

Association, Inhibition, and Object Permanence in Dogs' (*Canis familiaris*) Spatial Search

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The relative role of associative processes and the use of explicit cues about object location in search behavior in dogs (*Canis familiaris*) was assessed by using a spatial binary discrimination reversal paradigm in which reversal conditions featured: (1) a previously rewarded location and a novel location, (2) a previously nonrewarded location and a novel location, or (3) a previously rewarded location and a previously nonrewarded location. Rule mediated learning predicts a similar performance in these different reversal conditions whereas associative learning predicts the worst performance in Condition 3. Evidence for an associative control of search emerged when no explicit cues about food location were provided (Experiment 1) but also when dogs witnessed the hiding of food in the reversal trials (Experiment 2) and when they did so in both the prereversal and the reversal trials (Experiment 3). Nevertheless, dogs performed better in the prereversal phase of Experiment 3 indicating that their search could be informed by the knowledge of the food location. Experiment 4 confirmed the results of Experiments 1 and 2, under a different arrangement of search locations. We conclude that knowledge about object location guides search behavior in dogs but it cannot override associative processes.

Keywords: dog, cognition, spatial learning, discrimination reversal, object permanence

The cognitive abilities of dogs are attracting increasing interest in comparative cognition. This is partly because dogs seem to be more successful than apes in some cognitive tasks. This has led to the hypothesis that some cognitive abilities may have come about through domestication without having been selected for directly (see Hare, Brown, Williamson, & Tomasello, 2002; Hare & Tomasello, 2005a, 2005b; Miklosi & Topal, 2005; Miklosi, Topal & Csanyi, 2004, for a discussion). In particular, dogs seem to perform at a higher level of accuracy than apes in tasks requiring the identification of the correct location of hidden items following communicative signals provided by humans, such as reaching, gazing, and the placement of a wooden block acting as a marker of the location of the hidden object (Brauer, Kaminski, Riedel, Call, & Tomasello, 2006; Hare et al., 2002; Hare & Tomasello, 2005a; Miklosi et al., 2004).

Variations of these types of search task have often featured in object permanence studies within the Piagetian approach to comparative psychology (see Antinucci, 1989; Doré & Dumas, 1987;

Pepperberg, 2002; Vauclair, 1996, for reviews). Within this tradition, the ability of animals to retrieve a hidden object can be classified according to different stages. These range from the absence of attempts to retrieve an object that is only partially occluded, to the ability to solve invisible displacement tasks that require tracking the position of the object following a series of displacements of a device inside which the object had been hidden earlier in full view of the subject. It is often assumed that success in the most difficult of these search tasks is indicative of the ability to mentally represent an out-of-view object (see Vauclair, 1996, for a review) and attempts have been made to clarify in detail the level of representation required to solve different object permanence tasks (Perner, 1991; Suddendorf & Whiten, 2001). However, some authors have questioned whether representational skills may be required at all to search successfully for hidden objects in some of these tasks as it is possible that animals may solve some so-called object permanence tasks by just sensing that something interesting has been hidden in a particular location, without any representation of even basic object characteristics (see Pepperberg, 2002, for a discussion).

Early evidence suggested that dogs are able to track the location of objects subjected to invisible displacements (Gagnon & Doré, 1992; Gagnon & Doré, 1994; Triana & Pasnak, 1981). Nevertheless, it was soon recognized that this evidence was far from indicative of a sophisticated mental ability as it is possible that simple or relatively narrow strategies can sometimes lead to successful searches in these tasks. The use of simple search strategies in dogs has often been discussed in terms of whether their acquisition is based on associative principles, which should produce gradual learning and not an all-or-none solution to the problem at hand. The observation that the use of these strategies can some-

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times develop in one trial has been taken as evidence for the fact that they may not be acquired by means of associative processes (see Gagnon & Doré, 1992, 1993, for a discussion of this point). It has however been recognized that, albeit unlikely, even one-trial learning in such tasks can be based on associative processes (see Gagnon & Doré, 1992, 1993). This would be the case for example if the spatial or temporal contiguity between the sight of the food reward or highly preferred object and a particular location was a cue that was powerful enough to induce a bias toward searching in its vicinity. Although this latter possibility has been discounted on the basis of careful evaluations of the number of trials administered to dogs in different tests (Gagnon & Doré, 1992) it cannot be ruled out completely on the basis of existing literature.

Although it is very relevant in this type of study, the role played by associative processes in guiding dogs' search for objects, that they have seen disappearing in particular hiding locations, has seldom been investigated in detail. One exception is a thorough study by Watson and colleagues (2001), which specifically looked at this issue using a task that evaluated the relative role of inferential and associative processes in dogs' search for a hidden object. The authors looked at dogs' searches of an array of three screens behind which a toy was hidden. The dogs were shown the toy in a container that was then moved behind three screens and shown to be empty after it emerged from behind the last screen. Thus, the information that the toy disappeared behind one of the three screens was conveyed to the dogs but no explicit cue was given about which specific screen hid the object. The dogs were then allowed to search behind the screens. The duration of each search of the three screens was then analyzed, in trials in which dogs found the objects after searching all locations. According to Watson et al. (2001), the use of inferential skills by the dogs should have increased their degree of certainty that the object was behind one of the unexplored screen following each unsuccessful search. Therefore, the authors predicted that if the dogs' choices were mainly controlled by inference, their third search (i.e., behind the last remaining unsearched screen of the three) should be faster than their second search (with two unvisited screens left to search). By contrast, the prevalence of associative principles in dogs' search behavior would have determined the inhibition of a general "commitment to search" (p. 221). Watson and colleagues did not specify exactly what would be formed by association in this scenario but listed a number of possibilities such as an "acquired disposition" or "habit" or "tendency" to search which would be weakened by unsuccessful searches.

Because from this perspective each unsuccessful search would have increased the inhibition of search behavior, having performed two rather than one unsuccessful search would have produced "declining response strength" (Watson et al., p. 221). This would have resulted in a slower third search. Thus, opposite predictions were derived from an associative learning or an inferential model of dog search behavior. The results confirmed an associative search mode in dogs with slower searches observed following successive unsuccessful attempts to find the hidden object.

Nevertheless, it is possible to envisage some alternative predictions to those proposed there. For example, an inferential process, deployed when searching the last screen of the set of three following two unsuccessful searches, could require the integration of more information and the monitoring of the outcome of previous

searches (1) the object is either in A, B, or C; (2) not-A, therefore B-or-C; (3) neither-A-nor-B, therefore C, thus increasing the time required to make a choice following two unsuccessful searches compared to the time required to decide where to search after only one incorrect choice, which requires the integration of only two premises (1) the object is either in A, B, or C; (2) not-A, therefore B-or-C (see also McGonigle & Chalmers, 1992, for a discussion of a similar point albeit in a different type of task).

Similarly, it is possible to conceive a different outcome to that envisaged by Watson and colleagues (2001) for the response speed predicted by an associative model of search. In fact, an unrewarded search could result in the inhibition of the response to that specific location rather than in an inhibition of a "commitment to search" in general. If that is the case, faster responses would occur after two (rather than one) unsuccessful searches, as the only location left at the third attempt would not have any inhibitory potential attached to it. The fact that Watson et al. obtained opposite response time patterns in dogs and children seems to indicate that the two species tested in their study approached their tasks differently. Nevertheless, it seems that the role of association and inhibition in dogs' search needs to be assessed in more detail.

It is also worth noting that, as in similar types of search tasks, in the study by Watson and colleagues (2001) the object was shown to be present in a box before the box was moved and shown empty only after it had been transported behind all the screens. The dogs were not provided with any explicit information about which screen the object should have been hidden behind. Thus, learning could only occur on the basis of trial and error and this may have forced the animals to rely on associative principles. Object permanence tasks in which dogs witness the hiding of the object in one specific place, by contrast, offer the animal the possibility to use the information available to them to select the correct object location without having to rely on blind trial and error.

A very clear indication of the fact that witnessing the hiding of an object is a particularly salient cue in dogs would be provided by situations in which the informative value of this event can be contrasted with the informative value deriving from previously having repeatedly found a reward in a particular location. Human infants undergo a specific stage of their development in which, if they have successfully searched for an object in a particular spatial location A, they will search in this location in a subsequent trial even though they have witnessed it being hidden in a novel location B. This A-not-B error is typical of stage three of object permanence and has been linked to the prevalence of associative processes in infants (Diamond, 1985, 1998; Piaget, 1954) and a lack of inhibitory control mediated by the development of the dorso-lateral prefrontal cortex in both human infants and rhesus monkeys (Diamond & Goldman-Rakic, 1989). It has been recently claimed that dogs have a tendency to make more perseverative A-not-B errors than preschool children (Watson et al., 2001) even if previous developmental studies carried out on dog pups (Gagnon & Doré, 1994) suggested that, in general, dogs are not prone to A-not-B errors (see however, Pepperberg, Willner & Gravitz, 1997, for a thorough discussion of the reasons why this may be the case).

The literature reviewed above indicated that the cognitive underpinnings of dogs' search behavior still needs to be characterized in detail. Sometimes dogs' searches seem to be correctly informed by the perceived location of the target object but are occasionally

biased by lingering effects of having found an attractive object elsewhere or by deploying rules that are no longer appropriate. Therefore, there seems to be a need for a detailed assessment of whether dogs rely mostly on associative or on other processes to guide their search. The aim of the present study was to address this issue by means of a spatial version of the mediational learning (ML) paradigm (Beran et al., 2008; De Lillo & Visalberghi, 1994; Rumbaugh & Pate, 1984), which has been used to classify different primate species according to whether their prevalent mode of learning is associative or mediated by rule use. In its original, nonspatial form, the ML paradigm is a modified version of a binary discrimination reversal task (see also, Clayton, 1963; McDonald, King, & Hong, 2001; Robinson & Storm, 1978, for a discussion of relevant factors affecting discrimination reversal performance in related tasks). In the ML paradigm, during a prereversal training phase the animals learn which of two objects, varying on a number of different dimensions, occludes an item of food (A+, B-; where the letters indicate the objects and the plus sign [+] and the minus sign [-] the presence or absence of reward, respectively). Following the achievement of a performance criterion, the reward contingencies are switched and the performance in the reversal trial is assessed in three different reversal conditions: (1) one featuring the original pairs of occluding objects (A-, B+); (2) the second featuring the previously rewarded object paired with a novel object not present during training (A-, C+); and (3) the third where the previously unrewarded occluding object is paired with a new one (B+, D-). An associative learning mode would predict a different level of performance in the three reversal conditions and a particularly poor performance in reversal Condition A-, B+ because this condition would require the inhibition of the positive association with food acquired by Object A during training and the disinhibition of the response to the previously unrewarded Object B.

By contrast, if reversal performance is mediated by the use of a rule, such as win-stay, lose-shift, then reversal performance should be similar in the three different reversal conditions. We considered that, if appropriately modified, the ML paradigm is a powerful tool for the assessment of the relative role of associations and use of cues related to the location of objects in a search task in dogs. Because dogs are particularly proficient in a variety of spatial tasks (Fabrigoule & Sagave, 1992; Pongracz et al., 2001) and are more efficient when searching for hidden objects when a spatial rather than a nonspatial discrimination has to inform their choices (Dumas, 1998), we developed a spatial version of the ML paradigm. Two identical containers were placed in different locations and the dog had to learn which of the two contained an item of food to retrieve. In the first experiment we assessed the extent to which dogs displayed associative rather than rule mediated learning when searching for food in the absence of explicit information about the object location. In Experiment 2 and 3 explicit cues concerning the object locations were provided by allowing the dogs to witness the baiting of the container performed by a hand movement of the experimenter. Finally, in Experiment 4 we controlled for possible effects due to the specific arrangement of containers used in Experiment 1 and 2. The general rationale of Experiments 2, 3, and 4 was that the prevalent use of explicit cues (such as the witnessing of the baiting of a container) about the object location in dogs should have produced a similar performance in the three reversal conditions. By contrast, the prevalence

of associative processes in search would have predicted different reversal performance in the three conditions.

Experiment 1

Method

Subjects. Ten dogs (five males and five females) of the following breeds: two Labrador Retrievers, three Collies, one Spaniel, one large cross breed, one Dalmatian, one Bull Mastiff, and one Weimaraner, with an age range of 2 to 6 years were originally recruited to take part in the study. However, the Weimaraner showed signs of anxiety during testing and soon after the completion of the study was diagnosed with a severe form of epilepsy and excluded from the sample. Therefore, the results of nine dogs were analyzed. The dogs always had free access to water and were fed 4 hr before testing. Dogs were recruited from among the pets of customers of a commercial boarding kennels and were tested during their stay at the kennels. At the time of arrival at the kennels, written consent for participating dogs was obtained from their owners who signed a consent form after having read a description of the study. During the dogs' stay at the kennels, the experimenter had care of the dogs for a minimum of 3 days and thus had some familiarity with them. None of the dogs were working dogs, had received any prior instruction beyond basic obedience or had taken part in other psychological experiments.

Apparatus. The testing took place in an indoor facility, part of the boarding kennels, away from the main dog housing. A sketch of the apparatus is presented in Figure 1.

A rubber mat 2 m \times 4 m was marked with a semicircular array of 12 dots, equidistant from the dog. A schematic presentation of the array of dots in relation to the dog and the experimenter is presented in Figure 2a. The dots were 20-cm apart and their distance from the dog was 90 cm. Each dot indicated a possible location for each container. Each trial only featured two locations

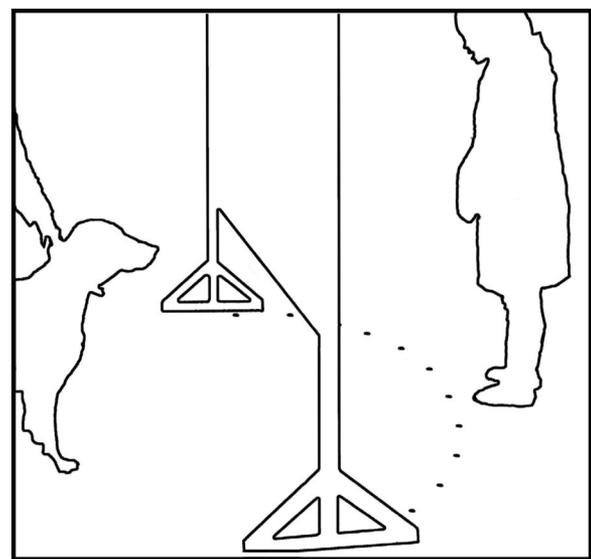


Figure 1. Schematic representation of the experimental set-up and apparatus used in Experiments 1 to 4.

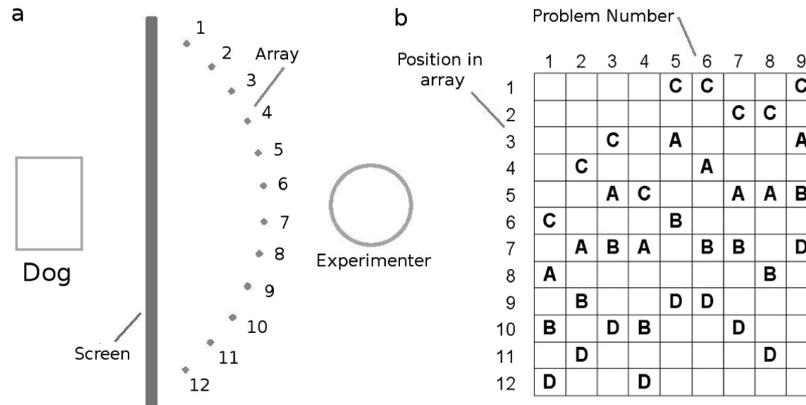


Figure 2. (a): The position of the hiding screen and its relation to the dog and the experimenter when hiding the bait in one of the containers. The semicircular arrangement of dots indicates possible hiding locations (not to scale). (b): A grid is presented with position in the circular array (rows) of Locations A, B, C, and D used in each problem from a pool of nine (columns). Please note that only two locations are used in any given trial (see text for details of the procedure).

and these varied according to the procedure described below. Plastic plant pots of 15-cm diameter were used as containers. A dry meat flavored biscuit (approximately 2 g) was used as bait and was placed in one of the containers where it could be easily obtained by the dogs following a correct search. A fabric screen was used to obstruct the top half of the body of the experimenter to prevent the involuntary transmission of cues such as posture or gaze direction at any time during the test. A dark curtain attached underneath the screen could be lowered to prevent the dogs from observing the baiting of the relevant container. To avoid providing discriminative auditory cues at the time of baiting, the containers were moved so that they simultaneously made a rattling noise. The curtain was raised to allow the dog to search for the bait that was not directly visible once hidden. Testing sessions were recorded with a video camera that was placed at hip height behind and to the side of the dog.

We controlled for spurious olfactory cues by using, as each container, two stacked plant pots. Inaccessible bait was placed in the space created between the bases of the two stacked pot. This allowed the scent of the bait to emanate through the drainage holes of the pots. Thus, the same olfactory cue was present at both the correct and at the incorrect search location. This precaution was taken even though it has been shown that dogs do not seem to rely on olfaction in object permanence tasks (Gagnon & Doré, 1992).

Familiarization. Each daily testing session started with a familiarization period of 3 min during which the dog was left free to explore the room and apparatus, without any containers or baits in place. This familiarization period was followed by the presentation of two trials with the bait located outside and adjacent to a single container, which was placed in a central location in front of the screen, for the dog to retrieve it. Then, three warm-up trials were administered in which the dog retrieved the bait from inside the container. In all these trials, one experimenter restrained the dog and the second experimenter placed the bait in the container. The dog did not witness the baiting of the container. The dog was then released and allowed to retrieve the bait. Following this familiarization phase the testing proper ensued following the procedure described below.

Design and procedure. In Experiment 1 the dogs did not witness the hiding procedure at any point. Each dog was presented with three binary spatial discrimination reversal problems. A *problem* was defined as a prereversal training phase featuring a binary spatial discrimination, followed by trials pertaining to the three reversal conditions described below. In the prereversal phase of each problem, the dogs learned to search at the rewarded location (here referred to as A+) and avoid searching at the nonrewarded location (here referred to as B-). Following a standard procedure for this type of paradigm (see Beran et al., 2008; De Lillo & Visalberghi, 1994; Rumbaugh, 1971; Rumbaugh & Pate, 1984) prereversal training lasted until a criterion performance of nine correct searches in the last 10 trials was met.

For each problem, there followed a reversal phase that comprised three conditions: (1) A- B+ featuring the same two locations used during the prereversal phase but with their reward contingencies reversed; 2) A- C+ in which the reward contingencies for Location A were reversed and a container was placed at a novel Location C, which was now baited, whereas the container at the original unrewarded Location B was no longer present; and 3) B+ D-, in which the previously unrewarded Location B was now rewarded and paired with a novel Location D, which was not baited and was used instead of the previously baited Location A. In different problems a different set of Locations A, B, C, and D was selected, according to the procedure described below. Each dog was presented with three of such problems, selected at random from a pool of nine problems. The set of possible locations in relation to the dog and experimenter are presented in Figure 2a. Figure 2b presents a grid with the locations that could be used in any given problem in the pool. Any given trial within a problem only featured two locations. The two locations featured in each discrimination, in either the prereversal or the reversal phase of each problem, had to satisfy the following constraints. They had to be at a minimum of 40-cm apart on the array to make them easily discriminable and a maximum of 60-cm apart so that both locations were within the dogs' visual field. This was done to avoid any major discrepancies in the distance between the locations

chosen in any particular condition, which may have had a spurious effect on the results.

Each reversal condition comprised seven reversal trials. The required order of the presentation of the trials in the reversal phase was that the first three reversal trials were randomly selected, without replacement, from the three different conditions. Then, trials for different conditions were intermixed and administered in a pseudorandom order, so that trials of the same condition could not be presented more than twice consecutively. As typically done with this type of paradigm (Rumbaugh & Pate, 1984) the first reversal trial of each condition was removed from the analysis as they were used to convey to the dog the information that the reward contingencies had now changed. Reversal performance was measured as the proportion of searches in the baited locations in Trials 2 to 7 of each reversal condition. A summary of the experimental procedure and design is presented in Table 1.

In each trial the dogs were allowed to perform one search and retrieve the bait if they searched in the baited container. When a dog searched the incorrect container the trial was interrupted. The dog was taken back to the starting position and a new trial was then administered.

Results

The dogs took an average of 14.43 trials to reach criterion during training (95% CI [12.16, 17.69]). The proportion of correct trials observed in the three reversal conditions (excluding the first trial of each condition) can be observed from Figure 3. One-sample t tests carried out on the proportion of correct responses observed in the three conditions revealed that dogs were significantly above chance in the A- C+, $t(8) = 2.51, p < .05$, and B+ D-, $t(8) = 5.66, p < .001$, condition and significantly below chance in the A- B+ condition, $t(8) = -5.37, p < .001$.

A one-way, repeated-measures analysis of variance (ANOVA) used to compare the proportion of correct responses observed in the three reversal conditions revealed a significant effect of condition, $F(2, 16) = 17.98, p < .001, \eta_p^2 = .69$. Pairwise comparisons indicated that the proportion of correct responses used in the condition featuring a full reversal A- B+ was significantly lower than that observed in each of the conditions featuring a novel location during reversal, A- B+ versus A- C+, $t(8) = 3.91, p < .001$; A- B+ versus B+ D-, $t(8) = 6.89, p < .001$. By contrast, the dogs showed similar levels of performance in the two conditions featuring a novel stimulus, A- C+ versus B+ D-, $t(8) = 1.50, ns$.

Our paradigm was not designed for the study of learning curves during reversal. Nevertheless, we considered it interesting to assess whether some degree of learning had occurred in any partic-

ular reversal condition. We did so by comparing the first and the last problem of each condition given to the dogs. We carried out these comparisons using paired sample t tests. None of them proved significant, $-1.55 < t(8) < 0.95, ns$.

Discussion

This first experiment was carried out to assess the basic mode of learning of dogs before implementing three further experiments based on the same paradigm and aimed at investigating the role of explicit cues about object location in dogs' search.

The results of this essential initial exploration of dogs' learning mode in spatial search indicated that the animals found it more difficult to master a reversal condition in which both the locations featured during training were present but with the reward contingencies switched (A- B+) compared to conditions featuring a novel and therefore neutral location paired with one of the locations experienced by the dog in the prereversal phase (either A- C+ or B+ D-).

It seems, therefore that the dogs did not use a search strategy based on a principle such as "Win-stay, lose-shift" (Harlow, 1949) or other rules that would have produced an errorless performance in Trials 2 to 6, which followed the first informative trial in all the conditions. The fact that we observed different levels of performance in the three different conditions tells us that learning was unlikely to be primarily mediated by rules in this experiment (see Rumbaugh & Pate, 1984, for a discussion of associative as opposed to rule mediated learning in a nonspatial version of this paradigm).

Experiment 1 helped us characterize the main mode of learning displayed by dogs in this type of task. Thus, we could now progress with the study of the effectiveness of the availability of explicit information about object location. We did this in Experiment 2 by allowing the dogs to witness the hiding procedure.

Experiment 2

With the second experiment we aimed to assess whether dogs exploit the presence of more explicit information about the object location during reversal. We did so by displaying the hiding event and the hand movements performed by the experimenter when baiting the appropriate container in the reversal condition. If these cues were particularly effective they should have been able to override the associative bias build up during training toward the selection of the rewarded location and the negative bias toward the selection of the unrewarded location.

Table 1
Prereversal Criterion, Number of Trials per Condition, and Order of Presentation Used in Experiments 1 to 3

Prereversal phase 9/10 correct criterion	Reversal phase (Trials 1 to 3 in random order)	Reversal phase (Trials 4–21 in pseudorandom order)
A+ B-	A- B+ (no novel, 1 trial) A- C+ (novel S+, 1 trial) B+ D- (novel S-, 1 trial)	A- B+ (6 trials) A- C+ (6 trials) B+ D- (6 trials)

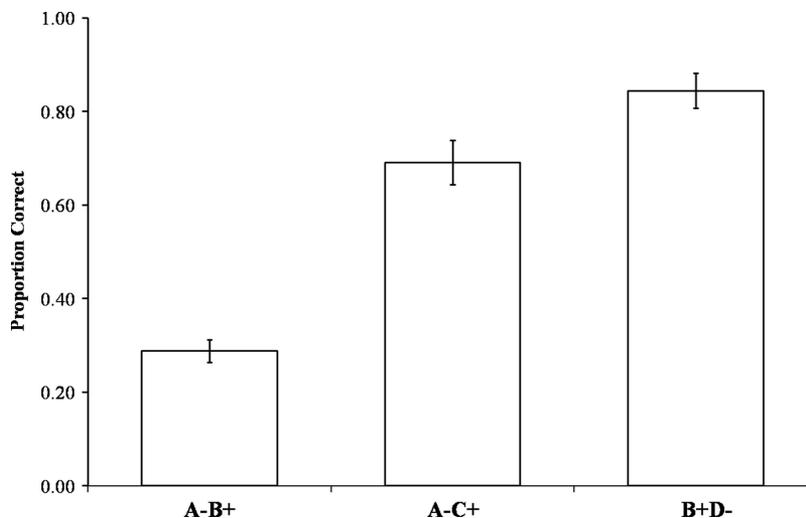


Figure 3. Proportion of correct searches in the three reversal conditions (A- B+, A- C+, and B+ D-) of Experiment 1. Error bars represent 95% confidence intervals of the mean.

Method

Subjects. A new sample of 10 dogs, five male and five females with an age range of 2 to 8 years, took part in the study. Two Dalmatians, four Labrador Retrievers, two Alsatians, one Pointer, and one small cross-breed were tested. As in Experiment 1, all dogs always had free access to water and were fed 4 hr before testing. They were recruited using the same procedure described for Experiment 1 and from the same commercial boarding kennels. None of the dogs had taken part in similar studies.

Design and procedure. The familiarization phase was carried out exactly as in Experiment 1. The locations to be used for each problem in Experiment 2 were selected using the procedure described in Experiment 1. As for Experiment 1, each dog was presented with a total of three problems.

The prereversal phase in this experiment was similar to the one adopted in Experiment 1 and required the animals to master a binary spatial discrimination (A+ B-). The hiding of the bait during the prereversal phase took place behind the lowered curtain.

The reversal phase was also similar to that used in Experiment 1 (see Table 1 for a summary of the procedure), however, in the reversal phase of the present experiment the curtain was not lowered and therefore the dogs had the opportunity to witness the baiting event during reversal. As such, the dog had all the necessary information to choose correctly in each of the reversal trials and the empirical question addressed here was whether they would have been able to benefit from it.

To prevent the dog from using spurious cues during the baiting event or making the baited cup more salient than the other by virtue of it being associated to the human hand (Reidel, Buttelmann, Call, & Tomasello, 2006), the baiting of the relevant container was paired with a manipulation of the unbaited container (inner cup was lifted 1 cm and dropped) so that a similar gesture was performed and a similar noise was produced in both cases, but the bait was only seen at the rewarded container. Trials were counterbalanced and randomly interspersed so that in half the manipulation of the unbaited containers preceded the baiting of the other and in the other half the inverse order occurred.

Results

The dogs took an average of 12.93 trials to reach criterion during the prereversal phase (95% CI [11.22, 14.65]).

The proportion of correct responses observed in the reversal phase for the three different conditions are presented in Figure 4.

The results of a one-sample *t* test showed that the dogs performed significantly above chance in the A- C+, $t(9) = 6.16, p < .001$, and B+ D-, $t(9) = 10.89, p < .001$, reversal conditions but significantly below chance in the A- B+ reversal condition, $t(9) = -2.89, p < .01$.

A one-way repeated-measures ANOVA carried out on the proportion of correct responses observed for the different conditions in the reversal phase revealed a significant difference between conditions, $F(2, 18) = 26.42, p < .001, \eta_p^2 = .75$. Pairwise comparisons carried out using paired-sample *t* tests revealed that the reversal Condition A- B+ generated a lower proportion of correct responses than reversal Conditions A- C+, $t(9) = 5.43, p < .001$, and B+ D-, $t(9) = 6.33, p < .001$, but performance in reversal Condition A- C+ did not differ significantly from that observed for reversal Condition B+ D-, $t(9) = 0.24, ns$. As in Experiment 1, no learning occurred between the presentation of the first and the last problem in each condition, $-1.64 < t(9) < -0.80, ns$.

Discussion

The results of Experiment 2 confirmed that even in a situation in which dogs received explicit information, which would have allowed them to select the correct location of the bait in every trial, their searches were still influenced by the reward contingencies experienced in the prereversal condition. In fact, if their searches were informed by the baiting event, they should have performed at the same level in the three reversal conditions. Nevertheless, their level of performance was significantly lower when the reversal included both the locations used during prereversal.

It should, however, be noted that in this experiment dogs had to learn the correct location of the bait by trial and error in the

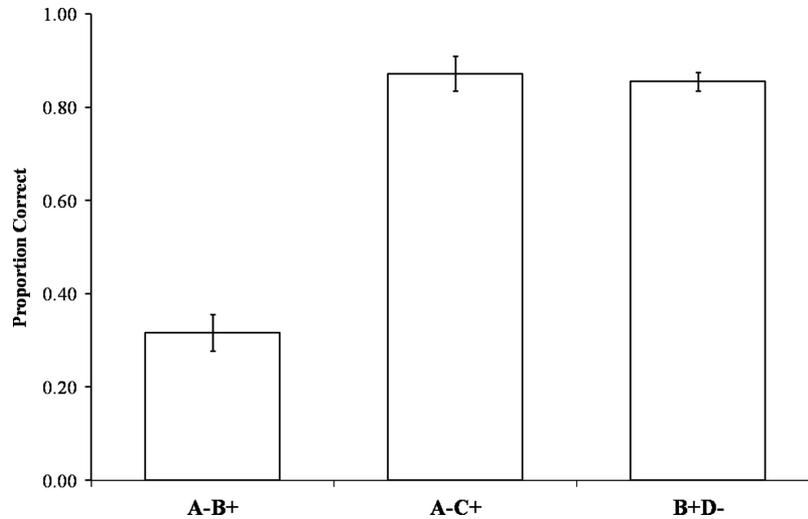


Figure 4. Proportion of correct searches in the three reversal conditions (A- B+, A- C+ and B+ D-) of Experiment 2. Error bars represent 95% confidence intervals of the mean.

prereversal phase as they did not witness the baiting event there. Thus, they were forced to use rote learning in the training to criterion before the reversal. It is possible that this type of learning overshadowed the presentation of more explicit cues during reversal.

In Experiment 3, we aimed to assess whether the same results would have been obtained if the dogs were given the opportunity to use relevant information concerning the location of the bait in the prereversal phase of the experiment too. Therefore, in Experiment 3 dogs were not forced to rely on associative learning during training. They could have spontaneously chosen to use explicit information about the object location available to them from the outset.

Experiment 3

In contrast with Experiments 1 and 2, in Experiment 3 we provided the dogs with the opportunity to witness the baiting of the correct container from the beginning of the prereversal phase.

Method

Subjects. Ten new dogs were recruited from the same commercial boarding kennels used for Experiments 1 and 2, following consent obtained from the owners. One dog, out of the 10 initially recruited for Experiment 3, had to be withdrawn because it showed a high level of anxiety during testing. Five male and four female dogs (age range 2 to 9 years) eventually took part: three Collies, one Great Dane, one Golden Retriever, one Alaskan Malamute, one Labrador-Poodle cross, one Doberman, and one Irish Terrier. As in previous experiments, dogs had free access to water and were fed 4 hr before testing. None of the dogs had taken part in similar studies.

Design and procedure. The familiarization procedure was the same as that used in Experiments 1 and 2. The prereversal and reversal phases of this experiment were similar to those of the previous experiments with the only difference that in Experiment

3 dogs witnessed the baiting event during both the prereversal and reversal phases. Also the procedure used to control for the presence of spurious cues during the baiting in the reversal phase of Experiment 2 was used both during the prereversal and reversal phase of Experiment 3. The same criterion of nine out of 10 trials correct choices in the last 10 trials was required before the administration of the reversal phase. In the reversal phase exactly the same procedure and conditions of Experiment 2 were used.

Results

The proportion of correct responses observed in the three reversal conditions of Experiment 3 is presented in Figure 5. The dogs took an average of 10.93 trials to reach criterion (95% CI [10.15, 11.70]).

As in the previous two experiments, the proportion of correct responses observed in the two reversal conditions in which a novel location replaced one of the locations used during prereversal learning was significantly above chance, A- C+, $t(8) = 4.62, p < .01$, and B+ D-, $t(8) = 6.31, p < .001$; but the search performance of the dogs was significantly below chance in the A- B+ reversal condition, $t(8) = -4.52, p < .01$. A one-way ANOVA performed on the proportion of correct responses observed in the three reversal conditions proved significant, $F(2, 16) = 26.42, p < .001, \eta_p^2 = .79$. Paired-sample t tests were used for the comparison of the different reversal conditions. They revealed that the proportion of correct responses in Condition A- B+ was significantly lower than that observed in the A- C+, $t(8) = 6.05, p < .001$, and B+ D- condition, $t(8) = 6.93, p < .001$, but that observed in the A- C+ was not significantly different from that observed in the B+ D- condition, $t(8) = 0.87, ns$. As in Experiments 1 and 2, no learning was observed between the presentation of the first and the last problem in each individual condition, $-1.72 < t(8) < -1.22, ns$.

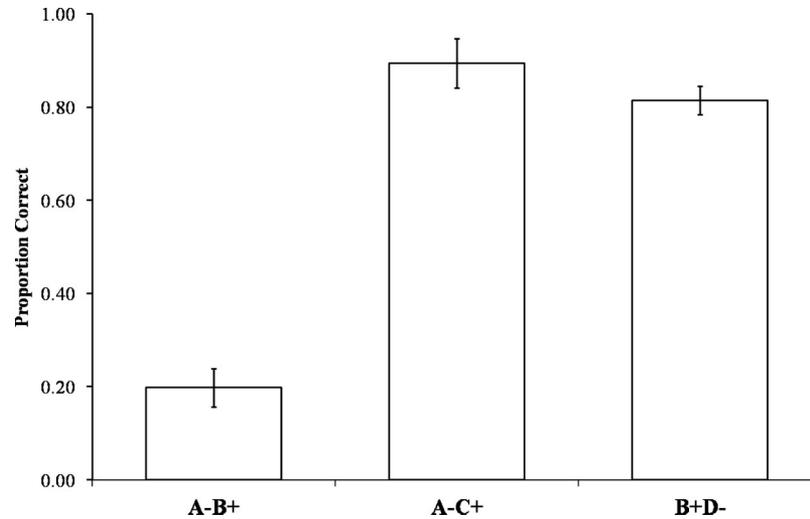


Figure 5. Proportion of correct searches in the three reversal conditions (A– B+, A– C + and B + D–) of Experiment 3. Error bars represent 95% confidence intervals of the mean.

Discussion

The results of Experiment 3 confirm that the two conditions in which a novel location was introduced during reversal (A– C+ and B+ D–) produced a higher level of performance than the reversal condition featuring the two locations used in the prereversal phase (A– B+).

This therefore indicates that associative learning took place despite the fact that dogs had all the information necessary to locate the bait from the outset and that what was learned in the prereversal phase affected dogs' choices during reversal.

One could argue that the dogs were not paying attention to the baiting event during the prereversal phase of this experiment and that because of this, associative processes prevailed there. Therefore, to confirm that dogs were indeed using the observation of the baiting event as a cue for identifying the correct location of the bait we carried out an analysis to compare the number of trials to criterion and prereversal performance in the three experiments. If the dogs ignored the baiting event completely and did not use it as a cue for determining the correct location of the bait we should expect similar trials to criterion and performance in the pretraining of the three experiments, whether the baiting event was witnessed by the dogs. By contrast, if the dogs were making use of the information provided by the fact that the baiting was performed in their full view then we should expect less trials to criterion and higher pretraining performance in Experiment 3, compared to Experiments 1 and 2.

A first one-way ANOVA was used to compare the number of trials to criterion in the three experiments. A significant difference was observed between the three experiments, $F(2, 25) = 5.51$, $p < .01$, $\eta^2 = .31$. Post hoc analyses revealed that this difference was mainly accounted for by a significant difference between Experiment 1 ($M = 14.93$, 95% CI [12.16, 17.69]) and 3 ($M = 10.93$, 95% CI [10.15, 11.70]), $p < .05$, as the mean for Experiment 2 ($M = 12.93$, 95% CI [11.22, 14.65]) did not differ significantly from that of the other experiments.

To clarify better these results we carried out a one-way ANOVA to compare the proportion of correct responses observed in the

training phase of the three experiments. This measure in fact would have given us a direct indication of whether the animals were more successful in Experiment 3 in which they had a chance to infer the location of the bait from the beginning of the training phase. It also proved significant, $F(2, 25) = 8.08$, $p < .01$. Post hoc analysis using the Tukey's honestly significant difference test indicated that the proportion of correct responses during the pretraining phase of Experiment 3 where the baiting was visible ($M = 0.94$, 95% CI [0.90, 0.97]) was significantly higher than that observed in the training phase of both Experiment 1 ($M = 0.87$, 95% CI [0.81, 0.88]), $p < .01$ and Experiment 2 ($M = 0.83$, 95% CI [0.79, 0.89]), $p < .01$ in which the baiting was not visible. The proportion of correct responses observed in the pretraining phase of the three experiments is reported in Figure 6.

From the results of this latter analysis we can conclude that, although dogs were able to use the information conveyed by the baiting event, spatial associative learning took place despite the fact that other learning options were available to the animals.

In accordance with previous studies (Beran et al., 2008; De Lillo & Visalberghi, 1994; Rumbaugh & Pate, 1984) in Experiments 1, 2, and 3 we measured the reversal performance from the second reversal trial. The first trial is normally excluded from the analysis being the one in which the animals are given the opportunity to learn that the reward contingencies have been reversed. Nevertheless, an analysis of the performance observed for trial one in each condition could be of some interest, as it would give us the opportunity to assess the presence of a differential transfer of learning in the different reversal conditions. In fact, when we carried one-sample t tests to assess whether the probability of searching correctly on the first reversal trial was different from the 0.5 expected by chance, it emerged that it was significantly below chance (negative transfer) in the A– B+ condition and significantly above chance in the A– C+ and the B+ D– conditions in Experiment 2 and 3, A– B+, $0.11 < M < 0.29$, $-4.95 < t(8) < -2.34$, all $ps < .05$; A– C+, $0.77 < M < 0.81$, $3.07 < t(9) < 3.90$, all $ps < .05$; B+ D–, $0.81 < M < 0.83$, $4.47 < t(8) < 5.37$, all $ps < .01$. In Experiment 1 we observed that performance was

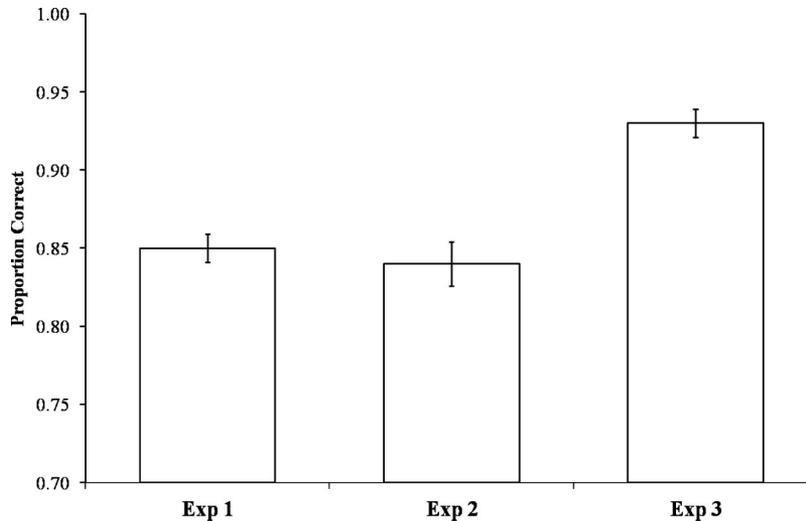


Figure 6. Proportion of correct responses observed in the prereversal phase of Experiments 1, 2, and 3. In Experiments 1 and 2 the baiting procedure in this phase was performed behind a curtain and was not visible to the dogs. In Experiment 3, the dogs had the opportunity to witness the baiting procedure in this phase. See text for further explanation. Error bars represent 95% confidence intervals of the mean. Exp = experiment.

significantly lower than chance in A- B+, $M = 0.30$, $t(8) = -2.35$; $p < .05$, and significantly above chance in B+ D-, $M = 0.78$, $t(8) = 3.54$, $p < .05$, but in Condition A- C+ it was not significantly different from chance. These results have to be considered with caution, as our study was not designed for Trial 1 analysis. The order of presentation of the first trial of each condition was selected at random and this may have created noise in Trial 1 data given the limited number of problems used in the study. Nevertheless, the results of this analysis of Trial 1 performance could be indicative of a higher propensity for the dogs to perform correctly at the outset of reversal in the two conditions featuring a novel location.

This could be due to the presence of a novel item that facilitates reversal performance as it eliminates the need to inhibit (A- C+) or disinhibit (B+ D-) as explained in previous studies that have used nonspatial version of the ML paradigm (Beran et al., 2008; De Lillo & Visalberghi, 1994; Rumbaugh & Pate, 1984).

However, an alternative explanation also is possible. Although dogs have proved to be able to use both egocentric and allocentric cues in spatial tasks (Milgram et al., 1999), it is still possible that in this study dogs coded the searched location prevalently egocentrically rather than in relation to other landmarks in the testing room. In fact, the particular constraints used in the experiments to determine the locations used in each discrimination determined that only Condition A- B+ featured a reversal of the reward consistencies in respect to the left or the right of the animal approaching the pair of containers, it is possible that only this condition was affected by a negative transfer of learning. As such, we carried out a further experiment explicitly aimed at evaluating the relative role of left-right response learning in the pattern of result observed in the previous experiments.

Experiment 4

Experiment 4 was carried out to assess whether a pattern of differences between reversal conditions similar to that observed in

all previous experiments also pertained to a situation in which a full reversal of the egocentrically defined left-right reward contingencies, which could be used by the dog approaching the containers, was maintained in all the reversal conditions. We tested two groups of dogs. One group was tested in absence (Experiment 4a) and one in presence (Experiment 4b) of explicit information about object location during reversal. Thus, apart from a different spatial arrangement of the containers, the procedure followed in Experiment 4a and 4b was the same as that followed in Experiment 1 and 2. This enabled us to make a direct comparison of the results obtained here and those of previous experiments.

Method

Subjects. There were 20 dogs who took part in these experiments. Ten (four males and six females with an age range of 1 to 8 years) were randomly assigned to Experiment 4a. The breed types were one Doberman, five Labrador Retrievers, two medium sized cross breeds, one Staffordshire Terrier, and one Weimaraner. The other 10 dogs (five males and five females, age from 1 to 9 years) were assigned to Experiment 4b. The breed types were one Border Collie, one Great Dane, one German Shepherd, two Labrador Retrievers, two medium sized cross breeds, one Pyrenean Mountain Dog, and two Spaniels.

All of the dogs were recruited from the same commercial boarding kennels as in all previous experiments and had not taken part in any previous experiments.

Design and procedure. A similar pool of problems to that used in Experiments 1 to 3 was used in Experiment 4a and 4b with the proviso that the left-right arrangement of the containers was always reversed in all the reversal conditions. To do so we had to violate the constraints used in Experiment 1 to 3, which required that the locations chosen in any given problem were never more than 60-cm or less than 40-cm apart. A diagram with the possible locations used in the present experiments is presented in Figure 7.

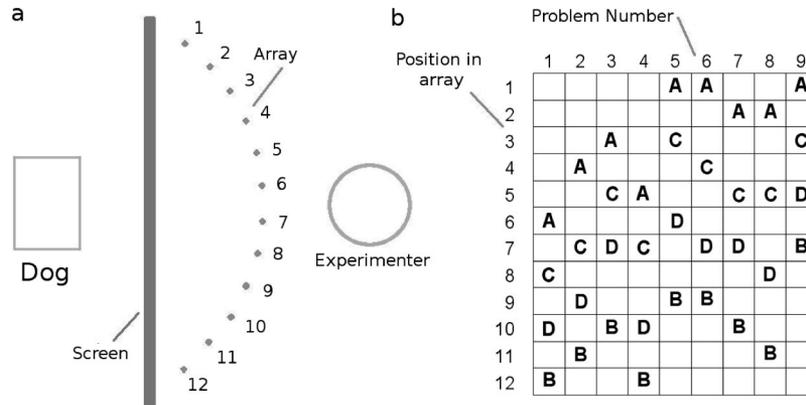


Figure 7. Schematic representation of the position in the circular array (rows) of the locations A, B, C, and D used in each problem from the pool of nine (columns) used for Experiment 4 (a and b). The experimental set-up and apparatus was the same used in Experiments 1 through 3.

This resulted in Condition A– B+ having containers further apart than the other two Conditions A– C+ and B+ D– in Experiments 4a and 4b in contrast with the procedure selected in Experiments 1 to 3, which ensured that the containers were at a similar distance in all different reversal conditions.

Apart from the difference outlined above, Experiment 4a followed exactly the same procedure as Experiment 1 (with dogs not witnessing the baiting either in the training or reversal condition) and Experiment 4b followed the procedure of Experiment 2 (the dogs witnessed the baiting in the reversal phase).

Results

The average number of trials required to reach criterion in the training phase of Experiment 4a was 14.47 (95% CI [12.74, 16.19]) and the average proportion of correct trials was 0.81 ([0.76, 0.85]). The average proportion of correct trials observed in each reversal condition was: A– B+ 0.34 ([0.21, 0.48]), A– C+ 0.62 ([0.52, 0.72]) and B+ D– 0.57 ([0.47, 0.66]).

In the training phase of Experiment 4b, the average number of trials to criterion was 12.00 (95% CI [13.98, 20.29]) and the proportion of correct trials was 0.78 ([0.72, 0.85]). The proportion of correct reversal trials was 0.62 ([0.50, 0.74]) for Condition A– B+, 0.63 ([0.52, 0.74]) for Condition A– C+ and 0.67 ([0.58, 0.76]) for Condition B+ D–.

A one-way, repeated-measures ANOVA carried out on the proportion of correct trials recorded in the different reversal conditions of Experiment 4a showed a significant difference among conditions, $F(2, 18) = 10.69, p < .05, \eta_p^2 = .54$.

Post hoc analysis was performed with paired-sample t tests. Similarly to what was observed in Experiments 1 to 3, it revealed a significant difference between the two conditions featuring novel items in the reversal phase and the control Condition A– B+ featuring the same locations used in the training phase, A– B+ versus A– C+, $t(9) = -2.50, p < .05, 95\% \text{ CI } [-0.44, -0.02]$, A– B+ versus B– D+, $t(9) = -2.38, p < .05, [-0.42, -0.01]$. No significant difference emerged between the two reversal conditions featuring novel locations, A– C+ versus B– D+, $t = 0.27, [-0.12, 0.15]$.

Similarly, in Experiment 4b a one-way, repeated-measures ANOVA carried out on the proportion of correct responses recorded in the three reversal conditions revealed a significant difference among them, $F(2, 18) = 4.94, p < .05, \eta_p^2 = .36$. Post hoc analyses revealed, as in the previous experiment that Condition A– B+ was significantly different from both Conditions A– C+, $t(9) = -3.38, p < .01$ and B+ D–, $t(9) = -3.42, p < .01$. The two reversal conditions featuring a novel location during reversal did not differ, $t(9) = 0.27, ns$.

The following results were obtained when Experiments 4a and 4b were compared with Experiments 1 and 2, respectively. A 2 (Experiment) \times 3 (Reversal Conditions) mixed model ANOVA carried out to assess whether the same pattern of performance was observed in Experiment 4a and Experiment 1 revealed a main effect of reversal condition, $F(2, 34) = 28.24, p < .001$, and of experiment, $F(1, 17) = 5.15, p < .05$, with Experiment 4a showing a higher level of reversal performance overall. The interaction reversal condition by experiment was also significant, $F(2, 34) = 4.44, p < .05$.

The interaction is explained by the fact that Condition B+ D– was performed at a higher level of accuracy in Experiment 4a, $t(17) = 3.80, p < .01$, compared to Experiment 1. By contrast, Conditions A+ B–, $t(17) = 0.74, ns$, and A– C+, $t(17) = 0.79$ did not differ significantly in the two experiments.

A 2 (Experiment) \times 3 (Reversal Conditions) mixed model ANOVA carried out to compare the results of Experiment 4b and Experiment 2 also revealed a significant main effect of reversal condition, $F(2, 36) = 38.45, p < .001$, with Experiment 4b showing a higher level of reversal performance than Experiment 2 and a significant interaction between experiment and reversal condition, $F(2, 36) = 4.00, p < .05$. Planned comparisons revealed a significantly higher level of reversal performance in Experiment 4b for Condition A+ C–, $t(18) = 3.50, p < .01$, and for Condition B+ D–, $t(18) = 4.78, p < .001$. By contrast, the reversal performance observed in Condition A– B+ did not differ in the experiments, $t(18) = 0.07, ns$. As in previous experiments no learning was observed between the presentation of the first and the last problem in each individual condition in either Experiment 4a or 4b, $-1.09 < t(9) < 1.73, ns$.

Discussion

The results Experiment 4a and 4b confirmed that the dogs found the two conditions featuring a novel location during reversal easier. This result enables us to rule out that this pattern of differences, as observed in previous experiments, was due exclusively to the absence of a reversal of left–right reward contingencies Conditions A– C+ and B+ D– in Experiments 1 and 2. Thus, the presence of a novel item in the reversal trials of Conditions A– C+ and B+ D– contributes to the higher level of reversal performance observed in these conditions. Nevertheless, Conditions A– C+ and B+ D– recorded a lower level of performance in Experiment 4a and 4b than in Experiments 1 and 2. This indicates that there was indeed an effect related to left–right response learning in Experiments 1 and 2. This effect contributed to the particularly high level of reversal performance recorded for Conditions A– C+ and B+ D– in those experiments. More important, however, this on its own is not sufficient to explain the difference between conditions as a similar pattern was observed in Experiments 4a and 4b in which all the conditions featured a complete reversal of the left–right reward contingencies.

The rationale for the particular choice of hiding locations in Experiments 1 and 2 was to keep the distance between the pair of containers within a similar range in the different reversal conditions. It was this constraint that determined a different left–right reward contingency shift in Condition A– B+ and the other two conditions. In Experiments 4a and 4b the fact that we kept the same left–right reward contingencies in all reversal conditions produced a larger distance between containers in Condition A– B+ than in the other two conditions (see Figure 7). As a matter of fact, the lack of a significant difference between the level of reversal performance observed for Condition A– B+ in the different experiments proved that that distance does not affect reversal performance in the reported experiments reported here.

General Discussion

Considering the importance attributed to the cognitive skills of dogs in recent comparative cognition literature, we judged it important to characterize in more detail the pervasiveness of associative processes, rule use, and reliance on explicit information about object location in a search task.

In the first experiment we determined which type of processes control search in dogs when no explicit information is conveyed regarding the location of the object to be retrieved. It was important to establish the prevalent mode of learning shown by dogs in absence of more explicit information about the object location. In the prereversal phase of this experiment, the dogs had to learn by trial and error which of the two possible locations was baited. Similarly, no explicit information about the bait location was provided in the reversal phase. The only relevant information available to the dogs, concerning the change in reward contingencies that had taken place during reversal, was the outcome of the first reversal trial.

On the basis of the mediational versus associative dichotomy we tested the following prediction: Relatively simple associative processes would have predicted a lower level of performance in the reversal condition featuring both the locations used during the prereversal phase (A– B+) compared to the other two. Moreover, within an associative mode of learning the relative performance in

the reversal conditions featuring a novel location in the place of either the previously rewarded location (A– C+) or the previously nonrewarded location (B+ D–) would have indicated the relative weight of associative and inhibitory processes, respectively, during spatial learning. By contrast, if learning mediated by the use of simple rules, such as “Win–stay, Lose–shift” (Harlow, 1949), had occurred we would have expected a similar level of performance in the three conditions in the reversal phase. This is because the outcome of the first reversal trial would convey the fact that the previously rewarded location was not to be chosen anymore. In Experiment 1, dogs clearly displayed an associative learning mode as reflected by their lower performance in the reversal Condition A– B+ compared to the other two that did not differ from each other. It appears that dogs can overcome inhibition (B+ D–) and they can disinhibit learnt responses (A– C+), but they have difficulty in overcoming both at the same time (A– B+).

It is possible that a nonspatial version of this task would produce a shift to a mediational mode of learning in dogs. However, the relatively poor color vision and visual acuity of dogs, compared to that of primates, combined with the fact that dogs perform better in spatial tasks rather than tasks requiring the use of nonspatial visual information (Dumas, 1998) make this possibility unlikely. Future studies could assess it by testing dogs with a similar paradigm but requiring learning and reversal learning of object discriminations. It would also be of interest to evaluate the extent to which dogs may develop a ML mode given enough exposure to a series of similar problems, in analogy with what is done with learning set paradigms (Harlow, 1949).

Once it was established that the basic learning mode of dogs is associative, we moved on to the assessment of whether dogs benefit from explicit cues concerning the bait location. We did this in Experiment 2 by allowing dogs to witness the baiting event in the reversal phase. In Experiment 2, dogs had all the necessary information that would have enabled them to search in the correct location during reversal and did not have to rely on previous learning to locate the bait. Therefore, the use of such information should have allowed the dogs to perform equally well in each reversal condition. Nevertheless, we observed that even with this explicit cue available to them, dogs still displayed a lower level of performance in the reversal Condition A– B+ in comparison to the other two reversal conditions (A– C+ and B+ D–).

The results of Experiment 2 indicated that even when other unambiguous cues about the bait location are given during reversal, the associative strength built-up in the course of previous learning overrides the use of other relevant information. However, with the method used in Experiment 2 we could not evaluate whether associative strength and inhibition would have built-up during training in situations in which all the information required to locate the bait was available from the outset. The results of Experiment 3, in which dogs witnessed the hiding procedure from the very beginning of testing in the prereversal phase, indicated that even in such a situation associative learning takes place in relation to the locations explored by the dog. Moreover, the comparison of the prereversal performance in the three experiments showed that dogs performed better when they witnessed the baiting, thus ruling out the possibility that the prevalence of associative learning occurred because the dogs were completely ignoring the hiding event.

Experiment 4 allowed us to rule out that the differential assignment of left–right reward contingencies or relative distance between search locations explained the pattern of results observed in our previous experiments.

Perseverative searches in locations in which the bait had previously been found even in presence of visual cues indicating that it has now been hidden elsewhere shares some resemblance with the A-not-B error reported in the Piagetian literature. Performance on these tasks would indicate that the provision of explicit cues about the bait location is not sufficient to override the association between a particular location and the presence of the reward developed in prereversal trials. It may also be indicative of relatively underdeveloped frontal functions in dogs as overcoming A-not-B errors has been put in relation to the development of the frontal cortical lobe (Diamond & Golman-Rakic, 1986). However, our procedure required repeated experience with successful searches at one location before the switch of rewarded locations and only some studies of A-not-B with human infants required multiple responses at A before a trial requiring the retrieval of the object at location B (see Diamond, 1998, for a discussion). It is possible that fewer perseverative errors would occur in dogs in conditions not requiring the stringent criterion used for this study or a less stringent criterion. The extent to which this is the case is a matter of empirical investigation to be carried out in future studies. However, as the issue of whether associative learning would occur in dogs in situations in which task demands do not require it was an important issue to address here.

In previous studies the prevalence of associative processes in dogs' search has been suggested on the basis of the lack of evidence that dogs can infer the location of a hidden object by default following a search of all the other incorrect locations in the search space (Watson et al., 2001). Our procedure allowed us to further characterize the role of such associative processes in dogs. Dogs used associations also in situations in which all the relevant information is explicitly provided to them without the need to be inferred. This is true at least in conditions featuring the same amount of repeated exposure to a reward in a given location as that required by our learning criterion and the type of explicit information used in our study. It was not obvious that dogs would have done so and it was important to assess this issue experimentally as done in this study. Also our results highlight an important consequence of associative learning. It can produce long-lasting effects that can be counterproductive when the task requirements change. Our paradigm allowed us to find out that inhibition of responses to an unrewarded location in dogs develops together with the associative strength acquired by the rewarded location. If this were not the case, we should have found reversal Condition B+ D– to be easier to solve than Condition A– C+. By contrast we observed in all experiments that performance in these two conditions was similar. This pattern of results is particularly remarkable considering that dogs easily acquired the spatial discrimination during the prereversal phase and as such did not experience many occasions in which their search of an incorrect location was unsuccessful.

However, in light of more recent developments in associative learning theory (see, e.g., Zentall & Sherburne, 1994) the role of inhibition in this type of tasks could be less prominent than previously assumed (e.g., Rumbaugh & Pate, 1984). The high level of performance observed in reversal Condition B+ D– could in fact be explained by assuming that the animals during training do not develop

a negative association to the nonrewarded stimulus B– that by contrast according to the value transfer hypothesis would acquire associative strength by virtue of Pavlovian conditioning because it appears together with A at the time of finding a reward following a search to A. This would induce a tendency to select it during reversal.

Moreover, as our paradigm is closely related to that used in traditional reversal learning studies it is important to assess the possibility that some effects observed in the literature on reversal learning could pertain to our results too. In discrimination reversal tasks a change of context can produce an increase in reversal performance (McDonald et al., 2001). Thus, it is possible that, in conditions featuring a novel location, reversal was easier because the dogs perceived them as featuring a different learning context. Other results provided within the literature on reversal learning indicate that explicit instructions during training facilitate reversal (Robinson & Storm, 1978). A full use of the informational content of the hiding gesture in dogs should have positively affected the A– B+ reversal performance in Experiment 3 compared to Experiments 1 and 2. A comparison of the A– B+ reversal performance in the three experiments that we carried out did not yield significant results, $F(2, 25) = 0.57, ns$, suggesting that this may not have been the case here. Thus, the hiding gestures conveyed to the dogs in this study do not seem to have the same instructional value as the verbal instructions used by Robinson and Storm (1978) with children. The failure to find a difference in reversal performance in the three experiments also points against the presence of a potential change of context effect (McDonald et al., 2001) produced by the provision of a hiding gesture in the reversal condition in Experiment 2.

It is possible that the predictive value of the baiting event itself was acquired in Experiment 3 via association. However, the fact that performance in the reversal phase of Experiment 3 was different in the three conditions indicates that either the baiting event was not used as a simple discriminative cue about the location to be chosen or, at least that the baiting event as a cue was not as salient as the learned prereversal location of the object. In fact, if the latter was the case, we should have observed a similar performance in the three conditions as in each of them the visible baiting event would provide the same discriminative cue. By contrast we have observed that it is the location repeatedly associated with the retrieval of the bait that seems to act as the most salient cue for the animals. The particular salience of spatial location relative to other types of cues also has been reported in other studies (Dumas, 1998) and our results would not be in contradiction with those reported there.

It has been convincingly proposed that cues that are socially transmitted by humans are particularly effective in guiding search for hidden objects in dogs (Agnetta, Hare, & Tomasello, 2000). In object permanence and other search tasks, it is possible that hiding events that are conveyed by movements of the human hand can acquire salience if seen by the animals as a communicative gesture and it has been stressed that these two components of the task may need to be separated to fully characterize, on the one hand, object concept and logical skills in animals and their social skills, on the other (see De Lillo & McGonigle, 1996, for a discussion). In the present study we saw that dogs picked up the information conveyed by the hiding of the object but this was not enough to completely override previous associative learning. Future studies could focus on the amount of repeated association between a given location and a reward necessary to determine these effects. They also could aim to evaluate the

conditions that provide most salient information about the bait location. For example, it is possible that dogs may be more prone to exploit the adaptive value of explicit information about changed circumstances when it is conveyed by ostensive gestures performed by humans during the visible hiding of the bait. We are currently carrying out studies to evaluate this possibility.

In conclusion, our results indicate that, at least within the scope of the conditions featured in our study, associative learning affects dogs' search for hidden objects more than explicit information about the objects' location. Further studies, using basic variations of the paradigm featured here, could clarify further the predictions of different associative learning models and the effectiveness of other sources of explicit information about object location in guiding spatial search in dogs.

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