I saw where you have been – the topography of human demonstration affects dogs' search patterns and perseverative errors

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Abstract

Performance in object search tasks is not only influenced by the subjects' object permanence ability. For example, ostensive cues of the human manipulating the target markedly affect dogs' choices. However, the interference between the target's location and the spatial cues of the human hiding the object is still unknown.

In a five-location visible displacement task, the experimental groups differed in the hiding route of the experimenter. In the 'direct' condition he moved straight towards the actual location, hid the object and returned to the dog. In the 'indirect' conditions, he additionally walked behind each screen before returning. The two 'indirect' conditions differed from each other in that the human either visited the previously baited locations before (proactive interference) or after (retroactive interference) hiding the object.

In the 'indirect' groups, dogs' performance was significantly lower than in the 'direct' group, demonstrating that for dogs, in an ostensive context, spatial cues of the hider are as important as the observed location of the target. Based on their incorrect choices, dogs were most attracted to the previously baited locations that the human visited after hiding the object in the actual trial. This underlines the importance of retroactive interference in multiple choice tasks.

Keywords: visible displacement, ostensive cues, spatial cues, perseveration, retroactive interference

1. Introduction

Finding hidden food or tracking and remembering the location of predators, prey or conspecifics is vital to the survival of many species. We can identify four factors contributing to a successful search.

Dogs' (*Canis familiaris*) object permanence ability has been the subject of extensive investigation over the past few decades. Numerous studies have shown that dogs are capable of solving tasks involving simple visible displacement (Triana and Pasnak, 1981; Gagnon and Doré, 1992, Gagnon and Doré, 1994). Dogs can reliably find a hidden object if a delay of 20 seconds (Gagnon and Doré, 1993) or even 4 minutes (Fiset et al. 2003) is introduced between the hiding event and the start of the search. There is some evidence suggesting that dogs are capable of simple invisible displacement (Gagnon and Doré, 1992). However more recent findings indicate that dogs' search behavior in an invisible displacement task is guided by the final position of the displacement device (Collier-Baker et al. 2004) or by the position of the experimenter (Fiset and LeBlanc, 2007).

Studies regarding how dogs encode the position of hidden objects show that they can use several sources of spatial information. **In a series of experiments, Fiset et al. (2000, 2007) found that** dogs primarily rely on egocentric information to encode the position of a hidden object**; however if** the egocentric information was made irrelevant, dogs were able to use allocentric information **and dead reckoning** as well to orient themselves (Fiset et al. 2007).

Geometric relationship of landmarks is not the only source of information that can guide an animal's choice when searching for hidden objects. Findings suggest that in object search tasks the position or the route taken by the experimenter (who hides the object) can also influence dogs' choices. In an invisible displacement task, where dogs had no information about the exact location of the target object, dogs tended to start searching at the location which was last passed by the experimenter whilst hiding the object (Watson et al. 2001). In an experiment of Fiset and LeBlanc (2007) the target object was not visible during the hiding, but was inside a container and this container was moved by a human experimenter. In one of the experimental conditions during the whole test the experimenter was

standing behind the hiding locations (closer to the two middle locations). In this situation dogs searched for the object more often at the locations close to the experimenter who hid the target object than at locations further away. Thus it seems that if dogs have insufficient information about the location of the target object they rely on local enhancement to solve the tasks.

These findings reveal a potentially important factor for the dogs' search performance: the information gained from social partners that until recently has been largely ignored in object search tasks. Human communicative signals can also guide the dogs' attention and influence their inferences and interpretations in object search tasks. For example, in a two-way choice task when dogs had no direct information about the location of the target they selected the location indicated by the human's ostensive-communicative referential cues (Erdőhegyi et al. 2007). In another two choice object search task Topál and colleagues (2009) found that dogs commit perseverative search errors when (and only when) the hiding events are presented in an ostensive communicative context.

Numerous studies suggest that dogs could be subject to proactive and retroactive interference. Positive evidence that proactive interference could have an effect on dogs' performance to our knowledge has been found in one study only (Tapp et al. 2003). In this experiment dogs had to solve a spatial list learning task. On the other hand Fiset and colleagues (2003) found no evidence for proactive interference in a delayed visible displacement task. On the other hand it was shown that in a radial maze dogs performance in a spatial memory task decreases due to the retroactive interference caused by the arms of the maze that have been already visited by the dog (Macpherson and Roberts, 2010). Gagnon and Doré (1993) found that dogs' errors in an invisible displacement task can be partially attributed to retroactive interference caused by the postdisappearance movement of the container. At the same study the researchers also found that dogs also seem to be subject to retroactive interference in a visible displacement task.

These findings and the earlier presented studies raise the possibility that dogs' search performance in object hide-and-search tasks is fundamentally affected by both the ostensive communicative nature of

the hiding event (by inducing perseverative errors) and the interference between the events perceived before or after witnessing the object disappear. Therefor we asked the question whether in a visible displacement task in a uniformly ostensive communicative context dogs' location choices would be affected by the hider's movement prior or after the disappearance of the object.

The object hide-and-search task in our study was designed so that dogs, after witnessing the placing of an object to one of five locations could search for the toy until they found it. A test consisted of five trials and the object was placed to all five locations once in a consecutive order. In the direct conditions the hider moved on a direct route (in a straight line towards the actual location) and dogs were either released right after the hiding (Direct group) or after 1 min distraction (Delayed Direct group). In the indirect conditions however, the hider walked behind each hiding location moving along an arc and the toy was placed behind one of the hiding locations. The hider's route was designed so that he either walked behind the previously baited locations before (Indirect group) or after (Reverse Indirect group) hiding the object. With this design we intended to discriminate the effects of the proactive interference caused by the hider's movement before hiding the object and the retroactive interference caused by the hider's movement after hiding the object. The hiding of the object was always performed in an ostensive communicative context. In the frame of this study by communicative context we mean that the hider expresses communicative intent by looking toward the dog while showing the ball (or his empty hands) and addressing the dog in a relatively high pitched voice, with the aim of attracting the dog's attention to himself and the task.

In our experiment the cues given by the hider can be categorized into two types. (1) The ostensive communicative cues that are intentional, uniformly present in all conditions throughout the entire hiding event and serve to direct dogs' attention to the hider and the task. (2) Spatial cues which refer to the position or the movement of the hider during the hiding event. These cues can be regarded as non-intentional and differ between the experimental conditions (except between the Direct and the Delayed

Direct conditions where they are identical). The spatial cues of the hider could affect dogs in several ways. Based on the effect of these we can form four hypotheses and make the following predictions:

1) If dogs rely exclusively on direct visual information about the location of the object in each condition, and ignore any other spatial cues of the hider (object location dominance hypothesis). In this case **(hypothesis 1)** we expect no difference in dogs' choices between the Direct and the two indirect groups. Based on the experiments of Fiset and colleagues (2003), we expect a lower performance in the Delayed Direct group due to the one minute of delay introduced. **However, according to hypothesis 1, no differences are expected among the trials in all groups (Table A.1).**

2) If spatial cues act as a general distraction, then dogs in the two indirect conditions will encode the position of the correct location less accurately and this would result in a decrease of performance. Since the total amount of potentially distracting spatial cues are the same in the Indirect and Reverse Indirect groups we would expect no difference in performance, location choices or the distribution of erroneous choices between the two groups**. In case of hypothesis 2 it is an open question, whether spatial distraction in t**he two indirect groups**, or the higher requirement of working memory in the Delayed Direct group would cause** lower performance**. However, according to this hypothesis again, we do not expect any difference among the trials in all groups (Table A.2).**

3) It is possible, however, that spatial cues act as attractors. Namely that in the indirect groups the hider by walking behind the locations does not simply distract dogs' attention from the location where the object is hidden, but directs it towards the locations behind which he was walking.

One of the possible **scenarios for** the spatial cues **(hypothesis 3A)** is whe**n** the hider walks behind the locations before hiding the object, thus possibly causing proactive interference, or walking behind the locations after performing the hiding and causing retroactive interference.

The amount and localization of "proactive spatial cues" and the "retroactive spatial cues" differ in each of the corresponding trials between the two indirect groups (See Fig. 2; e.g., 2nd trial: Indirect group: the

hider walks behind location 1 (proactive) and behind locations 3 to 5 (retroactive); Reverse Indirect group: the hider walks behind locations 5 to 3 (proactive) and behind location 1 (retroactive)). Because of this if there is a difference in the influence of the proactive and retroactive spatial cue types on dogs then that would cause a difference in overall location choices, correct choice distribution and the amount of perseverative and non-perseverative errors between the groups (**Table A.3**).

According to a second option (hypothesis 3B – 'the last spatial cue as attractor'), in line with the findings of earlier papers (Pongrácz et al. 2001; Watson et al. 2001) we could expect that dogs will show a preference for the location that the hider passed by last on his route and thus they will choose more often the location from where the hider returned to the starting position. This bias would lead to dogs having a lower ratio of correct choices in the two indirect groups, and a higher ratio of choosing the 1st or the 5th locations than expected by chance (**Table A.4**).

4) Because the local enhancement caused by the hider's movement could interfere with the information about the location where the object disappeared, we could expect dogs to shift their choices towards the locations based on the interaction between their previous experience and the 'new' spatial cues (Hypothesis 4). One possible difference is whether at the actual trial the given locations (behind which the hider walks) were already baited in a previous trial (spatial cues in the proximity of already baited locations) or were not baited in any of the previous trials yet (spatial cues in the proximity of non-baited locations). The 'baited spatial cues' and the 'non-baited spatial cues' are always at the same locations in each of the corresponding trials in the two indirect groups (See Fig. 2; e.g., 2nd trial: Indirect group: the hider walks behind location 1 (baited) and behind locations 3 to 5 (non-baited); Reverse Indirect group: the hider walks behind locations 5 to 3 (non-baited) and behind location 1 (baited)). Because of this if there is a difference in the influence of the baited and non-baited spatial cue types on dogs then that would cause no difference between the groups. However the overall location choices, the distribution of correct choices between trials and the amount of perseverative and non-perseverative errors would be biased (Table A.5).

2. Methods

2.1 Experimental arrangement

All tests were conducted outdoors so that a large scale setup could be used by increasing the distance between the hiding locations and the dog. Five hiding locations were used. Each one was comprised of a plastic panel (40cm×40cm with two bent 10cm extensions on each side); each panel was painted with a different black and white geometric pattern (Fig. 1). The patterns were only used in order to increase the salience of the hiding locations and to help dogs distinguish between the individual locations. The hiding locations were arranged along an arch at a distance of 2m from each other and were equidistant (15m) from the starting position (SP). The position of the individual patterns was randomized for each subject. A plastic flower pot (diameter 16cm) was placed behind each panel; these pots served for hiding the target object during the trials. We used a rubber squeezable toy or a ball as targets, depending on the dogs' preference. All tests were performed at a Hungarian dog training school between the spring of 2004 and the spring of 2006.

<place of Fig 1>

2.2 Subjects

Dogs (N = 84; 21 per group) and their owners were recruited from clients of various dog training schools and participants of competitions for dogs. Participation in the tests was voluntary. Owners were instructed how to behave and what to do (and not do) during the test. Only dogs older than 1 year were tested (33 females and 51 males, mean age = 2.06 years, range = 1–10 years) and various breeds were included. The dogs were required to be highly motivated to retrieve a ball or rubber toy. Dogs were assigned randomly to one of the four experimental groups. It should be noted that Gagnon and Doré (1992) showed that domestic dogs from various breeds showed similar performance in a visible displacement task similar to the one used in the present experiment.

2.3 Procedure

A test consisted of five trials. Each trial started with the owner, the dog and the hider (H) standing at the SP facing the hiding locations. The H took the target object, showed it to the dog and started walking towards the hiding locations with the object constantly visible in his hand. The H continuously maintained the dogs' attention on himself by frequently turning his head back and calling the dog's name and waving the target object.

When the H reached the actual location he walked behind it and placed the object in the pot. After this the H displayed his empty hands and returned to the SP. During this the H continued to keep the dog's attention on himself by talking to the dog. After the H returned to the SP, the owner released the dog from its leash. The dog was allowed to search for the target object for one minute and could visit any number of hiding locations during this time. During this period the dog was continuously encouraged by both the H and the owner to search for the object, but no directional cues were allowed to be given to the dog (pointing at the correct location, verbally directing the dog, etc.). If the dog found the object it was praised by the H and the owner, and recalled to the SP. The owner took the object from the dog, handed it to the H and the next trial began.

We chose to let dogs continue to search for the object even after an incorrect choice because we were specifically interested in which locations dogs' would choose only by observing the hider's movement and based on their memory about the object's location in the previous trials. We did not want to interfere with dogs' choices by actively restricting them to choose any of the locations.

During a test the target object was hidden behind each location once in a consecutive order either starting from the left-most or from the right-most hiding location counterbalanced in each group. The H hid the target object only once to each location to minimize the chance of dogs forming strong associations between one particular location and the target object. Three of the experimental groups differed in the route the H took while carrying the object to the hiding location and returning to the SP.

In the 4th group one minute of retention interval was introduced between the return of the H to the SP and the search of the dog.

In the Direct (D) group the H moved in a straight line from the SP to the actual hiding location, and returned directly to the SP after hiding the object (Fig. 2). The entire hiding procedure (from starting to walk from the SP, to arriving back and releasing the dog) lasted on average 25 seconds.

In the Indirect (I) group the H started walking always towards the right- or leftmost hiding location (the one where the object was hidden in the first trial of the actual test), then walked behind the line of the hiding locations to the actual location. After hiding the object, the H continued to walk towards the other end of the location line**. Importantly, during this part of his route, the H held his hands such way that the dog could see that the object was not in them anymore. From the last location in the line the H** walked back to the SP (Fig. 2). The whole procedure of hiding the object lasted on average 33 seconds.

The Reverse Indirect (rI) group was similar to the Indirect group in the experimenters' route. The only difference was that the H started to walk towards the location where the object was hidden in the fifth trial and not toward the location where the object was placed in the first trial (Fig. 2). The whole procedure of hiding the object lasted as long as in the Indirect group.

To control for the longer delay between the act of hiding the object and the return of the experimenter in the indirect conditions (4 seconds on average), we included a group where we introduced one minute delay between the return of the experimenter and the release of the dog (Delayed Direct group (dD)). In this group the route of the hider was the same as in the Direct group. The only difference was that after the H arrived back to the SP from hiding the object, the dog was not released immediately from the leash. Instead the dog was led by the owner 15 meters away from the SP where they walked for one minute around in a designated circle (diameter 6m). At the signal of the H, the owner and the dog returned to the SP. The owner released the dog from the leash and from this point the experiment proceeded as described above.

<place of Fig 2>

The difference between the Direct and the two indirect groups is in the number and localization of spatial cues the hider presents during the hiding event. The only common element in each group is the conspicuous placing of the object to the actual hiding location. In the direct groups the “walking to” and “walking back” elements are focused on the actual location, so every spatial cue given by the hider is directed towards the location where the object was placed.

In the indirect groups the “walking to” and “walking back” elements are focused on the first and last locations respectively. There are two elements which do not occur in the direct groups: walking behind the line of hiding locations before and after hiding the target object. This also means walking behind locations where the object was hidden in the previous trials or behind locations where the object was not hidden yet. In the indirect groups only the “hide the object” cue is associated with the correct location, the other spatial cues are focused on the incorrect locations (except the first and last trials when either the “walking to” or “walking back” spatial cue coincides with the correct location).

2.4 Data collection

The dogs’ behavior was recorded with a handheld camcorder fixed on a tripod and the video footage digitalized and analyzed later. We coded dogs’ search behavior by recording the number and sequence of hiding locations visited until the object was found. Visiting (searching at) a hiding location was defined as the dog lowering its head just behind one of the plastic panels and looking inside the pot behind it. We followed the principle that hiding locations were numbered from 1 to 5 according to the order of hiding events across trials 1-5.

In this study we analyzed dogs’ first choices: the hiding location visited first in each trial. A correct first choice was defined as the dog choosing the location where the object was hidden by the experimenter in that trial, choosing any other hiding location first was considered an erroneous choice. We also

analyzed the distribution of incorrect choices, therefor if a dog did not find the hidden object after searching for one minute in any of the trials that dog was excluded from the survey.

2.5 Data analysis

Our main statistical tool for data analysis here were the Monte Carlo tests. Requiring only minimal assumptions for validity, Monte Carlo tests provide a flexible and intuitive methodology for statistical analysis (Nichols & Holmes 2002). They are preferable to parametric and traditional non-parametric methods as they do not require a specific distribution shape. Monte Carlo tests apply to a variety of test statistics having a more complicated distribution. This property of Monte Carlo tests made us possible to conduct statistical tests which simultaneously take in account the differences between individual trials or regard the differences between all possible choices in all trials and compare these distributions across experimental groups.

To control for the increased chance of Type I errors resulting from multiple comparisons, we applied a false discovery rate control (FDRC) from Benjamini and Hochberg (1995) to all the p values obtained each time multiple comparisons were executed in parallel. The Monte Carlo tests and the FDR control used in this article were implemented using MATLAB® (R2008a, Copyright 1984-2008, The MathWorks, Inc.).

To find out whether the four experimental groups differed in performance we compared the ratio of correct choices in all trials with a Monte Carlo analysis. The test statistic was calculated as follows. The ratios of correct choices were calculated in all groups and all trials (Table A.6). Afterwards the square of differences were calculated for the corresponding trials between all groups pairwise and summed. According to the H_0 that all four experimental groups should come from the same population we generated random samples by permuting the labels denoting group membership among the data for each individual. We generated 10^6 random samples. For each sample the test statistic was calculated thus constructing the sampling distribution. To determine the probability that the observed difference between all four groups can be attributed to chance (p), we determined the ratio of random samples

where the summed square of differences was equal or greater than in the original sample. Our criterion to reject the H_0 was a p value smaller than 0.05.

In case of significant differences were found between particular pairs of groups, to ascertain which trials are responsible for these differences, we determined for each trial the probability of obtaining an equal or greater difference between the ratios of correct choices. The Monte Carlo test was the same as previously used, with one exception. The squared differences of correct choice ratios between trials were not summed, but the probability of obtaining an equal or greater difference was calculated separately for each trial.

In case of between-group differences, we counted for each subject the number of correct trials (min.: 0, max.: 5) and calculated the summed squared differences of correct choices compared to the value expected by chance (1 in case of 5 trials with 0.2 success rate). Then we run a Monte Carlo simulation generating random correct choices across five trials for each subject with the rate expected by chance (0.2) and repeated the above described difference calculation with the simulated data and the theoretical value expected by chance. We repeated the process 10^6 times and compared the differences with the one obtained with the empirical data set. The p value was obtained by calculating the ratio of simulated differences that were equal or larger than the difference of the empirical data set from the theoretically expected values. We repeated the calculation for each of the four experimental groups and applied a FDR correction to the obtained four p values.

We also analyzed the distribution of dogs' first choices among all hiding locations in the experimental groups. We conducted a Monte Carlo test similar to the one carried out when comparing performances, except that now we used a different test statistic. Instead of calculating the ratio of the correct choices we calculated the ratios of choices of all the hiding locations in each trial (Table A.7). As previously we first conducted an overall Monte Carlo test comparing the sum of squared differences of first choices between all four groups.

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In case if the distribution of the first choices differ from that expected by chance, to find out which locations are the ones chosen more or less often than 20% by the dogs, we conducted five binomial tests in the given group. We calculated the total number each of the locations was chosen throughout the test. Then for each location we compared the ratio the given location and any other location being chosen (e.g., for location 1: total number location 1 was chose / total number location 2 + 3 + 4 +5 was chosen) to the one expected by chance (0.2 / 0.8) with a binomial test.

We analyzed also the distribution of dogs' erroneous choices. We compared the number of errors made by choosing locations where the object was hidden in a previous trial (perseverative errors) and by choosing locations where the object had not been hidden yet (non-perseverative errors). Since altogether in the five trials there is an equal chance to make perseverative or non-perseverative errors, we compared the total number of perseverative and non-perseverative errors in each group. We conducted four Monte Carlo tests, one for each group. Our test statistics were the differences between the total number of perseverative and non-perseverative errors made in the group of interest. The samples were generated by randomly rearranging the errors in a way that for each dog we swapped the perseverative errors with the non-perseverative ones with 50% chance. Then on the rearranged dataset we calculated the difference between the total number of perseverative and non-perseverative errors and determined whether this difference was equal or larger than the original one. We counted the number of runs where the difference was equal or larger than the original one and divided this by the total number of runs (10^6) resulting in our p value.

3. Results

3.1 Analysis of the dogs' correct choices

The Monte Carlo analysis indicated that the observed difference between the four experimental groups cannot be attributed to chance (MC test: N_D=21, N_{dD}=21, N_I=21, N_{rI}=21, p=0.00). So we conducted six pairwise Monte Carlo tests comparing each group with the others. The tests were identical to the method **described in 2.4,** except for that at each test only two groups participated in the analysis (**Table 1**). Our results show that both of the direct groups differ significantly from both of the indirect ones but there is no significant difference between the Direct and the Delayed Direct groups and also no difference between the Indirect and Reverse Indirect groups.

Table 1 Results of the six pairwise Monte Carlo tests comparing the differences in performance between experimental groups (FDRC sig.: stars mark p values passing the Benjamini & Hochberg FDR control; Experimental groups: D: Direct, dD: Delayed Direct, I: Indirect, rI: Reverse Indirect).

	D-dD	**D-I**	**D-rI**	**dD-I**	**dD-rI**	**I-rI**
p	0.0716	0.0002	0.0000	0.0305	0.0007	0.1272
FDRC sig.		*	*	*	*	

Our first hypothesis (object location dominance) predicted that there should be no difference between the performance of the Direct, the Indirect and the Reverse Indirect groups, but the Delayed Direct group should have a lower performance than the other three. However we found that dogs' performance was significantly higher in the Direct and Delayed Direct group than in the Indirect or in the Reverse Indirect groups. The difference between the direct and the indirect groups was in the localization of the spatial cues presented by the hider during the hiding event. Thus we can conclude that the spatial cues of the hider have an influence on dogs' **performance**.

In the next step we determined, which trials caused the above described between-group differences. Our results revealed that the Direct and Indirect groups differed in performance at trials three and four **(Table 2).** The Direct and Reverse Indirect groups differed between trials three, four and five. In the Delayed Direct and Indirect groups none of the individual trials differed significantly after applying the FDR correction. The Delayed Direct and Reverse Indirect groups differed in performance also between trials three and four.

Table 2 Results of the pairwise Monte Carlo tests comparing the differences in performance at each trial (FDRC sig.: stars mark p values passing the Benjamini & Hochberg FDR control; Experimental groups: D: Direct, dD: Delayed Direct, I: Indirect, rI: Reverse Indirect).

		Trial 1	**Trial 2**	**Trial 3**	**Trial 4**	**Trial 5**
D-I	p	1.0000	0.5061	0.0108	0.0048	0.1004
	FDRC sig.			*	*	
D-rI	p	0.7186	0.0578	0.0000	0.0048	0.0043
	FDRC sig.			*	*	*
dD-I	p	1.0000	0.3547	0.3542	0.0127	0.5309
	FDRC sig.					
dD-rI	p	0.4531	1.0000	0.0025	0.0128	0.0628
	FDRC sig.			*	*	

In order to determine the factors contributing to the **between-group differences in** performance, we started our analysis by comparing dogs' performance in each group to the one expected by chance. **We found** that in all four groups the summed performance of dogs was significantly above the level expected by chance (MC test: Direct: N=21, p=0.00; Delayed Direct: N=21, p=0.00; Indirect: N=21, p=0.00; Reveres Indirect: N=21, p=0.02). However since we obtained significant differences between the groups when comparing the performances in separate trials we also compared the performance in each trial to the success rate expected by chance.

In order to accomplish this, we conducted a series of binomial tests where we compared the correct / incorrect first choice rate expected by chance (0.2 / 0.8) to the total number of correct / incorrect

choices at the particular trial. In the Direct and Delayed Direct groups, dogs found the object with their first choice significantly above chance level in all trials (Binomial test: Direct: N=21, Trial 1: p=0.00, Trial 2: p=0.00, Trial 3: p=0.00, Trial 4: p=0.00, Trial 5: p=0.00; Delayed Direct: N=21, Trial 1: p=0.00, Trial 2: p=0.02, Trial 3: p=0.00, Trial 4: p=0.00, Trial 5: p=0.00) (Fig. 3). In the Indirect group, dogs were not able to find the object with their first choice in trial three and four and also in the Reverse Indirect group in trials three, four and five (Binomial test: Indirect: N=21, Trial 1: p=0.00, Trial 2: p=0.00, Trial 3: p=0.05, Trial 4: p=0.41, Trial 5: p=0.00; Reverse Indirect: N=21, Trial 1: p=0.00, Trial 2: p=0.02, Trial 3: p=0.29, Trial 4: p=0.41, Trial 5: p=0.17). These findings also underpin the results of the previous Monte Carlo tests where we found that there is a difference between the two direct groups and the two indirect groups based on performance, but with no difference within them.

<place of Fig 3>

3.2 Analysis of the distribution of dogs' first choices

We found a significant difference between the distributions of first location choices between the groups (MC test: N_D=21, N_{dD}=21, N_I=21, N_{rI}=21, p=0.00). After this we conducted six pairwise Monte Carlo tests comparing each group with the others (**Table 3**). The test detected a significant difference between the Direct and Reverse Indirect groups and between the Delayed Direct and Reverse Indirect groups.

Table 3 Results of the six pairwise Monte Carlo tests comparing the differences in the ratios of locations chosen between experimental groups (FDRC sig.: stars mark p values passing the Benjamini & Hochberg FDR control; Experimental groups: D: Direct, dD: Delayed Direct, I: Indirect, rI: Reverse Indirect).

	D-dD	**D-I**	**D-rI**	**dD-I**	**dD-rI**	**I-rI**
p	0.1930	0.1940	0.0008	0.4494	0.0025	0.0408
FDRC sig.			*		*	

Only in the case of the Reverse Indirect group did the distribution of first choices differ from that expected by chance **(Table 4).** This finding suggests that the Reverse Indirect group differs from the other three in respect to first location choices.

Table 4 Results of the four multinomial tests comparing the number of first choices towards the hiding locations in each experimental group to the level expected by chance (0.2 at all five locations) (FDRC sig.: stars mark p values passing the Benjamini & Hochberg FDR control).

	Direct	**Delayed Direct**	**Indirect**	**Reverse Indirect**
p	0.9003	0.1483	0.1089	0.0000
FDRC sig.				*

After performing five separate Binomial tests, the results showed that dogs in the Reverse Indirect group chose the first and second locations more often than that expected by chance and locations three and five less often (Binomial test: N=21, Location 1: p=0.00, Location 2: p=0.00, Location 3: p=0.00, Location 4: p=0.18, Location 5: p=0.00) (Fig. 4).

<place of Fig 4>

These results are not in accordance with our hypothesis 2 according to which no differences are expected in dogs' first choices among trials within all groups and between the Indirect and Reverse Indirect groups. Our hypothesis **3B** predicted that dogs would show a preference for following the hider's route. This could manifest as a preference for choosing one or both of the hiding locations on the edges more often than the ones in the middle in the indirect groups. However the analysis of first location choices (**Table 4**) demonstrated that only in the Reverse Indirect group did dogs' choices differ significantly from a homogenous distribution. In this group dogs chose the first location more often than expected by chance which could support the hypothesis that they prefer to choose the location last passed by the hider (for the route of the experimenter see Fig. 2).

3.3 Analysis of the dogs' erroneous choices

Finally we analyzed the distribution of dogs' erroneous choices. The results of the Monte Carlo tests showed that in all groups, except in the Direct group, the distribution of errors was biased towards the locations where the object had been hidden in a previous trial **(in other words, dogs committed the so-called perseverative error)** (**Table 5**).

Table 5 Results of the Monte Carlo tests comparing the total number of perseverative and non-perseverative errors in the four experimental groups (FDRC sig.: stars mark p values passing the Benjamini & Hochberg FDR control).

	Direct	**Delayed Direct**	**Indirect**	**Reverse Indirect**
p	0.2225	0.0016	0.0163	0.0000
FDRC sig.		*	*	*

Next we compared the two error types separately to find out whether the numbers of perseverative or non-perseverative errors made by the dogs differ among the four experimental groups. This Monte Carlo test was identical to the one conducted when we compared dogs' performance with the exception that the test statistics were either the squared differences between the total number of perseverative, or the squared difference between the total number of non-perseverative errors in each group. We compared the number of errors in each group to the number of errors in all other groups.

We found no difference between the groups in regard of non-perseverative errors but we found a significant difference in the amount of perseverative errors between the groups (MC test: N_D=21, N_{dD}=21, N_I=21, N_{rI}=21; Non-perseverative errors p=0.69, Perseverative errors p=0.00). To ascertain which groups differ from each other in respect to perseverative errors, we conducted six pairwise Monte Carlo tests between the groups using the same test statistics as previously (**Table 6**).

Table 6 Results of the six pairwise Monte Carlo tests comparing the differences in the total number of perseverative errors made between experimental groups (FDRC sig.: stars mark p values passing the

Benjamini & Hochberg FDR control; Experimental groups: D: Direct, dD: Delayed Direct, I: Indirect, rI: Reverse Indirect)

	D-dD	**D-I**	**D-rI**	**dD-I**	**dD-rI**	**I-rI**
p	0.0296	0.0067	0.0000	0.3511	0.0001	0.0084
FDRC sig.	*	*	*		*	*

We found that the **total number of perseverative errors was the lowest in the Direct group, while it was the highest in the** Reverse Indirect group (Fig. 5**). There was no significant difference between the number of perseverative errors in the Delayed Direct and the Indirect groups**. These results demonstrate that **the larger proportion** of errors made in the indirect groups compared to the Direct group is due to the increase in perseverative errors.

<place of Fig 5>

Our second hypothesis (spatial cues as distractors) predicted that the Direct group should have a higher performance than the Indirect and Reverse Indirect groups, but the two indirect groups should not differ from each other. In terms of performance this is true, however there is a significant difference in location choices and, as we could see above, in the number of perseverative errors between the Indirect and the Reverse Indirect groups. These findings indicate that regarding the spatial cues only as factors that distract dogs' attention from the action of hiding, does not completely explain our findings. **However, if we take in consideration the movement of the Hider as a source of differently influential socio-spatial information, like hypothesis 3A, we can get a more plausible explanation for the uneven distribution of perseverative errors.**

4. Discussion

While analyzing the result of our experiment, we found evidence that contradicted three of the hypotheses proposed in the introduction. Our first hypothesis (object location dominance) predicted no

difference between the performance of the Direct, the Indirect and the Reverse Indirect groups. In contrast, we found that dogs' performance was significantly higher in the Direct group than in the two indirect groups. This finding was in accordance with our second hypothesis (spatial cues as distractors). This hypothesis on the other hand also predicted that there should be no difference between the two indirect groups. Our analysis revealed however, that the Indirect and Reverse Indirect groups differed in location choices and the number of perseverative errors, which findings refute this hypothesis. **H**ypothesis **3B** expected that dogs would choose one or both of the hiding locations on the edges more often than the ones in the middle in the indirect groups. However there was no clear evidence indicating a similar choice pattern.

Contrary to the previously mentioned ones, hypotheses 3A and 4 remained **still** unrefuted. **In these we expected spatial cues acting as attractors alone (hypothesis 3A), or in interference with local enhancement caused by the previously found hidden targets (hypothesis 4). Hypothesis 4** predicted specific distribution of location choices, correct choices and erroneous choices in the two indirect groups depending on the relative influence of the baited and non-baited spatial cues on dogs' choices (**Table A.5**). Since the baited locations are mostly the lower-numbered ones (Trial 1: none; Trial 2: 1; Trial 3: 1-2; Trial 4: 1-2-3; Trial 5: 1-2-3-4) in both of the indirect groups, this means that if the baited spatial cues are more salient to dogs, then they should choose the lower-numbered locations more often than expected by chance. This subsequently leads to a better performance in the initial trials and more perseverative than non-perseverative errors. On the other hand if the non-baited spatial cues (Trial 1: 2-3-4-5; Trial 2: 3-4-5; Trial 3: 4-5; Trial 4: 5; Trial 5: none) are more salient, then the higher-numbered locations will be chosen more often. This naturally leads to a better performance in the later trials and more non-perseverative than perseverative errors.

Looking at the ratio of perseverative and non-perseverative errors we found that in both of the indirect group's dogs committed significantly more perseverative errors **than in the Direct group**. This finding fits to the predicted outcome of **Hypothesis 4** in which the baited spatial cues are more salient to dogs

than the non-baited ones. Analyzing the ratios of correct choices at each trial revealed that in the Indirect group dogs performed above chance level in the 1st, 2nd and 5th trial and that in the Reverse Indirect group their performance was above chance only in the 1st and 2nd trials. Since dogs' performance was above chance mainly in the initial (1st and 2nd) trials, these results match best the expected outcome of the case when the baited spatial cues have more influence on dogs' choices than the non-baited ones.

The ratios of first location choices only differed from the level expected by chance in the Reverse Indirect group. In this group the dogs chose more often the 1st and 2nd locations and less often the 3rd and 5th locations. This is also in accordance with the results above. All the results of our statistical analysis are in concordance with the predictions **of Hypothesis 4 (positive interference between spatial and local enhancement cues),** based on the assumption that the spatial cues presented while walking behind locations where the object was hidden in the previous trials have a stronger effect of attracting dogs' attention, than the spatial cues at non-baited locations.

However, Hypothesis 4 does not predict difference between the location choices, correct choices and error patterns of the two indirect groups. Therefore we investigated our results in the light of the question whether the spatial cues before the act of hiding (proactive), or the spatial cues after the act of hiding (retroactive), have a greater influence on dogs' choices. **Hypothesis 3A** predicted specific differences between the Indirect and Reverse Indirect groups if either of the spatial cues had stronger influence on dogs' choices than the other (**Table A.3**).

The locations affected by the proactive spatial cues are the lower-numbered ones in the Indirect group (Trial 1: none; Trial 2: 1; Trial 3: 1-2; Trial 4: 1-2-3; Trial 5: 1-2-3-4) and the higher-numbered ones in the Reverse Indirect group (Trial 1: 2-3-4-5; Trial 2: 3-4-5; Trial 3: 4-5; Trial 4: 5; Trial 5: none). In the case dogs location choices are more influenced by proactive spatial cues then we would expect dogs to choose the lower numbered locations with higher frequency in the Indirect group and the higher numbered locations with higher frequency in the Reverse Indirect group. This at the same time would

lead to better performance in the initial trials and more perseverative errors in the Indirect group versus the Reverse Indirect group. Consequently the locations affected by retroactive spatial cues are the higher-numbered ones in the Indirect and the lower-numbered ones in the Reverse Indirect group, leading to better performance in the initial trials and more perseverative errors in the Reverse Indirect group versus the Indirect group .

According to these predictions we will now concentrate on the differences between the two indirect groups. When analyzing the distribution of errors we found that dogs committed significantly more perseverative errors in the Reverse Indirect group than in the Indirect group. This result fits to **hypothesis 3A**, in which the retroactive spatial cues have a stronger effect on dogs' choices than the proactive ones.

By looking at the ratios of correct choices, we can see that in both indirect groups dogs perform above chance level in the 1st and 2nd trials, but only in the Indirect group is their performance above chance in the 5th trial. This indicates that dogs' correct choices are more evenly distributed in the Indirect group whereas in the Reverse Indirect group dogs only choose correctly in the initial two trials**, which again shows similarity to what hypothesis 3A (with retroactive cues having the stronger effect) predicted.** The distribution of first location choices shows a similar picture **(although no direct significant difference was found between the location choices of the two indirect groups).** In the Indirect group none of the locations were chosen more often than that expected by chance, but in the reverse Indirect group dogs choose the lower-numbered locations (1st and 2nd) significantly more often and the higher-numbered ones (3rd and 5th) significantly less often. The results of analyzing dogs' correct and first location choices both support the assumption that the retroactive spatial cues have a stronger effect on dogs' choices than the proactive spatial cues.

By summarizing the findings above we can say that dogs' choices are strongly influenced by the spatial cues of the experimenter and are not only guided by the information gained from seeing the object disappear at one of the locations. The spatial cues of the experimenter influence dogs' by directing their

choices towards the locations where the cues were presented. After analyzing the results of the two indirect groups it is clear that dogs were influenced more by the spatial cues presented at locations where the object was hidden / found in a previous trial (baited spatial cues) then by spatial cues at locations that were not baited previously. Additionally when analyzing the differences between the Indirect and the Reverse Indirect groups we came to the conclusion that the spatial cues presented after the act of hiding (retroactive spatial cues) had a stronger effect on dogs' choices then the spatial cues presented before it (proactive spatial cues).

In conclusion dogs' location choice behavior in our experiment can be explained by **three** factors: the observed location of the object's disappearance; baited spatial cues; retroactive spatial cues. Below we enumerate these **three** factors, their influence on dogs' location choices and the interaction of the factors.

1) The observed location of the objects disappearance. This factor must have a ubiquitous effect on dog's location choices since in all experimental groups dogs' summed correct choices were significantly above the chance level. However we found significantly lower performance in the two indirect groups than in the two direct groups suggesting that dogs' choices are influenced by additional factors in the indirect groups.

2) A logical candidate for the decreased performance in the indirect groups and the increased level of perseverative errors in the Reverse Indirect group is that the hider walks behind the locations where the object was hidden in the previous trials (baited spatial cues). By doing this the hider directs dogs' attention towards the previously baited locations more than it was done in the direct groups.

However this factor does not account for the difference of perseverative errors and location choice patterns between the two indirect groups. It also does not explain why in the Indirect group dogs' perseverative errors are not higher than in the Delayed Direct group. Since there is a difference between the two indirect groups, we need a fourth factor that influences dogs' choices to explain this difference.

3) As the **third** factor we identified the post-object-disappearance part of the hider's route (retroactive spatial cues). The retroactive spatial cues interact with the previously discussed baited spatial cues. In the Indirect group the two cue types act against each other (the hider walks behind the already baited locations, then hides the object and finally walks behind the not yet baited locations). In the Reverse indirect group however the two cue types direct dogs' attention to the same locations (the hider walks behind the not yet baited location, then hides the object and finally walks behind the already baited locations). This difference is sufficient to explain why dogs commit less perseverative errors in the Indirect group than in the Reverse Indirect group and it also explains why dogs' location choices are biased towards the lower numbered locations in the Reverse Indirect group whereas in the Indirect group this is not the case.

However in regard of the **third** factor there is an alternative, equally possible explanation for the result we found. It is possible to take the notion to its extreme that dogs' location choices are influenced strongest by spatial cues that happen closest in time to the dogs' release. In this case dogs would be only attracted by the location where from the hider returned and not by the other locations he walked behind. In consequence dogs would be in a conflict between this location and the location where they observed the object disappear.

Since this mechanism would lead to the same results as the one we proposed originally we cannot decide in the frame of this experiment between the two. However this difference does not affect the essential conclusion that dogs are influenced by the spatial cues of the hider after the object is hidden and that this influence is probably due to a mechanism similar (or equal to) retroactive interference.

Next we discuss how the baited and the retroactive spatial cues can be interpreted in the light of similar object search tasks done with dogs. The baited spatial cue when the hider walks behind previously baited locations is similar to the sham baiting behind location A in the B trials used in the experiment of Topál and colleagues (2009). Similarly to us, they found that in an ostensive communicative context when the object was hidden to location B, but a sham baiting was performed behind location A, dogs

581 tended to choose location A. The two main differences compared to our experiment are that prior to
582 the B trials the object was hidden four times to location A and that at the B trials a sham baiting was
583 performed by moving the object behind location A. In our experiment the object was not hidden more
584 than once to any of the locations and although in the indirect conditions the hider walked behind all
585 locations, he held the object high and visible in his hands until placing it behind the actual location.

586 A possible explanation of why the spatial cues at previously baited locations had a higher effect on dogs'
587 performance than those at previously non-baited locations is that the locations where they have already
588 found the object were more salient for the dogs. Meaning that dogs regarded only those hiding
589 locations as potential locations for the object where they previously found it.

590 Our finding that the retroactive spatial cues of the hider (the cues after hiding the object) have stronger
591 effect on dogs choices, than the proactive spatial cues, can be compared with the experiment of Watson
592 and colleagues (2001). In a task where dogs had no information about the exact location of the target
593 object, dogs tended to start searching at the location which was last passed by the experimenter whilst
594 hiding the object. We did not find unambiguous evidence that dogs had preference for the location from
595 where the hider returned. However the retroactive spatial cues can be interpreted as if these cues
596 would be only directed to the location where the hider returned **from**. The finding that dogs might be
597 subject to retroactive interference in our study is in accordance with other studies demonstrating that
598 dogs are subject to retroactive interference in spatial memory related tasks (Gagnon and Doré, 1993;
599 Macpherson and Roberts, 2010).

600 A potential explanation of this finding is that the hider continues to talk to the dog even after leaving the
601 object behind one of the locations. This might give the dog the impression that the important part of the
602 demonstration is still not over. Thus the dog's attention shifts from the actual location to the hider and
603 subsequently to the locations behind which the hider is walking, which in turn leads to the dog choosing
604 one of those locations with a higher probability.

One could argue that according to this interpretation the results of our study are due to dogs simply misunderstanding the aim of the task and does not tell much about dogs' use of spatial cues in ostensive contexts. According to this argument dogs would be insecure about the aim of the task because the hider keeps on talking to the dog after hiding the object and focuses dogs' attention on himself. However dogs' insecurity should be the highest in the first trial of the Indirect condition. During the phase of this trial when the hider is walking on his route and performing the hiding, dogs should have no prior knowledge whether this task will be about finding the object or, for example, about following the hider's route. In the two direct conditions and the Reverse Indirect condition the two rivaling interpretations of the task would lead to the same location choice. In the Indirect condition however dogs should be more confused and consequently show a much lower performance than in any of the other three groups. Our results contradict this interpretation showing that the performance of dogs in the first trials is not lower in the Indirect group than in the other three groups (**Table A.6**).

Thus we can conclude that the experimenter's continuous communication is not a 'design failure' but an important point of the procedure that makes it possible to demonstrate that the ostensive communicative context normally helps dogs learn from dog-directed communicative cues but may easily mislead them as well.

The novel aspect of our experiment was that dogs had direct visual information about the location of the target object as it was hidden in plain sight of the dog. Additionally the object was placed only once to each location, this way the chance that dogs form a strong association between a location and the target object was minimized. Finally during the entire hiding event the hider kept the dog's attention on himself by continuously talking to the dog.

Earlier research has shown that dogs' choices in an object search task are influenced by the position of the human performing the hiding (Fiset and LeBlanc, 2007; Watson et al. 2001). However in these experiments dogs had no information about the objects location or could only infer it by following the movement of a container. Our experiment demonstrated that dogs' choices are significantly influenced

630 by the position of the hider, even when they received direct visual information about the location of the
631 object.

632 In the experiment of Topál and colleagues (2009), they found that dogs tend to choose a location where
633 they have seen the object disappear in previous trials, even if they could see that it was placed to
634 another location at the current trial. The researchers concluded that the reason why dogs committed
635 these perseverative errors was the ostensive communicative context. However in our Direct group, dogs
636 showed no signs of perseverative errors despite the fact that the hiding was performed in an ostensive
637 communicative context. This is not surprising if we take into account that in the experiment of Topál and
638 colleagues (2009), the object was placed four times to location A before the B trials, and even during the
639 B trials the object was passed behind screen A, prior to being placed behind screen B.

640 This comparison suggests that the ostensive communicative context alone is not enough to induce
641 perseverative errors in a situation where neither the spatial cues of the hider, nor the placement of the
642 object is biased toward any of the locations (as in our Direct group). However in our two indirect groups,
643 dogs committed significantly more perseverative errors than in the Direct group, and the only added
644 elements were the spatial cues of the hider which, as we showed earlier, are clearly responsible for
645 these erroneous choices. This demonstrated that the ostensive communicative context was only
646 effective in our experiment in influencing dogs' choices when it was combined with the spatial cues of
647 the hider.

648 In an experiment where dogs had direct visual information about the location of the target object and
649 could witness the experimenter manipulate another hiding place, Erdőhegyi and colleagues (2007)
650 found that dogs still chose the correct location significantly above chance. At first glance this seems to
651 contradict our findings, suggesting that dogs are not influenced by the social or visual cues of a human
652 when they have direct visual information about the location of the object. However Erdőhegyi and
653 colleagues (2007) only compared the performance of the dogs to the level expected by chance. In our
654 experiment in the indirect groups dogs also performed above chance when analyzing the performance

off all five trials together. However when comparing the performance of the different conditions to each other, we found significant differences between the direct and the indirect conditions, showing that the spatial cues of the human does affect dogs' choices in our task.

Our study provided evidence that dogs are strongly influenced by the spatial cues of the hider in an object search task even when they have visual information about the location of the object's disappearance. The hider did not touch, point at, or sham bait any of the other locations, only walked behind them. Based on this, it is clear that dogs' performance in an object search task is extremely easily influenced by the presence of a human. Based on previous research it is probable that the ostensive communicative context greatly magnified this effect and that signals of ostensive communication specifically interacted with the spatial memory of the object in the dog.

It still remains an open question that besides the spatial cues of the hider, what other factors could have a significant effect on dogs' choices? One likely candidate **is** a common element of A-not-B tasks: hiding the object multiple times to the same location. The minimal amount of repetition to influence dogs' choices **was tested recently (Péter et al., 2015), where we found that in an ostensive context it is enough to hide the target twice at location A for eliciting perseverative error in the next 'B' trial in dogs.**

As a part of our study we also analyzed that which part of the hider's route and which spatial cues (baited and retroactive spatial cues) had the greatest effect on dogs' choice patterns. We took in account the interplay of these and other factors to explain the observed choice patterns. Perhaps in a future analysis, it would be more fruitful to construct models of the hypothetical factors and their interactions and compare the prediction of these models with the actual results to be able to assess in amore exact manner the factors and their interactions affecting dogs' choices. Such a model would also enable us to analyze not only the first, but the later choices of dogs in this task. This could lead to a more detailed understanding of the processes that guide dogs' choices on the individual level.

5. Acknowledgements

The authors are thankful to two anonymous reviewers for their valuable comments on the earlier version of this manuscript. This study was supported by grants from the Hungarian NSF No. T047235 and by grants from the European Union FP7-ICT-2007 LIREC 215554; ETOCOM project (TÁMOP-4.2.2-08/1/KMR-2008-0007), also through the Hungarian National Development Agency in the framework of the Social Renewal Operative Programme supported by the EU and co-financed by the European Social Fund.

6. Appendix

Table A.1 According to Hypothesis 1 ('object location dominance'), the differences in dogs' location choices, correct choices and erroneous choices between the Direct, Delayed Direct and the two indirect groups.

	Location choices	Correct choices	Erroneous choices
Direct group	Not affected	Not affected	Not affected
Delayed Direct Group	Not affected	Weaker performance than in the other groups	More than in the other three groups
Indirect and Reverse Indirect groups	Not affected	Same as in Direct	Same as in Direct

Table A.2 According to Hypothesis 2 ('spatial cues as general distractors'), the differences in dogs' location choices, correct choices and erroneous choices between the Direct and the two indirect groups.

	Location choices	Correct choices	Erroneous choices
Direct group	Not affected	Not affected	Not affected

Indirect Group	Not affected	Weaker performance than in Direct	More than in Direct
Reverse Indirect group	Not affected	Weaker performance than in Direct	More than in Direct

Table A.3 According to Hypothesis 3A, the differences in dogs' location choices, correct choices and erroneous choices between the two indirect groups, depending on the relative influence of the proactive and the retroactive spatial cues on dogs' choices.

Relative Strength	Location choices	Correct choices	Erroneous choices
Proactive > Retroactive	lower-numbered locations chosen more often in Indirect	better performance at the initial trials in Indirect	more perseverative in Indirect
Proactive < Retroactive	lower-numbered locations chosen more often in Reverse Indirect	better performance at the initial trials in Reverse Indirect	more perseverative in Reverse Indirect
Proactive = Retroactive	similar	similar	similar

Table A.4 According to Hypothesis 3B ('the last spatial cue as attractor'), the differences in dogs' location choices, correct choices and erroneous choices between the Direct and the two indirect groups.

	Location choices	Correct choices	Erroneous choices
Direct group	Not affected	Not affected	Not affected
Indirect Group	5th location is chosen over the chance level	Weaker performance than in Direct	More than in Direct
Reverse Indirect group	1st location is chosen over chance level	Weaker performance than in Direct	More than in Direct

Table A.5 According to Hypothesis 4, the distribution of dogs' location choices, correct choices and erroneous choices in the two indirect groups, depending on the relative influence of the baited and the non-baited spatial cues on dogs' choices.

Relative strength	Location choices	Correct choices	Erroneous choices
Baited > Non-baited	lower-numbered locations chosen more often	better performance at the initial trials	more perseverative
Baited < Non-baited	higher-numbered locations chosen more often	better performance at the final trials	more non-perseverative
Baited = Non-baited	uniform	uniform	uniform

Table A.6 Ratios of correct choices as a proportion of sample size.

	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5
Direct	0.81	0.76	0.81	0.76	0.81
Delayed Direct	0.86	0.43	0.57	0.71	0.67
Indirect	0.86	0.62	0.38	0.29	0.52
Reverse Indirect	0.71	0.43	0.10	0.29	0.33

Table A.7 Ratios of first choices towards the five hiding locations, all trials.

	Location 1	Location 2	Location 3	Location 4	Location 5
Direct	0.20	0.21	0.22	0.21	0.16
Delayed Direct	0.30	0.15	0.19	0.21	0.15
Indirect	0.30	0.22	0.17	0.13	0.18
Reverse Indirect	0.34	0.37	0.08	0.14	0.07

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Figure captions

Figure 1 An actual photograph of the test. In the foreground the two crouching persons are the owner of the dog and Experimenter/ Hider. The dog has just passed Location 3 in the middle. At each location there is a plastic panel, painted to different black-and-white patterns. The Experimenter hid the target behind one of these panels in each trial.

Figure 2 The hider's route (grey arrows) while hiding the object depicted at the second trial in each experimental group. Uninterrupted lines represent the part of the route where the experimenter has the target object, broken lines show the portion where the experimenter's hands are empty. In the example shown here the object was hidden first to the left-most hiding location. The order of the hiding events (and trials) is denoted by numbers 1 to 5 (SP: starting position; *: act of hiding the object).

Figure 3 Ratios of correct choices at each trial and experimental group. Binomial test comparing the number of correct choices to the ratio expected by chance (0.2) (stars mark trials passing the Benjamini & Hochberg FDR control; black lines mark the ratio of correct choices expected by chance).

Figure 4 Ratios of first choices of hiding locations in all trials at the Reverse Indirect group. Binomial tests comparing the number of first choices of hiding locations to the ratio predicted by chance (0.2) (N=21; stars mark trials passing the Benjamini & Hochberg FDR control; black line marks the ratio of first choices expected by chance).

Figure 5 Total number of errors made towards hiding locations where the object was hidden in a previous trial (Perseverative errors) and errors made towards locations where the object was not hidden yet (Non-perseverative errors) in the four experimental groups (lowercase letters mark the differences found between groups with the Monte Carlo test comparing the non-perseverative errors, uppercase letters mark the differences found comparing perseverative errors; groups with different letters differ significantly from each other, groups with the same letter do not differ).

Figure1

Figure2

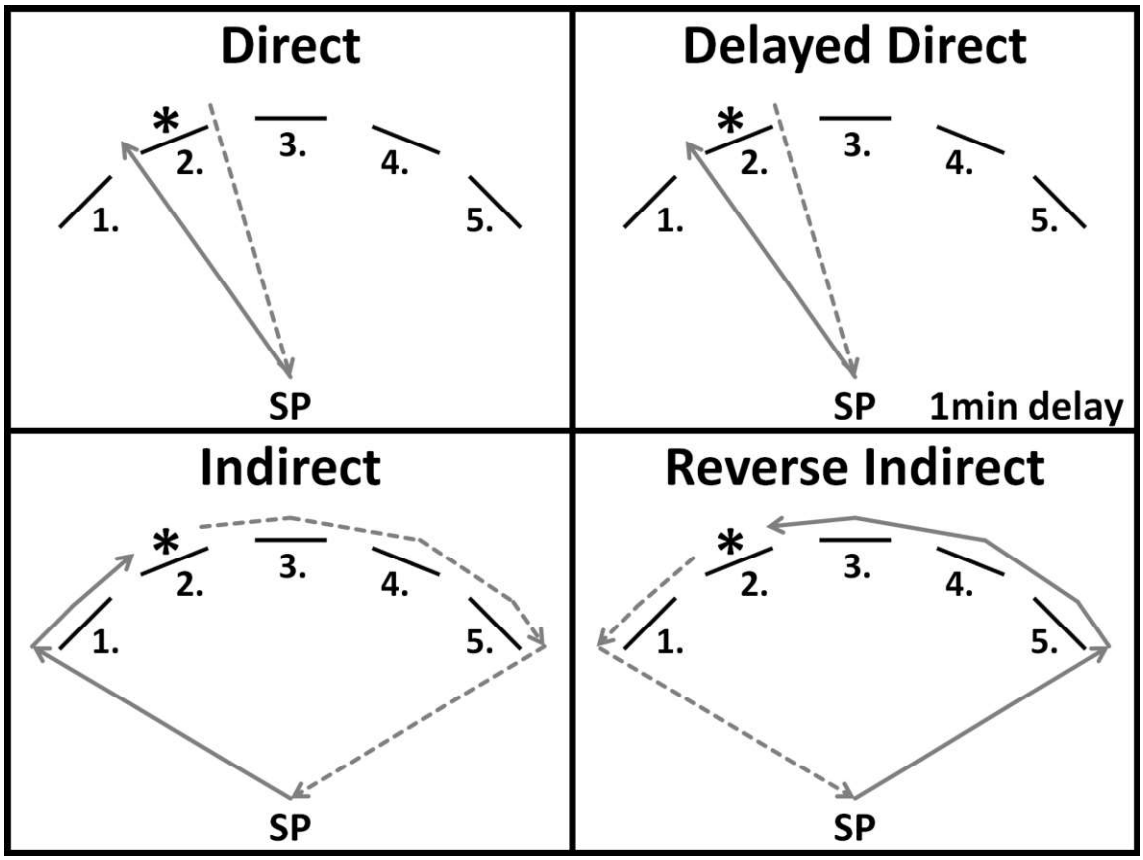

Direct
*
2.
3.
4.
1.
5.
SP
Delayed Direct
*
2.
3.
4.
1.
5.
SP
1min delay
Indirect
*
2.
3.
4.
1.
5.
SP
Reverse Indirect
*
2.
3.
4.
1.
5.
SP

Figure3

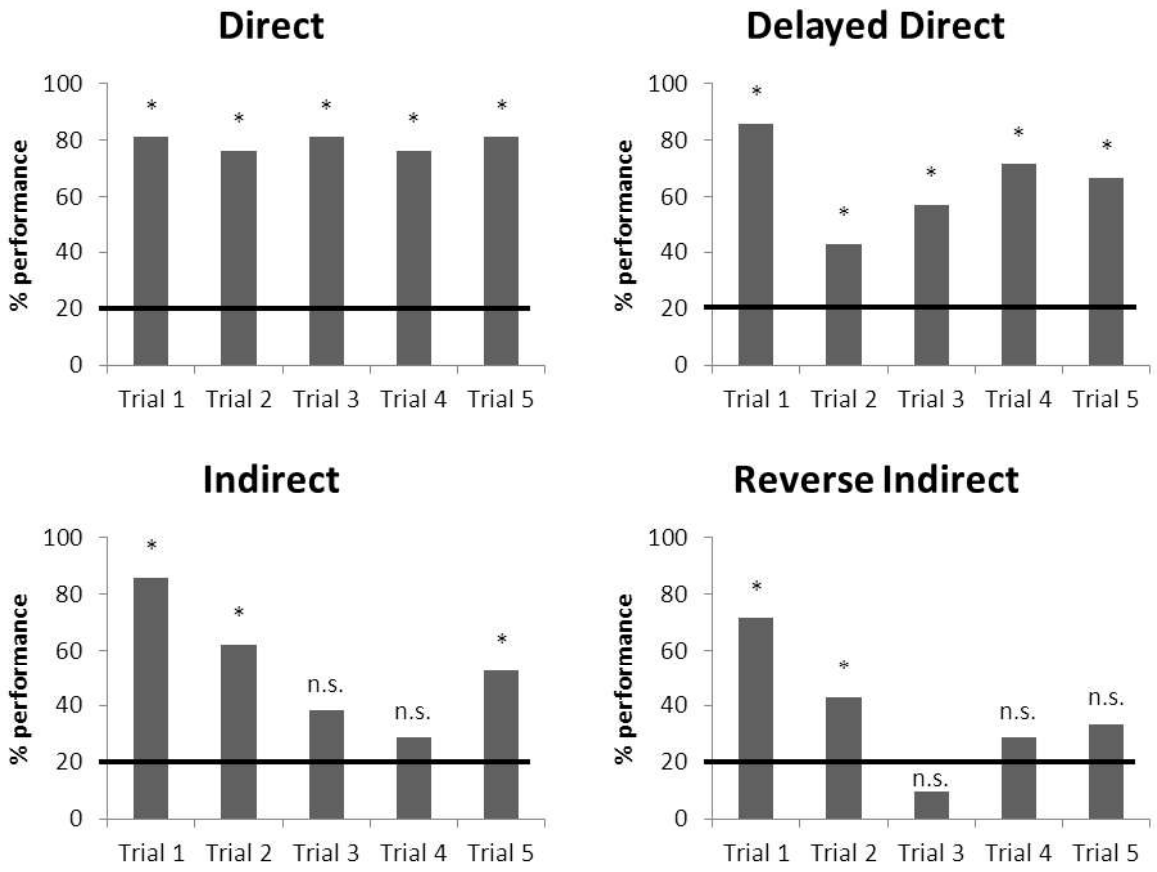

Direct
Delayed Direct
Indirect
Reverse Indirect
% performance
100
80
60
40
20
0
Trial 1
Trial 2
Trial 3
Trial 4
Trial 5
*
n.s.

Figure4

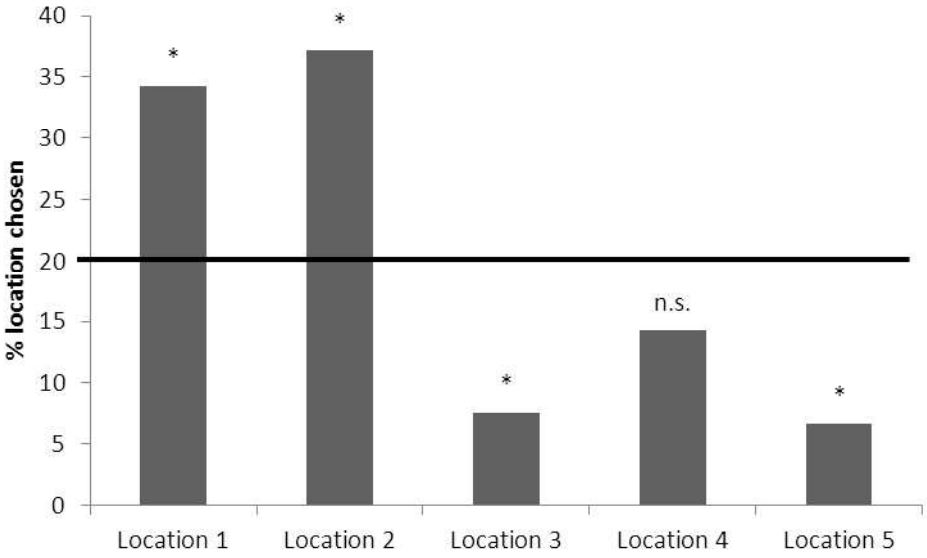
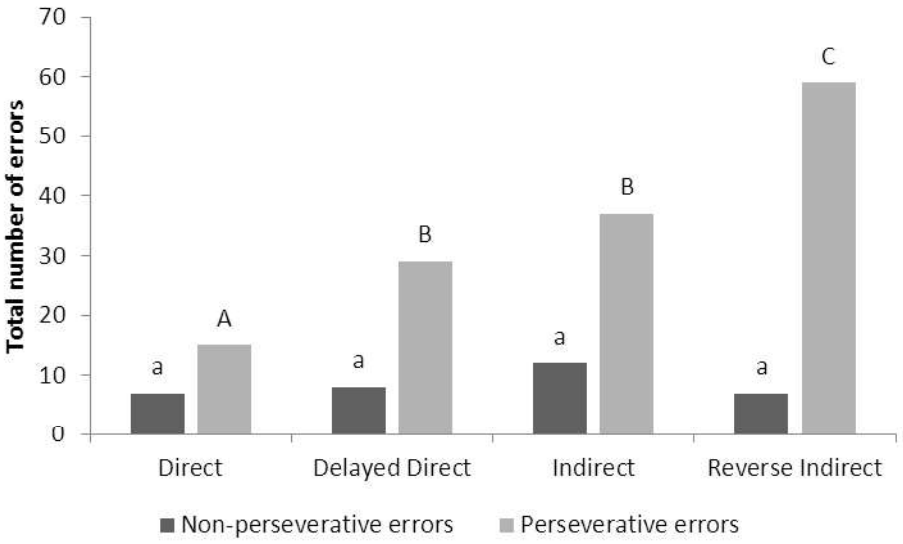

% location chosen
40
35
30
25
20
15
10
5
0
*
*
*
n.s.
*
Location 1
Location 2
Location 3
Location 4
Location 5

Figure5


Total number of errors
70
60
50
40
30
20
10
0
a
A
a
B
a
B
a
C
Direct
Delayed Direct
Indirect
Reverse Indirect
Non-perseverative errors
Perseverative errors