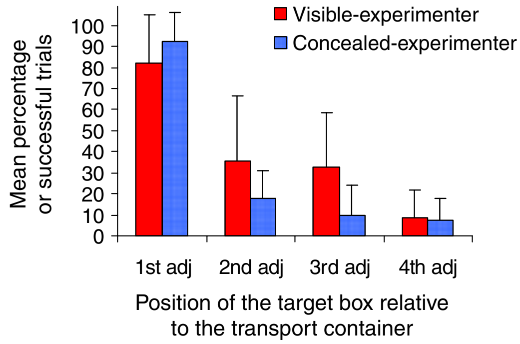

Fig. 3 Mean percentage of successful trials in the ID trials as a function of the final position of the displacement device relative to the target box. *Errors bars* = standard deviations

To confirm these impressions, a factorial within-subject ANOVA with visibility of the experimenter (2) × position of the target box (4) was performed. It revealed a significant effect of visibility of the experimenter, $F(1, 9) = 7.31$, $P = 0.024$; the performance of dogs was higher in the Visible-experimenter condition than in the Concealed-experimenter condition. The analysis also showed a significant effect of the position of the target box, $F(3, 27) = 64.54$, $P = 0.0001$. A series of *a posteriori* t tests revealed that the percentage of success was higher at the box adjacent to the final position of the displacement device than at the three nonadjacent boxes, which did not differ. Finally, the ANOVA also revealed a significant interaction, $F(3, 27) = 3.91$, $P = 0.019$. When the target location was the second or third box relative to the final position of the displacement device, the analyses of simple main effects indicated that the performance of dogs was higher when the experimenter was visible than when she was not, $F(1, 34) = 5.98$, $P = 0.020$ and $F(1, 34) = 9.84$, $P = 0.004$, respectively. However, the performance was similar in both experimental conditions when the target box was the first or the fourth box relative to the position of the displacement device. Finally, the mean percentage of success was above chance level only when the target box was adjacent to the displacement device (Visible-experimenter condition, $t(9) = 7.88, P = 0.001$; Concealed-experimenter condition, $t(9) = 15.89$, $P < 0.0001$). All other one-sample t tests revealed that the performance of dogs was at chance or below chance level when the target location was one of the three nonadjacent positions.

In summary, these last analyses show that the dogs solely succeeded the ID trials when the target box was adjacent to the final position of the displacement device. Otherwise, the dogs failed to find the target object. Nevertheless, when the experimenter was visible and the target box was nonadjacent to the final position of the displacement device, the performance of dogs increased if the object was hidden behind one of the two boxes adjacent to the central position of the experimenter. This suggests that the visibility of the experimenter influenced the search behavior of dogs but was not sufficient for the dogs to succeed the ID trials.

Analysis of errors

The analysis of errors was aimed at further determining the specific role of the experimenter on the search behavior of dogs in the ID trials as a function of the hiding location and the position of the displacement device. If the position of the experimenter and of the displacement device actually influenced the search behavior of dogs in the ID trials, then, the pattern of search distribution observed in the analysis of success should also be observed. When the dogs failed the ID trials, they should have primarily searched at the box adjacent to the final position of the displacement device in both experimental conditions. However, this tendency should be lower in the Visible-experimenter condition when the object was hidden behind the two central boxes because the performance of dogs was higher when the target position was adjacent to the position of the experimenter. Figure 4 illustrates, for each target position relative to the final position of the displacement device, the mean percentage of errors made by the dogs at the three nontarget boxes as a function of the visibility of the experimenter. A series of factorial within-subject ANOVAs with position of the nontarget box (3) × visibility of the experimenter (2) were performed on the percentage of errors made by the dogs for each of the four positions.

When the target location was the first adjacent box relative to the position of the displacement device, errors were rare. The factorial within-subject ANOVA revealed a significant effect of position of the nontarget boxes, $F(2, 18) = 8.13$, $P = 0.003$; a series of *a posteriori t* tests indicated that the mean percentage of errors made at the second adjacent nontarget position was higher than at the third and fourth adjacent nontarget positions, which did not differ. There was no effect of visibility of the experimenter nor of the interaction. Therefore, when the target location was the first adjacent box, the errors were uniquely distributed as a function of the position of the target location.

When the target location was the second adjacent box relative to the displacement device, the sphericity could not be assumed for the position of the nontarget boxes ($W = 0.305$, $df = 2$, $P = 0.009$) and the interaction ($W = 0.245$, $df = 2$, $P = 0.004$). The factorial within-subject ANOVA showed a significant effect of visibility of the experimenter, $F(1, 9) = 7.28$, $P = 0.021$; the percentage of errors was higher in the Concealed-experimenter condition than in the Visible-experimenter condition. The analysis also revealed a significant effect of position of nontarget boxes, $F(1.253,$

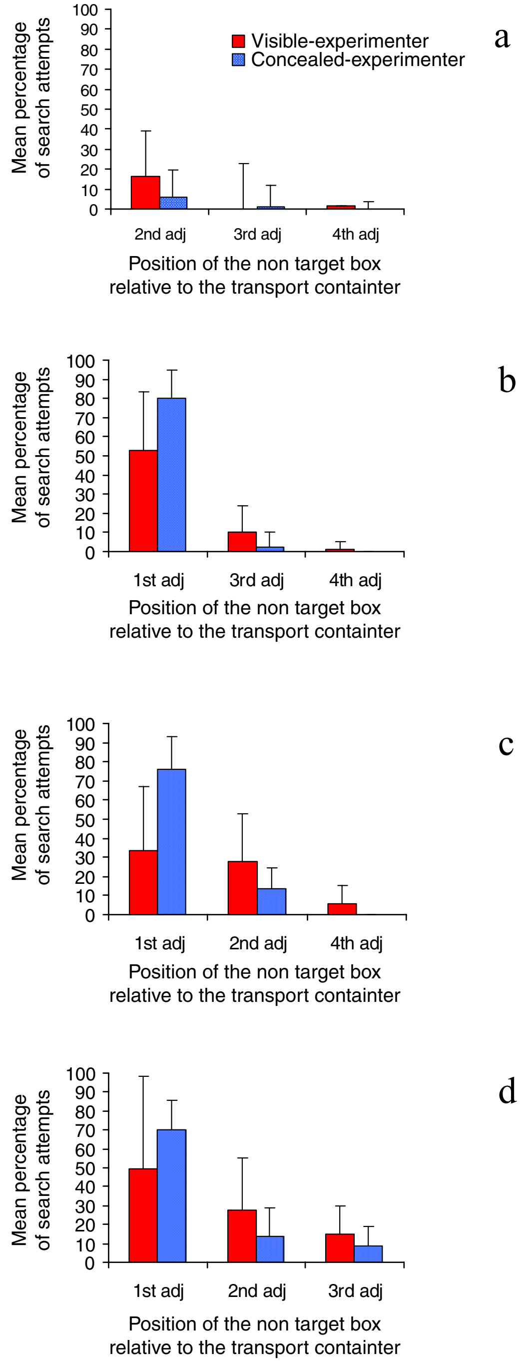

Fig. 4 Mean percentage of errors in the ID trials as a function of the position of each nontarget box relative to the final position of the displacement device. **a** the target box was the first adjacent box to the displacement device; **b** the target box was the second adjacent box; **c** the target box was the third adjacent box; **d** the target box was the fourth adjacent box. *Error bars* = standard deviations

11.279) = 72.44, $P < 0.0001$. A series of *a posteriori t* tests revealed that the mean percentage of errors was higher at the first nontarget position adjacent to the displacement device than at the third and fourth nontarget positions, which did not differ. Finally, the analysis also showed a significant interaction, $F(1.195, 10.756) = 12.51$, $P = 0.004$. The analysis of simple main effects for the first nontarget position adjacent to the displacement device indicated that the percentage of errors was higher in the Concealed-experimenter condition than in the Visible-experimenter condition, $F(1, 25) = 19.87$, $P = 0.002$. The simple main effects of visibility of the experimenter for the third and fourth nonadjacent positions were nonsignificant. Therefore, when the target box was the second adjacent to the displacement device, the dogs primarily searched behind the box located at the first adjacent location to the displacement device but the percentage of errors made at the first adjacent nontarget position was lower when the experimenter was visible than when she was not.

When the target location was the third adjacent box relative to the position of the displacement device, the sphericity could not be assumed for the factor position of the nontarget boxes ($W = 0.322$, $df = 2$, $P = 0.011$). The factorial within-subject ANOVA showed a significant effect of visibility of the experimenter, $F(1, 9) = 5.74$, $P = 0.040$; the percentage of errors was higher in the Concealed-experimenter condition than in the Visible-experimenter condition. The analysis also revealed a significant effect of position of the nontarget boxes, $F(1.271, 11.436) = 20.57$, $P < 0.0001$. A series of *a posteriori t* tests indicated that the mean percentage of errors was higher at the first adjacent nontarget position than at the second and fourth adjacent nontarget positions, and that the percentage of errors was higher at the second than at the fourth adjacent nontarget position. The ANOVA also showed a significant interaction, $F(2, 18) = 15.50$, $P < 0.0001$. The analysis of simple main effects indicated that the percentage of errors made by the dogs at the first nontarget position adjacent to the displacement device was higher in the ID trials of the Concealed-experimenter condition than in the ID trials of the Visible-experimenter condition, $F(1, 27) = 26.91$, $P < 0.0001$. The simple main effects of visibility of the experimenter for the second and fourth nonadjacent positions were nonsignificant. Thus, when the target location was the third box adjacent to the displacement device, the dogs primarily searched behind the box adjacent to the displacement device. However, the percentage of errors was lower at the first adjacent nontarget box when the experimenter was visible than when she was not.

Finally, when the target location was the fourth adjacent nontarget box, the factorial within-subject ANOVA revealed a significant effect of position, $F(2, 18) = 21.19$, $P = 0.0001$, but no other significant effects. A series of *a posteriori t* tests indicated that the mean percentage of errors was higher at the first adjacent nontarget position than at the second and third nontarget positions, which did not differ. Therefore, when the target location was the fourth adjacent box, the errors were primarily distributed as a function of the first box adjacent to the displacement device.

In summary, the analysis of errors in the ID trials supports the analysis of success and also indicates to which extent the search behavior of dogs was guided by the position of the experimenter relative to the target box. In the Concealed-experimenter condition, whatever the position of the target box, the dogs systematically searched behind the first nontarget box relative to the final position of the displacement device. However, in the Visible-experimenter condition, if the target object was hidden behind one of the two central boxes (the second and third adjacent boxes), that is, the two boxes located in closest proximity of the experimenter who manipulated the object, the percentage of errors made at the first adjacent box was lower than in the Concealed-experimenter condition. However, if the object was hidden behind the first or fourth adjacent box, the dogs searched as a function of the displacement device. These results, combined with those observed in the analysis of success, suggest that in the ID trials, the search behavior of dogs was partially guided by the presence of the experimenter when the target object was hidden behind one of the two boxes adjacent to the experimenter. Otherwise, the dogs searched mainly behind the first adjacent box relative to the displacement device.

Visits to the displacement device

In the ID trials, if the dogs first visited the displacement device, they were given a second chance to search behind one of the four boxes. Therefore, there was a possibility that the dogs primarily searched behind the box adjacent to the displacement device because after searching behind the displacement device, it was the first box they encountered. As a result, the dogs could have used an associative rule such as “Visit the displacement device and if the target object is not there, select the first adjacent box”. If the dogs relied on this alternative strategy, the number of search attempts made at the displacement device should be high and stable in both testing sessions of each experimental condition. In order to test this posthoc hypothesis, the number of visits made at the displacement device was transformed as a percentage of the total number of valid trials in which each dog watched the whole manipulation of the device.

First, a series of one-sample *t* tests indicated that the mean percentage of visits made at the displacement device was at chance (chance was 20% because the displacement device was identified as the fifth potential hiding location) in the first session of the Concealed-experimenter condition ($t(9) = 0.78$, $P = 0.79$) whereas it was lower than chance in sessions 1 and 2 of the Visible-experimenter condition

($t(9) = -5.09, P = 0.001$ and $t(9) = -9.96, P < 0.001$, respectively) as well as in session 2 of the Concealed-experimenter condition ($t(9) = -2.52, P = 0.03$). Second, a factorial within-subject ANOVA with visibility of the experimenter (2) $\times$ session (2) revealed that the percentage of visits made by the dogs at the displacement device was higher in the first session ($M = 12.92$, SD $= 8.10$) than in the second ($M = 6.82$, SD $= 7.10$), $F(1, 9) = 21.94$, $P = 0.001$. All other effects were nonsignificant.

In summary, these analyses reveal that the dogs visited the displacement device more frequently in session 1 than in session 2, suggesting that they learned over trials that the displacement device was not a hiding location. However, given the low percentage of visits made by the dogs to the displacement device in each session of both conditions, it appears that the dogs did not regard the displacement device as a potential hiding location. This observation is not surprising because the open side of the displacement device was facing the dog at the end of the manipulation and the dogs could easily perceive that the displacement device was empty.

General discussion

In the present study, although we have replicated the experimental setup (number of boxes and final position of the displacement device) used by Gagnon and Doré (1992, 1993), our data corroborate those observed by Collier-Baker et al. (2004), suggesting that domestic dogs do not understand invisible displacements. Most specifically, the dogs easily succeeded on visible displacement problems as well as on invisible displacements in which the final position of the displacement device was adjacent to the target box. However, they failed on invisible displacement problems in which the displacement device was nonadjacent to the target box. Moreover, the analysis of search distribution revealed that the dogs primarily searched as a function of the adjacency of the displacement device but also relied, to a lesser extent, on the position of the experimenter to determine where to search. The influence of the experimenter on the search behavior of dogs was also supported by the tendency of dogs to stare at the experimenter during the invisible displacement trials, suggesting that dogs were unable to infer the invisible displacement of the object but attempted up to a certain point to rely on visual cues involuntarily provided by the experimenter to locate the hidden object.

But why did dogs primarily search at the first adjacent box relative to the displacement device in invisible displacements? If the dogs do not have the mental capability to infer that the object was imperceptibly transferred from the displacement device to the target box, as a rule they should have searched for the object at the location where they saw it disappear, that is, inside the displacement device. However, perhaps because the dogs were given a direct perceptual cue showing that the target object was no longer inside the displacement device at the end of the manipulation, the dogs logically searched for the hidden object at the nearest location to the displacement device, that is, the first box adjacent to it. Recent investigations into domestic dog cognition support this interpretation. For example, Osthaus et al. (2003) performed a series of experiments aimed at investigating a gravity bias for falling objects in dogs. In their experiments, an attractive object was dropped into a small opaque chimney, which was diagonally attached with the help of an opaque tube to one of the three boxes located below. Their results indicated that dogs searched for the object inside the box located just below the target chimney (that is where the food was dropped off) and the authors concluded that dogs do not understand that falling objects can move diagonally on the vertical plane. Another plausible explanation to Osthaus et al. (2003)'s results, however, is that dogs do not understand that an object can unnoticeably move inside an opaque tube. Thus, in Osthaus et al. (2003)'s study, perhaps the dogs searched at the box directly located below the dropping chimney because it was the nearest location to the target chimney where they saw the object disappear. Fiset and Perreault (2004) tested this hypothesis by orienting the chimneys and boxes on the horizontal plane, eliminating the influence of gravity. They found that dogs searched for the target object inside the box located at proximity of the target chimney, suggesting that dogs searched for the object at the closest location where they saw it disappear. Doré et al. (1996) also reported a similar conclusion in a task in which the target hiding box was visibly moved to an empty adjacent location or transposed with an adjacent empty box. The performance of dogs was lower in the condition in which the initial target location was filled with an identical empty box, suggesting that dogs were unable to represent invisible displacements but rather searched at the location where they saw it last.

On the contrary, the present study also reveals that domestic dogs use the experimenter to increase their chance of success in invisible displacement problems. However, this effect was relatively subtle because it increased the performance of dogs solely in the invisible displacement trials in which the target location was one of the two boxes adjacent to the experimenter. But what kinds of cues were provided by the experimenter in the invisible displacement problems? We suggest that the dogs did not use subtle cues (e.g., hand pointing) involuntarily provided by the experimenter but rather used the experimenter as a local landmark for guiding their search behavior when the displacement device was moved behind one of the boxes adjacent to the experimenter. This interpretation is supported by recent studies (Agnetta et al. 2000; Hare et al. 2002; Riedel et al. 2006) that showed that dogs are able to use a physical marker placed in front of one of two boxes containing hidden food. Interestingly, our data revealed that the dogs did not use the position of the experimenter when the object was hidden behind the boxes located at either end of the row of boxes, suggesting that the capacity of dogs to encode and use local landmarks to localize a hidden object in invisible displacement problems is limited to the immediate objects surrounding the target position. This observation also supports the interpretation that the dogs did not use subtle visual cues involuntarily provided by the experimenter during the manipulation. If the dogs had used such visual cues, the experimenter would have influenced the search behavior of dogs whatever the position of the target location because the manipulations were the same for each ID trial. However, we did observe a difference in the search distribution of dogs as a function of the position of the target location. Nevertheless, one may raise the objection that the dogs did not use the experimenter to encode the position of the object but rather searched behind the boxes adjacent to the experimenter because they were attracted by the movements of the experimenter when she returned behind the two central boxes at the end of the manipulation. However, if the dogs had relied on this alternative strategy, they should also have searched behind the two central boxes adjacent to the experimenter when the target box was located at either end of the row of boxes but we did not observe this tendency in the analysis of errors. Interestingly, although the tendency of dogs to stare at the experimenter during the invisible displacement trials supports our interpretation, it may also reflect the importance of domestication in dogs, which has recently been put in evidence by studies on comparative social cognition. For example, Miklósi et al. (2003) first socialized dogs and wolves to humans at comparable levels and later trained them to solve two simple manipulation tasks (bin-opening and rope-pulling). Then, both species faced an insoluble version of the same two problems. Results revealed that dogs looked/gazed earlier and longer at their owner than socialized wolves, suggesting that while they face a complex task (as in the present study), dogs attempt to look at human face. Interestingly, this ability appears to be part of a complex form of dog–human communication system which possibly emerged through close cohabitation during the last 35,000–100,000 years, that is, after dogs diverge from their common ancestor, the wolf (Vilá et al. 1997).

Finally, although the present findings, as well as those reported by Collier-Baker et al. (2004), suggest that domestic dogs do not have the mental capacity to infer invisible displacements, they indicate that dogs are able to spontaneously use a variety of strategies to increase their chance of success. Put together, our study and the one conducted by Collier-Baker et al. (2004) reveal that the performance of dogs in invisible displacement problems is influenced by the final position of the displacement device, the visibility of the experimenter, and the last box visited by the displacement device. Nevertheless, it appears that dogs attribute more weights to some sources of information than others. The final position of the displacement device is undeniably more influential than the last box visited by the displacement device or the position of the experimenter. This hierarchical organization of the search behavior of dogs for hidden object has already been implicated by a study investigating the spatial encoding processes in dogs. Fiset et al. (2000) performed a series of experiments to examine whether dogs used egocentric or allocentric spatial information to locate a disappearing object in a single visible displacement task. In their experiments, all visual sources of allocentric spatial information (boxes, experimenter, walls) were systematically and drastically shifted to a new location in the room. The results indicated that the dogs did not use any of these sources of allocentric information but primarily searched as a function of linear egocentric information, that is, the direction by which they had seen the object disappear (Fiset et al. 2006). Furthermore, when the spatial position determined by linear egocentric information was not available, the search behavior of dogs was guided by allocentric information. This later observation supports the conclusion that the spatial encoding process of dogs is hierarchically organized: dogs prefer linear egocentric information but can also encode and use allocentric information. In the current study, it appears that the dogs also hierarchically organized the visual cues available in an invisible displacement task: the dogs primarily searched as a function of the displacement device but when the experimenter was visible, they showed a tendency to use both sources of information.

In conclusion, the present study supports the assumption that domestic dogs do not understand invisible displacement problems but rather search as a function of the final position of the displacement device and, to a lesser extent, the position of the experimenter. The current study also indicates that studies assessing the upper limits of object permanence must be carefully designed to avoid misinterpretation of the cognitive capability of nonhuman animals. Therefore, we strongly recommend that further studies investigating upper limits of object permanence in animals use the experimental controls introduced in the current study as well as those proposed by Collier-Baker et al. (2004, 2006).

Acknowledgements This research was supported by an operating research grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) and by a research grant from the Faculté des Études Supérieures et de la Recherche (FESR) of Université de Moncton. Valérie LeBlanc was supported by an Undergraduate Student Research Award from NSERC. The experiments received approval from the Comité de protection des animaux from the Faculté des études supérieures et de la recherche de l'Université de Moncton, which is responsible for the application and enforcement of rules of the Canadian Council on Animal Care. We thank the owners of the dogs who participated in these experiments.

References

Agnetta B, Hare B, Tomasello M (2000) Cues to food location that domestic dogs (*Canis familiaris*) of different ages do and do not use. Anim Cogn 3:107–112

American Kennel Club (1992) The complete dog book, 18th edn. Howell Book, New York

Barth J, Call J (2006) Tracking the displacement of objects: a series of tasks with great apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, and *Pongo pygmaeus*) and young children (*Homo sapiens*). J Exp Psychol Anim Behav Process 32:239–252

Bräuer J, Kaminski J, Riedel J, Call J, Tomasello M (2006) Making inferences about the location of hidden food: social dog, causal ape. J Comp Psychol 120:38–47

Call J (2001) Object permanence in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and children (*Homo sapiens*). J Comp Psychol 115:159–171

Collier-Baker E, Suddendorf T (2006) Do chimpanzees (*Pan troglodytes*) and 2-year-old children (*Homo sapiens*) understand double invisible displacement? J Comp Psychol 120:89–97

Collier-Baker E, Davis JM, Suddendorf T (2004) Do dogs (*Canis familiaris*) understand invisible displacement? J Comp Psychol 118:421–433

Collier-Baker E, Davis JM, Nielsen M, Suddendorf T (2006) Do chimpanzees (*Pan troglodytes*) understand single invisible displacement? Anim Cogn 9:55–61

De Blois ST, Novak MA (1994) Object permanence in Rhesus Monkeys (*Macaca mulatta*). J Comp Psychol 108:318–327

De Blois ST, Novak MA, Bond M (1998) Object permanence in Orangutans (*Pongo pygmaeus*) and squirrel monkeys (*Saimiri sciurus*). J Comp Psychol 112:137–152

Doré FY (1986) Object permanence in adult cats (*Felis catus*). J Comp Psychol 100:340–347

Doré FY, Dumas C (1987) Psychology of animal cognition: Piagetian studies. Psychol Bull 102:219–233

Doré FY, Fiset S, Goulet S, Dumas M-C, Gagnon S (1996) Search behavior in cats and dogs: interspecific differences in working memory and spatial cognition. Anim Learn Behav 24:142–149

Dumas C, Doré FY (1989) Cognitive development of kittens: a cross-sectional study of object permanence. J Comp Psychol 103:191–200

Dumas C, Doré FY (1991) Cognitive development in kittens (*Felis catus*): an observational study of object permanence and sensorimotor intelligence. J Comp Psychol 105:357–365

Fiset S, Perreault M (2004) Vertical invisible displacements in domestic dogs: gravity or linearity bias? Unpublished data, Université de Moncton, Moncton, New Brunswick, Canada

Fiset S, Gagnon S, Beaulieu C (2000) Spatial encoding of hidden objects in dogs (*Canis familiaris*). J Comp Psychol 114:315–324

Fiset S, Landry F, Ouellette M (2006) Egocentric search for disappearing objects in domestic dogs: evidence for a geometric hypothesis of direction. Anim Cogn 9:1–12

Funk MS (1996) Development of object permanence in the New Zealand parakeet (*Cyanoramphus auriceps*). Anim Learn Behav 24:375–383

Gagnon S, Doré FY (1992) Search Behavior in various breeds of adult dogs (*Canis familiaris*): object permanence and olfactory cues. J Comp Psychol 106:58–68

Gagnon S, Doré FY (1993) Search behavior of dogs (*Canis familiaris*) in invisible displacement problems. Anim Learn Behav 21:246–254

Gagnon S, Doré FY (1994) Cross-sectional study of object permanence in domestic puppies (*Canis familiaris*). J Comp Psychol 108:220–232

Gruber HE, Girgus JS, Banuazizi A (1971) The development of object permanence in the cat. Dev Psychol 4:9–15

Hare B, Tomasello M (1999) Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. J Comp Psychol 113:173–177

Hare B, Brown M, Williamson C, Tomasello M (2002) The domestication of social cognition in dogs. Science 298:1634–1636

Howell CH (1987) Statistical methods for psychology, 2nd edn. Duxbury, Boston

Mathieu M, Bouchard MA, Granger L, Herscovitch J (1976) Piagetian object permanence in *Cebus capucinus*, *Lagothrica flavicauda* and *Pan troglodytes*. Anim Behav 24:585–588

McKinley J, Sambrook TD (2000) Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). Anim Cogn 3:13–22

Mendes N, Huber L (2004) Object permanence in common marmosets (*Callithrix jacchus*). J Comp Psychol 118:103–112

Miklósi Á, Polgardi R, Topál J, Csányi V (1998) Use of experimenter-given cues in dogs. Anim Cogn 1:113–121

Miklósi Á, Kubinyi E, Topál J, Gácsi M, Virányi Z, Csányi V (2003) A simple reason for a big difference: wolves do not look back at humans but dogs do. Curr Biol 13:763–766

Natale F, Antinucci F, Spinozzi G, Poti P (1986) Stage 6 object concept in nonhuman primate cognition: a comparison between gorilla (*Gorilla gorilla gorilla*) and Japanese macaque (*Macaca fuscata*). J Comp Psychol 100:335–339

Neiworth JJ, Steinmark E, Basile BM, Wonders R, Steely F, DeHart C (2003) A test of object permanence in a new-world mondey species, cotton top tamarins (*Saguinus oedipus*). Anim Cogn 6:27–37

Osthaus B, Slater AM, Lea SEG (2003) Can dogs defy gravity? A comparison with the human infant and a non-human primate. Dev Sci 6:489–497

Parker ST (1977) Piaget's sensorimotor series in an infant macaque: a model for comparative unstereotyped behavior and intelligence in human and nonhuman primates. In: Chevalier-Skolnikoff S, Poirier FE (eds) Primate bio-social development: biological, social, and ecological determinants. Garland, New York, pp 43–112

Pasnak R, Kurkjian M, Triana E (1988) Assessment of stage 6 object permanence. Bull Psychol Soc 26:368–370

Pepperberg IM (2002) The value of the Piagetian framework for comparative cognitive studies. Anim Cogn 5:177–182

Pepperberg IM, Funk MS (1990) Object permanence in four species of psittacine birds: an African grey parrot (*Psittacus erithacus*), an Illiger mini macaw (*Ara Maracana*), a parakeet (*Melopsittacus undulatus*), and a cockatiel (*Nymphicus hollandicus*). Anim Learn Behav 18:97–108

Pepperberg IM, Kozak FA (1986) Object permanence in the African gray parrot (*Psittacus erithacus*). Anim Learn Behav 14:322–330

Pepperberg IM, Willner MR, Gravitz LB (1997) Development of Piagetian object permanence in a grey parrot (*Psittacus erithacus*). J Comp Psychol 111:63–75

Piaget J (1937) La construction du réel chez l'enfant. Delachaux and Niestlé, Neuchâtel, Paris, France

Pollok B, Prior H, Gunturkun O (2000) Development of object permanence in food-storing magpies (*Pica pica*). J Comp Psychol 114:148–157

Redshaw M (1978) Cognitive development in human and gorilla infants. J Hum Evol 7:133–141

Riedel J, Buttelmann D, Call J, Tomasello M (2006) Domestic dogs (Canis familiaris) use a physical marker to locate hidden food. Anim Cogn 9:27–35

Spinozzi G, Potí P (1993) Piagetian Stage 5 in two infant chimpanzees (Pan troglodytes): the development of permanence of objects and the spatialization of causality. Int J Primatol 14:905–917

Suddendorf T, Whiten A (2001) Mental evolution and development: evidence for secondary representation in children, great apes and other animals. Psychol Bull 127:629–650

Thinus-Blanc C, Poucet B, Chapuis N (1982) Object permanence in cat : analysis in locomotor space. Behav Process 7:81–87

Triana E, Pasnak R (1981) Object permanence in cats and dogs. Anim Learn Behav 9:135–139

Vilá C, Savolainen C, Maldonado JE, Amorim IR, Rice JE, Honeycutt RL, Crandall KA, Lundeberg J, Wayne RK (1997) Multiple and ancient origins of the domestic dog. Science 276:1687–1689

Wood S, Moriarty KM, Gardner BT, Gardner RA (1980) Object permanence in child and chimpanzee. Anim Learn Behav 8:3–9