Anim Cogn
DOI 10.1007/s10071-013-0656-5

ORIGINAL PAPER

Deferred imitation and declarative memory in domestic dogs

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Received: 11 April 2013 / Revised: 12 June 2013 / Accepted: 13 June 2013

Abstract This study demonstrates for the first time deferred imitation of novel actions in dogs (*Canis familiaris*) with retention intervals of 1.5 min and memory of familiar actions with intervals ranging from 0.40 to 10 min. Eight dogs were trained using the 'Do as I do' method to match their own behaviour to actions displayed by a human demonstrator. They were then trained to wait for a short interval to elapse before they were allowed to show the previously demonstrated action. The dogs were then tested for memory of the demonstrated behaviour in various conditions, also with the so-called two-action procedure and in a control condition without demonstration. Dogs were typically able to reproduce familiar actions after intervals as long as 10 min, even if distracted by different activities during the retention interval and were able to match their behaviour to the demonstration of a novel action after a delay of 1 min. In the two-action procedure, dogs were typically able to imitate the novel demonstrated behaviour after retention intervals of 1.5 min. The ability to encode and recall an action after a delay implies that facilitative processes cannot exhaustively explain the observed behavioural similarity and that dogs' imitative abilities are rather based on an enduring mental representation of the demonstration. Furthermore, the ability to imitate a novel action after a delay without previous practice suggests presence of declarative memory in dogs.

Keywords Deferred imitation · Dog · Declarative memory · Social learning

Introduction

Deferred imitation is the ability to encode, retain and retrieve a memory of an action and then to use it as the basis to reproduce the demonstrated action after a delay (Klein and Meltzoff 1999). Since Piagetian theories (Piaget 1952), deferred imitation has been considered a hallmark of mental representation as it indicates the emergence of the infant's ability to form a mental representation of the model's behaviour at the time of demonstration and recall of that image after a retention interval (Barr et al. 1996).

From a cognitive perspective, evidence for deferred imitation excludes alternative explanations of behavioural similarity between demonstrator and observer where the demonstration triggers a similar behaviour in the observer at the same time or shortly after it, such as contagion and response facilitation (Bandura 1969). Researchers generally agree that 1 min is a sufficiently long delay to exclude the kind of reflexive response thought to be responsible for immediate imitation (e.g., Zentall 2006). Accordingly, imitative behaviour after such a delay is considered as deferred imitation.

While imitation is usually studied between individuals of the same species, there is strong evidence that dogs can learn socially both from con- and heterospecific demonstrators. Dogs represent a particularly interesting species for the study of hetero-specific social learning abilities (Kubinyi et al. 2009) as they have undergone selection for

Electronic supplementary material The online version of this article (doi:10.1007/s10071-013-0656-5) contains supplementary material, which is available to authorized users.

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Published online: 16 July 2013

living in human groups through domestication, and these changes helped to form a species with surprisingly complex social skills (Reid 2009; Miklósi et al. 2007; Hare and Tomasello 2005, Miklósi and Topál 2013). Dogs are particularly keen on relying on human communicative cues (Hare et al. 2002; Miklósi et al. 2003; Miklósi and Soproni 2006), are able to learn by observing humans in detour tests and manipulative tasks (Pongracz et al. 2001, 2003, 2012; Kubinyi et al. 2003) and are easily influenced by humans in observational learning situations (Kupan et al. 2010). The selection for living in human social groups might therefore have favoured their general ability to learn from humans.

Two independent studies (Topál et al. 2006; Huber et al. 2009), using the 'Do as I do' procedure (Hayes and Hayes 1952), showed that dogs are able to match functionally their behaviour to an action demonstrated by a human experimenter. In one of these studies, the authors (Huber et al. 2009) found that the dog's matching degree decreased with the increased delay interposed before the 'Do it!' command: She could perform correctly with delays shorter than 5 s and only once she could match a familiar action after 35 s. Thus, dogs may lack the ability of (true) deferred imitation, but this negative result could be explained by problems with the procedure used. It is likely that through the 'Do as I do' procedure as applied by Topál et al. (2006) and Huber et al. (2009), the dog learns that it should copy the action that has been demonstrated immediately before the 'Do it!' command. Thus, dogs trained this way would not have learned that they were required to copy the action that was demonstrated before an interval.

The aim of the present study is to assess if dogs possess the cognitive ability of deferred imitation. For this purpose, dogs were first trained by their owners with the 'Do as I do' method, and then, before testing, they were trained to wait for short intervals (from 5 to 30 s) before they were allowed to display a copy of the observed action. By using this procedure, we taught our subjects that the 'Do it!' command referred to what had been demonstrated before an interval. In the following testing phase, the dogs participated in a series of tests looking at (1) generalisation ability, (2) deferred imitation and (3) emulative learning.

First, we investigated the dogs' ability to reproduce human-demonstrated actions after delays ranging from 0.40 to 10 min that also included distractions during the retention interval. The use of distractions engages dogs in a different activity, thus preventing them from keeping their mind active on the demonstration, so that the ability to encode and recall the demonstrated action after an interval can be tested.

In studies on children, their deferred imitation after long retention intervals is affected by changes in context between demonstration and retrieval, and it is supposed that context might serve as a retrieval cue that helps recalling the demonstration (e.g., Barnat et al. 1996). Thus, in the second part of the testing, dogs were given the 'Do it!' command in a different location from that of the demonstration.

Two-action or multi-action experiments (Dawson and Foss 1965) have become recognised methods (e.g., Akins and Zentall 1996; van de Waal et al. 2012) to test imitative abilities because they control for other non-imitative processes that may increase the probability of a similar response by the observer, such as local enhancement (Thorpe 1963) and stimulus enhancement (Galef 1988). In the case of emulation, the observer learns about the outcome of the demonstrator's action, but not about the action itself (Wood 1989; Tomasello 1990). Importantly, Horner and Whiten (2005) found that chimpanzee's tendency to use emulation or imitation to solve a tool-using task depended on the availability of causal information during demonstration, and they seem to be able to flexibly use the process that is more efficient, given the environmental constrains of the situation.

Accordingly, we included two tests that control for emulation learning using the two-action procedure because earlier studies on imitation in dogs (Topál et al. 2006; Huber et al. 2009) did not explicitly test for such alternative explanations. We designed our two two-action tests to be different in the kind of information shown to the dogs: In the first two-action test, the two actions did not lead to different outcomes, while in the second two-action test, two different outcomes were achieved by the demonstrators. If dogs were only able to engage in deferred emulation but not in deferred imitation, we would expect them to perform correctly only when two different outcomes were presented, but not to succeed when different actions without different outcomes were shown.

Finally, a test to control for Clever Hans effect and a control test in absence of demonstration were carried out.

Materials and methods

Subjects

The subjects in our study consisted of 8 adult pet dogs ranging from 2 to 10 years old and their owners who volunteered to participate in this experiment. The dogs were females of various breeds (4 Border Collies, 1 Shetland Sheepdog, 1 Yorkshire Terrier, 1 Czechoslovakian Wolfdog and 1 mixed breed).

Before the study began, all the subjects had previously been trained by their owners with the 'Do as I do' method to match their behaviour to demonstrated actions (based on Topál et al. 2006, see below).

Training phase

Preliminary 'Do as I do' training (based on Topál et al. 2006):

The training protocol had been previously explained to all the owners by the experimenter (C.F.) before the study began and consisted of two phases:

> Phase 1. The dogs learned to match their behaviour to 3 demonstrated familiar (i.e., already trained) actions using the 'Do it!' command through operant conditioning techniques. Each owner could decide what actions to use for the training. Once the dogs reached approximately 80 % of correct performance in at least two sessions in a row, they began the second training phase. Phase 2. The dogs learned to match their behaviour to 6 demonstrated familiar actions using the 'Do it!' command (in the training sessions 3, other familiar actions were added to the 3 used in phase 1). Both in phase 1 and 2 owners could decide what actions to use for the training, the only requisite being that they had to be already trained actions. The owners typically used both object-related actions and body movements.

The owners were allowed to train the dogs at home and were instructed to reward the dog using food or access to favourite toys only if their behaviour after the 'Do it!' command corresponded to the action that had been demonstrated. The definition of correspondence was based on Topál et al. (2006): The action that the dog performed immediately after the 'Do it!' command was considered as functionally matching the demonstration if it entailed the same goal and, given the species-specific differences in the behaviour repertoire of the two species, was executed in a similar way.

The owners were instructed to train their dogs two to three times per week in a single training session lasting no more than 5 min. A single training session typically included six to ten trials, but owners were not given restrictions about the number of trials.

The training of the dogs lasted on average approximately 1 month, but the duration varied from 2 to 7 weeks according to the time devoted by owners to the training.

Once the dogs reached 80 % of correct performance with the 6 familiar actions, owners were allowed to train their dogs to perform novel actions using this training technique.

Preliminary training for deferred imitation

Before the testing began, all subjects went through a training phase aimed at teaching dogs that the 'Do it!' command now referred to the action that had been demonstrated after the 'Stay' command, even if: (1) An interval elapsed between the demonstration and the 'Do it!' command and (2) the demonstrator performed other actions during the interval (i.e., walked in another direction). The procedure was as follows:

Owners made their dog stay in place while facing them and made them pay attention using cues known by the dog. Next, the owners demonstrated a familiar object-related action. Then, they returned to the starting position in front of their dog and waited for 5 s while looking straight ahead, before giving the 'Do it!' command. Dogs were rewarded using food or access to favourite toys only if their behaviour after the 'Do it!' command corresponded to the action that had been demonstrated. In case of failure, the procedure was repeated.

When the dogs were successful with this short delay in at least two trials in a row, owners increased the delay up to 10 s, repeating the same procedure. When dogs were successful with this delay in at least two trials in a row, owners were instructed to perform the demonstration and then walk with their dogs during increasingly longer delays, before returning to the starting position and giving the 'Do it!' command. The delay was gradually increased to approximately 30 s to allow owners to walk with their dog behind a curtain positioned at 14 m from the objects, before returning to the starting position and giving the 'Do it!' command (Fig. 1).

Owners trained the dogs in two different dog schools. They admitted the dog to the following testing procedure once they or the trainer who controlled the training procedure reported that the dogs could functionally match their behaviour to the demonstration of familiar actions in two trials in a row with a delay of 30 s.

Testing phase

The testing took place at the same two dog schools where the dogs were trained, in outdoor fenced areas. Before the testing, owners completed a list of all the actions that were already familiar to their dogs (i.e., the dogs were already trained to perform those actions either with traditional training methods or with the Do as I do method). For each subject, we randomly picked five object-related actions from this list to use in those testing conditions where familiar actions were demonstrated. Thus, in the Familiar action conditions, dogs were randomly shown actions that either were part of their training repertoire but had never been used in the Do as I do framework or were used for the Do as I do training.

In each test and for each dog, three object-related actions were randomly chosen out of those five for the Familiar action condition, Distracting condition and Changed context condition, and three completely novel object-related actions were presented in the Novel action

Fig. 1 Experimental setting: The dog is facing the owner in the starting position 4.5 m away from the objects; three objects on which actions can be demonstrated are placed in predetermined randomised positions at a distance of 3.5 m from each other; the curtain used to obstruct the view of the objects during the retention interval is behind the owner at a distance of 14 m from the objects

condition and in the Two-action tests (Table 1). The relative position of the objects on which the demonstration was performed (centre, right, left) was also randomised, their distance being 3.5 m from each other. The curtain used to prevent dogs from looking at the target object during the retention interval was placed at a distance of 14 m from the objects (Fig. 1).

The owners taking part in the tests helped to prepare the setting (i.e., they carried all the objects to the predetermined position). This was done to exclude that dogs could rely on olfactory cues for their performances, as all the objects were previously manipulated by the owners.

At the beginning of each trial, the owner made the dog stay at the same place (using verbal commands and hand gestures known by the dog) and demonstrated a randomly chosen object-related action. After the demonstration, dog and owner walked behind the curtain in order to prevent the dog from looking at the target object. When the predetermined retention interval elapsed, the experimenter told the owner to go back to the starting position and, having reached this position, the owner gave the 'Do it!' command to the dog while looking straight ahead. For the analysis, the length of the delay in each condition was calculated from the demonstration to the 'Do it!' command and could slightly vary (±30 s) according to the walking speed of each owner and dog when they went back from behind the curtain to the starting position.

Dogs were tested in different periods, according to their owners' availability for the testing. For each subject, an interval of at least 30 min passed between two consecutive tests, and the maximum number of tests per day was 4. The maximum interval between two consecutive tests for one dog was 53 days.

Each dog went through the same testing protocol (Table 2) consisting of 19 tests in eight different conditions (one trial per delay) in the following detailed order:

Familiar action Eight tests on familiar actions with different retention intervals (durations of retention intervals: 0.40 min; 1 min; 1.5 min; 2 min; 3 min; 4 min; 6 min; 10 min).

Novel action Three novel objects were placed in randomised positions, and the dogs were tested on a novel action (enter a wooden box) with a retention interval of 1 min.

Distracting action In five tests, the dogs observed the demonstration of a familiar action and were then distracted during the retention interval, before the 'Do it!' command was given (in 3 tests, owners distracted them by giving a different command 'lay down', with retention intervals of 0.50; 3; 4 min; and in two tests, owners distracted the dogs by throwing a ball and encouraging them to fetch it, with retention intervals of 1 min and 4 min).

Changed context Owners demonstrated a familiar action at one location, then walked with their dog to another location where 3 identical objects were placed in similar respective positions and gave the 'Do it!' command (retention interval: 1 min).

'Clever Hans' control A single test with the same procedure as the Familiar action condition, except that after the demonstration by the owner, he and the dog walked behind the curtain, where a familiar person who was not aware of what action was demonstrated was hiding. After a retention interval of 1.15 min, this naive person went with the dog to the predetermined starting position and gave the 'Do it!' command in the absence of the owner who stayed behind the curtain.

No demonstration control Two novel objects (a tube placed in vertical position and an umbrella stand) and the wooden box (already used in the Novel action condition) were placed at randomised positions. The owner commanded the dog to stay in the usual starting position and to pay attention as was done in the other tests. The owner remained still for 5 s and then gave the 'Do it!' command

Table 1 Behaviours used for the testing, description of the human demonstration and description of the expected dog's behaviour

Name of the behaviour	Description of the owner's demonstration	Description of the expected dog's behaviour
Familiar actions		
Walk around bucket	The owner walks around a bucket placed on the ground	The dog walks around a bucket placed on the ground
Muzzle in bucket	The owner puts his face in a bucket placed on the ground	The dog puts her muzzle in a bucket placed on the ground
Put muzzle in colander	The owner puts his face in a colander placed on the ground	The dog puts her muzzle in a colander placed on the ground
Climb on chair	The owner climbs with his feet on a chair	The dog climbs with all fours on a chair
Touch chair	The owner touches the seat of a chair with his hands	The dog touches the seat of the chair with her front paw
Walk around cone	The owner walks around a cone placed on the ground	The dog walks around a cone placed on the ground
Touch cone	The owner touches with his hand a plastic cone that is placed on the ground	The dog touches with her front paw a plastic cone that is placed on the ground
Pull rolling toy	The owner pulls a string attached to a children's toy with wheels using his hand and makes it move on the ground	The dog takes in her mouth a string attached to a children's toy with wheels and pulls it making it move on the ground
Ring bell	The owner rings a bell that is hanging from a bar	The dog rings a bell that is hanging from a bar
On table	The owner climbs on an agility table	The dog jumps on an agility table
Hoop	The owner puts his feet and hands in a hoop placed on the ground	The dog puts her four paws in a hoop placed on the ground
Open box	The owner removes the lid of a box using his hand	The dog removes the lid of a box using her mouth
Touch stool	The owner touches a small stool with his hand	The dog touches a small tool with her front paw
Drop bottle	The owner touches a bottle that is placed on the ground using his hand and makes it fall	The dog touches a bottle that is placed on the ground using her front paw and makes it fall
Take object	The owner takes with his hand one of two objects that are placed on a chair	The dog takes the other object that is placed on the chair with her mouth
Jump in high packaging box	The owner steps inside a cartoon packaging box raising his legs to enter in it	The dog jumps inside the packaging box
Roll ball	The owner touches a ball and makes it roll	The dog touches a ball and makes roll
Swing hanging object	The owner touches with his hand a toy that is hanging from a hurdle	The dog touches with his front paw a toy that is hanging from a hurdle
Touch target	The owner touches with his hand a small pad on the ground	The dog touches with her front paw a small pad on the ground
Jump over hurdle	The owner jumps over a hurdle	The dog jumps over a hurdle
Novel actions		
Enter wooden box	The owners put his feet and hands in a wooden box	The dog enters in a wooden box with her all fours
Look inside wooden box	The owner looks inside a wooden box	The dog looks inside a wooden box
Touch wooden box	The owner touches a wooden box with hand	The dog touches a wooden box with her front paw
Knock over tube	The owner knocks over a cartoon tube placed vertically on the ground using hand	The dog knocks over a cartoon tube placed vertically on the ground using her front paw
Walk around tube	The owner walks around a cartoon tube placed vertically on the ground, moving from left to right	The dog walks around a cartoon tube placed vertically on the ground, moving from left to right

to the dog. After the command, the owner was instructed to keep looking straight ahead for the duration of the test. The behaviour of the dog was video recorded for 30 s after the 'Do it!' command.

Two-action on box The setting was the same as in the No demonstration control test. Three dogs were shown an action on the box, and the other 5 dogs were shown a different action on the box. The demonstrations were 'Look

Table 2 Subjects (dog's name and breed) and actions chosen for each subject in the different testing conditions

Dog's name—breed	Randomly chosen familiar action
Familiar action condition	
Emma—Shetland Sheepdog	Roll ball, muzzle in colander, touch stool, muzzle in colander, muzzle in colander, touch stool, on table, muzzle in colander
Phoebe—Border Collie	On table, ring bell, muzzle in bucket, touch stool, touch stool, muzzle in bucket, touch stool*, touch stool
Bambù—Border Collie	Climb on chair, muzzle in bucket, walk around cone*, climb on chair, jump over hurdle, on table, climb on chair, on table
Lilly—Yorkshire Terrier	Pull rolling toy, open box, swing hanging object, jump in high packaging box, open box*, drop bottle, pull rolling toy, drop bottle
Adila—Mixed breed	On table*, ring bell, touch cone, on table, ring bell, touch chair, touch cone, walk around bucket
Minnie—Border Collie	Muzzle in bucket, touch stool, muzzle in bucket, on table, on table*, ring bell, on table, touch stool
Soley—Border Collie	Touch chair, jump over hurdle, on table, muzzle in bucket, on table, touch chair*, jump over hurdle*, touch chair
India—Czechoslovakian Wolfdog	Jump over hurdle, touch chair, drop bottle, drop bottle, touch chair, jump over hurdle, touch chair, on table

Dog's name	Novel action
Novel action condition	
Emma, Phoebe, Bambù, Lilly, Adila*, Minnie, Soley, India	Enter wooden box

Dog's name	Randomly chosen familiar action
Distracting action condition (distraction: lay down command)	
Emma	Hoop, roll ball*, hoop
Phoebe	Take object, ring bell, take object
Bambù	Climb on chair, muzzle in bucket, climb on chair
Lilly	Swing hanging object, drop bottle, pull rolling toy
Adila	Touch chair, walk around bucket, on table
Minnie	Take object, muzzle in bucket, touch stool
Soley	Jump over hurdle, touch chair, on table*
India	Drop bottle, on table, touch chair
Distracting action condition (distraction: play with ball)	
Emma	Muzzle in colander, hoop
Phoebe	On table, take object
Bambù	Jump over hurdle, muzzle in bucket
Lilly	Jump in high packaging box, open box
Adila	Ring bell, touch cone
Minnie	On table, ring bell
Soley	Touch chair*, walk around cone
India	Jump over hurdle, touch chair*
Changed context condition	
Emma	Touch target
Phoebe	Muzzle in bucket
Bambù	Muzzle in bucket
Lilly	Drop bottle
Adila	Touch cone
Minnie	Take object
Soley*	Walk around cone
India	Ring bell
Clever Hans control condition	
Emma	Roll ball
Phoebe	On table
Bambù	Muzzle in bucket
Lilly	Jump in high packaging box
Adila	On table
Minnie	Take object
Soley	Jump over hurdle
India	On table

Dog's name	Novel action
Two-action on box condition	
Emma, Phoebe, Bambù, Minnie, Soley	Touch box
Lilly, Adila, India	Look inside box
Two-action on tube condition	
Emma, Phoebe, Minnie, India	Walk around tube
Soley*, Lilly, Adila, Bambù	Knock over tube

Wrong performances of the dogs are marked by *. Actions and conditions are listed in the actual order of testing

inside the box' and 'Touch the box with hand', respectively. The two actions lead to the same outcome (i.e., the box did not move). The dogs that were already familiar with the action of 'Muzzle in the bucket' were shown 'Touch the box with hand' because we suspected that 'Look inside the box' would have been similar to the already familiar action. The retention interval was 1.30 min.

Two-action on tube The setting was the same as in the No demonstration control condition. Half of the dogs were shown an action on the tube, and the other half of the dogs were shown a different action on the tube. The actions were 'Walk around the tube from the left side to the right' and 'Knock over the tube' (retention interval: 1.30 min). In this case, the two demonstrations lead to different outcomes (the tube stayed in its vertical position when the experimenter walked around or the tube fell to a horizontal position when it was knocked over and was then repositioned by the experimenter while the dog and the owner were behind the curtain). For this test, the assignment of the subjects to the groups was randomised.

The testing sessions were recorded by two video cameras placed in two different positions in order to always have a view of the dog and the owner.

Data collection and analysis

The actions of the dogs after the 'Do it!' command were coded by the experimenter as 'match' (the dog performs an action that is functionally similar to the demonstrated task) or 'no match' (the dog performs any other action). In the conditions where novel actions were demonstrated (Novel action, Two-action on box and Two-action on tube), the behaviour of the dog was scored as matching only if there was a correspondence in both the goal (if a goal was present) and the body movement, taken into account the differences in the body schema of dogs and humans (i.e., a human's hand touch was considered corresponding to a dog's front paw touch). In the conditions where familiar actions were demonstrated, a mere functional correspondence was used as criterion because the expected response of the dog was already known since these were trained actions.

In addition to the main coder (C.F.), an independent observer coded 30 % of the videos in order to assess inter-observer reliability. The calculation of the kappa coefficient yielded $K = 1$.

The results were analysed using GraphPad software by comparing performances between the different conditions and the No demonstration control test using Fisher's exact test with α level at 0.05. However, since each testing condition was planned to answer a specific theoretical question, the above value was corrected by the method suggested by Bonferroni taking into account the number of 'Do as I do' tests performed within a specific condition.

Results

In the No demonstration control condition, no dog performed any action on the objects present in the testing area, all dogs but one did not perform any action at all for at least 5 s after the 'Do it!' command, which is matching with the demonstration (the owner did not perform any action for 5 s). One dog remained in a sitting position for the duration of the video recording (30 s) but slightly raised a paw 2 s after the 'Do it!' command was given. Three dogs did not move for the whole duration of the test, one dog did not move for 20 s and then stood up, one dog remained in place but barked, one dog moved a little backward while remaining in a sitting position, and one dog remained in a sitting position for 5 s and then ran away to play and then sniffed the ground.

We compared performances between the different conditions and the No demonstration control using Fisher's exact test. In the Familiar action condition, the subjects were tested with eight different retention intervals, and the Bonferroni-corrected α level is 0.00625. Comparing the number of correct performances of the demonstrated action after the different delays with the No demonstration condition, we found a statistically significant difference for the tests with delays of 0.40, 1, 1.5, 2, 4 and 10 min (Fisher's exact test, respectively: $P = 0.0014$, $P = 0.0002$, $P = 0.0014$, $P = 0.0002$, $P = 0.0014$ and $P = 0.0002$, respectively), while for the tests with 3 and 6 min delays, the difference was not significant after the Bonferroni correction ($P = 0.007$).

Subjects were tested two times on their memory of novel actions on the box (i.e., all dogs were tested on 'Enter the box', and then, some of them were tested on 'Touch the box with hand/front paw' and some of them on 'Look inside the box' in the subsequent Two-action test on box in which all dogs performed the demonstrated action). In this case, the Bonferroni-corrected α level is 0.025, and there is a significant difference between all the performances and the No demonstration condition ('Enter the box': $P = 0.0014$; 'Touch the box with paw' and 'Look inside the box': $P = 0.0002$). The dogs' performance was also significantly different from the No demonstration condition in the Two-action test on tube ($P = 0.0014$) in which only one dog performed a different action (entered the box) before performing the action that had been demonstrated ('Knock over the tube') and was scored as 'no match'.

In the Distracting action condition, dogs were tested with two different distractions in overall five tests with different delays, and the Bonferroni-corrected α level is 0.01. All the performances showed a significant difference from the No demonstration condition (Distraction: 'Lay down' with 1 min delay: $P = 0.0002$; with 3 and 4 min delay: $P = 0.0014$; Distraction: 'Play with ball' with 1 min delay: $P = 0.0002$ and with 4 min delay: $P = 0.007$, respectively).

In the Changed context and Clever Hans conditions, the dogs were only tested with one delay, so we did not use the Bonferroni correction for the statistical analysis. We found a significant difference between the dogs' performance and the No demonstration condition (Changed context: $P = 0.0014$ and Clever Hans: $P = 0.0002$).

Fisher's exact test was used to compare each different condition to the Familiar action condition to assess whether the matching performance changes with the increased delays, with the introduction of distractions, when changing the context of retrieval or when demonstrating novel actions. First, in order to assess whether the increased delay affects the performance, we compared with each other the results obtained after different delay durations in the Familiar action condition (e.g., comparing the performance of dogs with 1-min delay with their performance with 10 min delay) and no comparison reached the level of significance ($P = 0.4667$ for the comparison of the performance after delays of 3 and 6 min compared to the

performance after delays of 1, 2 and 10 min and $P = 1.000$ for the comparisons with all the other delay durations) (Fig. 2a). Second, we compared the performance of the dogs in the Familiar action condition with their performance in the Distracting condition with, respectively, similar delays, and no comparison reached the level of significance ($P = 1.000$ for all the comparisons). Then we also compared the performance in the Familiar action condition after 1 min delay with that in the Novel action condition and Changed context condition, in which the 'Do it!' command was also given after 1 min delay and not even in this case we found significant differences ($P = 1.000$ for both comparisons). The matching performance of the dogs did not even change when they were tested for emulation and imitation in the two Two-action tests, compared to the test in the Familiar action condition with a similar delay ($P = 1.000$ in both comparisons).

Throughout the testing procedure of 18 trials, 6 dogs made only one error, one dog made two errors and one dog made 6 errors (for the details see Table 2). Overall 130 (90.28 %) trials have been scored as 'match' and 14 as 'no match'.

Discussion

The robust performance of the dogs in the present study convincingly supports deferred imitation. Dogs were typically able to reproduce familiar and novel actions after different delays, in different conditions and also if distracted by their owners who engaged them in different types of activities before recalling the demonstrated action. Their performance in the tests where familiar actions were demonstrated are compatible with response facilitation (or 'deferred response facilitation'), defined as the ability to detect and encode a perceived action and to select and control an already known motor response, so that there is similarity between the observed action and the motor response (Byrne 1994). As we used object-related actions, in the tests where familiar actions were shown, also

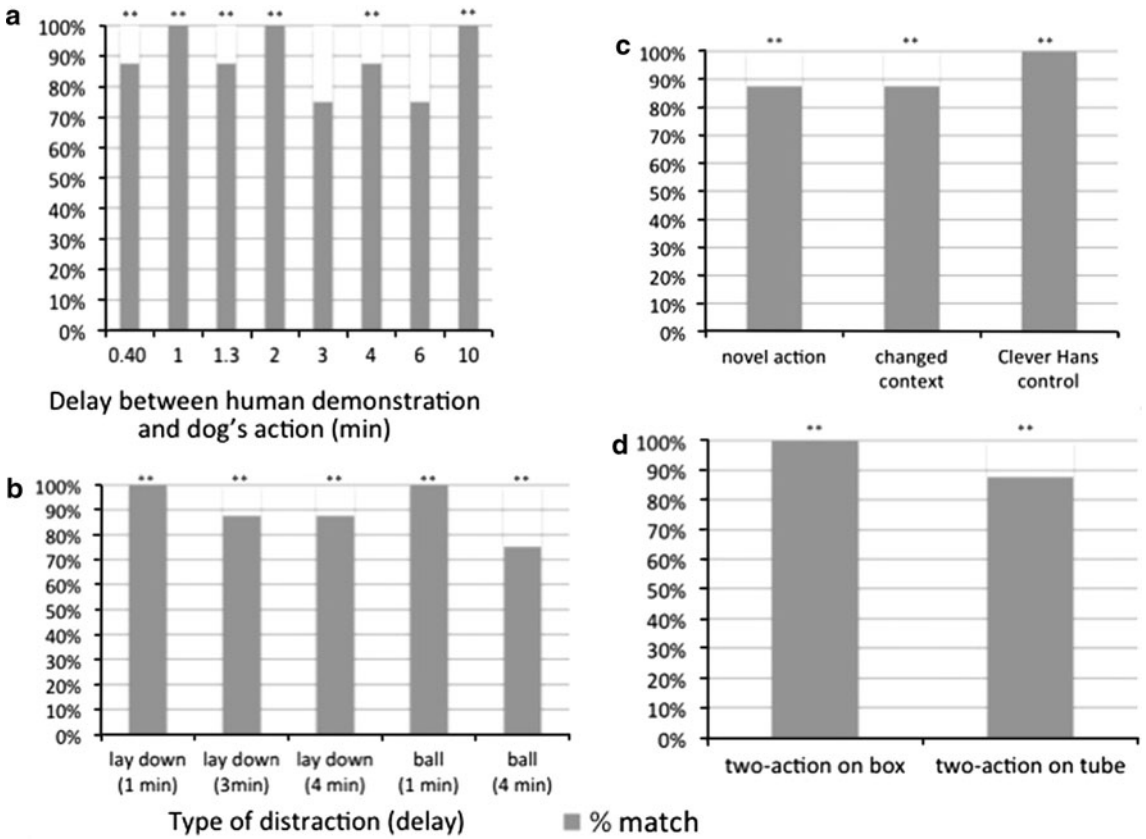

Fig. 2 Percentage of dogs' performances scored as 'match' in the different conditions. *Astreiks* indicate statistically significant difference compared to the No demonstration condition after Bonferroni correction. **a** Familiar actions after different delays; **b** familiar actions with distractions during the retention interval; **c** novel action after a delay of 1 min, familiar action in a different context after a delay of 1 min and 'Do it!' command given by a different 'naïve' experimenter after a delay of 1.15 min; **d** two-action tests on novel actions after a delay of 1.30 min. The figure shows that the matching percentage does not typically change with increased delays from 0.40 to 10 min (**a**), with the introduction of distractions (**b**), when novel actions are demonstrated, changing the context of retrieval and in the Clever Hans control test (**c**) and when different novel actions on the same objects are demonstrated (**d**)

'deferred stimulus enhancement' (Galef 1988) could explain the dogs' performance. However, the results of the Two-action tests reveal that subjects not only acted on the same object that was manipulated by the demonstrator, but also copied the different novel actions that were performed on that object. In particular, dogs were able to match their body movement to the demonstration not only when the two demonstrated actions lead to different outcomes, which could be explained by goal emulation, but also when the different body movements on the same object did not lead to different outcomes.

Given the anatomic differences between humans and dogs, we cannot be sure how human actions are encoded by a dog and the coding of the performance as 'match' or 'no match' has been adjusted to the differences in the behaviour repertoire of the two species, using the definition of 'functional imitation' (see Topál et al. 2006). The novel actions were considered as 'match' only if the body part used by the dog for performing the particular action was corresponding (e.g., the human's hand touch was considered corresponding to the dog's front paw touch), which is also a more stringent criterion for imitation than the one used by Miller et al. (2009) where a human demonstrator pulled a screen with hand, and the dog's performance was considered imitation if the dog used his muzzle.

In the Clever Hans control condition, all dogs were able to reproduce the demonstrated action when the 'Do it!' command was given by an unknowledgeable ('naïve') experimenter after a delay of 1.15 min. Thus, we can exclude any effect of involuntary cues given by the demonstrator or the owner on the dog's performance.

In the No demonstration control condition, dogs tended to stay still, without performing any action, which replicates the finding from Topál et al. (2006) and also excludes that the mere presence of the objects could elicit the target behaviours.

Imitation after some delay has been claimed to indicate representational abilities in human infants (e.g., Carpenter et al. 1998b; Meltzoff 1995). The ability to recall and reproduce actions after such delays as those used in the present study reveals that reflexive behaviour cannot exhaustively explain the observed behavioural similarity and we can exclude that facilitative processes played a role in triggering similar actions in the observer after attending the demonstrator (Bjorklund and Bering 2003).

Evidence for deferred imitation of a novel action without previous practice has been used to provide a direct measure of declarative (non-verbal) memory in infants (Barnat et al. 1996; Klein and Meltzoff 1999). Klein and Meltzoff (1999) assessed deferred imitation in 12-month-old infants using a procedure that did not allow subjects to motor practice on the tasks before the delay was imposed, therefore excluding that memory could be based on re-accessing a motor habit. The ability shown by children to recall the behaviour has been claimed by the authors to demonstrate declarative (non-procedural) memory. In the present study, we used a similar procedure: Dogs were not allowed to interact with the object before the 'Do it!' command was given (so-called 'observation-only procedure' Klein and Meltzoff 1999). In the Novel action condition and in both Two-action conditions, subjects imitated the novel behaviours after a delay without any previous practice of these particular actions, so that their memory and recall could not have been based on re-accessing a motor habit, because none was formed. Furthermore, they had to recall the action in the absence of any direct or indirect cue that, during the retention interval, could have functioned as a perceptual trigger, because the curtain obstructed the view of the objects. Therefore, dogs did not simply recognise and choose after a delay the object that was used during the demonstration, but also retrieved and reproduced an action they had not performed on this object before, without the possibility to base their recall on the aid of previous motor practice. Taken together, these results suggest the presence of some form of declarative (non-procedural) memory for imitative actions in dogs.

In the Novel action condition, all dogs were scored as matching the demonstrated action, with the exception of one. However, the dog that was scored as 'no match' approximated her behaviour to the demonstration: She entered the box only using her front paws, leaving the hind legs outside. We can therefore argue that she was able to at least partially encode and recall the demonstration. Novelty is a relative concept (Whiten and Custance 1996) as it can refer to various aspects of the behaviour (e.g., the object involved, the body movement, the context, etc.). In the current study, the behaviour was considered new if it had never been trained (Heyes and Sagerson 2002). We cannot state that our subjects had never performed these actions spontaneously during their lifetime, but this was not likely to have happened. In the Novel action condition, the behaviour was new regarding the body movement and the object for all dogs, with the exception of one dog who had been previously trained to enter a box, although this box was different from that used during testing (different in shape, size, material and colour). Thus, for this dog, that behaviour was new only with regard to the target object.

The Two-action test, in which two other different actions were shown on the same box, demonstrates that at least three different actions were conceivable for a dog on that object: 'Enter the box', 'Look in the box' and 'Touch the box with paw'. Thus, we can exclude that 'Enter the box' was the only achievable or probable action for a dog who could just match the object after a delay (delayed matching), or that the increased attention towards the stimulus alone can explain the observed behavioural similarity (stimulus enhancement).

In the Two-action condition on the tube, it may not be possible to distinguish between goal emulation and imitation, because the dogs both reached the same goal (i.e., caused the same movement of the object) and also used the same body action. In particular, for those dogs that witnessed a knock over action, the affordance of the object—the tube passed from a vertical to a horizontal position—might have helped to retrieve the goal to be reached. However, in the Two-action test on the box (or Multi-action test, if also the 'Enter the box' action is considered), neither affordance nor goal was available, as no modification in the object was possible. Thus, in the latter case, only deferred imitation can be considered as an explanation of the observed behavioural similarity.

In the present study, all dogs were exposed to the demonstration of 'Enter the box' in the Novel action condition, and seven dogs out of eight could match this action. In the first Two-action condition, two other different actions on the box were demonstrated ('Touch the box' was demonstrated to five subjects and 'Look in the box' to the other three), and all dogs imitated the particular action that was shown to them after a delay of 1.30 min. While the classical two-action procedure usually involves two different groups of subjects that are tested on two different actions (e.g., Akins and Zentall 1996; Dorrance and Zentall 2001; Van de Waal et al. 2012), the present results also reveal that dogs may be able to change their behaviour according to what they have observed in two different tests where two different actions without different outcomes are demonstrated to the same subject on the same object.

In our study, the dogs' performance was not affected by context change (Barnat et al. 1996; Klein and Meltzoff 1999) with retention intervals of 1 min, which further supports the deferred nature of dogs' imitative abilities. More importantly, this result provides compelling evidence that local enhancement (i.e., increased attention towards the location of the demonstration) cannot exhaustively explain the observed behavioural similarity. However, this does not imply that, during memory retrieval, context may not serve as a cue that might help recall under different conditions, such as with longer retention intervals that challenges the memory of dogs.

Studies on human infants (e.g., Klein and Meltzoff 1999; Óturai et al. 2012) show that the length of the delay affects performance. Very long retention intervals, such as 1 or 4 weeks, affect imitative behaviours, and it has been hypothesised that this forgetting pattern might be due to the transfer of the acquired information to 'very-long-term memory' (Klein and Meltzoff 1999).

Fiset et al. (2003) explored the duration of dog's working memory in an object permanence task and found that, although the performance decreased with increased delay, the dog's accuracy remained higher than chance level with retention intervals up to 4 min. In the present study, dogs did not decrease their performances with increased delay up to 10 min, and further experimental work should investigate the forgetting pattern in dogs and their memory of actions after longer delays.

In conclusion, previous studies and the present results strongly suggest that dogs possess a rudimentary form of deferred imitation that may also play a role in acquiring information from both con-specifics and heterospecific (humans). It is likely that this ability is not restricted to dogs and other canids may also possess it. Further investigation could reveal what functional role this skill might have in wild living canids.

Acknowledgments This study was supported by the Hungarian Scholarship Board by providing a fellowship to C. Fugazza. A.M. also receives funding from MTA-ELTE Comparative Ethology Group (MTA01 031), and the Hungarian Science Foundation (OTKA K81953). We are also grateful to the dog owners of the Good Boy and Happy Dog School who enthusiastically participated in this research with their dogs. We thank L. Marinelli for her comments on the manuscript, C.P. West for proofreading the English of this article and the anonymous reviewers for their valuable suggestions.

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