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ORIGINAL PAPER

Do as I … Did! Long-term memory of imitative actions in dogs (*Canis familiaris*)

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Abstract This study demonstrates long-term declarative memory of imitative actions in a non-human animal species. We tested 12 pet dogs for their ability to imitate human actions after retention intervals ranging from 1 to 24 h. For comparison, another 12 dogs were tested for the same actions without delay between demonstration and recall. Our test consisted of a modified version of the Do as I Do paradigm, combined with the two-action procedure to control for non-imitative processes. Imitative performance of dogs remained consistently high independent of increasing retention intervals, supporting the idea that dogs are able to retain mental representations of human actions for an extended period of time. The ability to imitate after such delays supports the use of long-term declarative memory.

Keywords Long-term memory · Deferred imitation · Declarative memory · Long-term recall · Dogs

Introduction

Deferred imitation is the ability to encode the demonstration of an action and to recall it after a delay in order to use it as the basis to perform a matching action (Klein and Meltzoff 1999). Presence of such cognitive ability offers evidence that behavioural similarity between demonstrator and observer is the result of an enduring representation of the demonstrator's behaviour (Huber et al. 2009), rather than the effect of facilitative processes (Zentall 2006).

Declarative memory, due to its role in recalling facts and events (Cohen and Squire 1980), provides an essential basis for deferred imitation. In preverbal human infants, declarative memory is typically assessed by testing their tendency to imitate after retention intervals during which the subjects are not allowed to motor practice on the observed actions (Klein and Meltzoff 1999). Deferred imitation after delays longer than 10 min indicates the existence and use of long-term memory (Barnat et al. 1996).

So far only a few studies have attempted to investigate deferred imitation in non-human species, and the delays used have been relatively short. Chimpanzees (*Pan troglodytes*) showed some evidence of behavioural similarity after delays of 10 min (Bjorklund and Bering 2003; Bjorklund et al. 2002). Japanese quail (*Coturnix japonica*) were shown to be able to match their behaviour to that of a demonstrator after a delay of 30 min (Dorrance and Zentall 2001). Deferred imitation after longer delays has not been tested in other non-human species. Dogs' ability to imitate has recently received attention from researchers (Huber et al. 2009; Range et al. 2011; Topál et al. 2006). Using a modified version of the Do as I Do paradigm (Topál et al. 2006), we previously found that dogs are able to imitate human actions after retention intervals ranging from 40 s to 10 min (Fugazza and Miklósi 2014a). These findings raise the compelling question of whether they could store the representation of others' actions in their long-term memory (Bauer and FIvush 2014).

In the present study, we investigated dogs' declarative memory of imitative actions after delays of 1, 2, 12 and 24 h. Imitative performance of dogs with delay between

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demonstration and recall was compared to a control group carrying out the same tasks in the same order but without delay. This split-plot experimental design (Fisher 1925; Jones 2009) allowed us to compare performance with delayed recall to an estimated baseline performance for each action, while precluding the possibility that the subjects' recall in deferred imitation tests was based on a memory of their own prior actions (Meltzoff 1988) because each dog was tested only once with a given action. To control for non-imitative processes that may enhance the probabilities of a similar response—e.g. stimulus enhancement (Thorpe 1963) and goal emulation (Tomasello 1990)—we combined the Do as I Do paradigm with the two-action procedure (Akins and Zentall 1996).

Materials and methods

Subjects

Our experiment needed significant effort from owners and their dogs, as they had to be available both during demonstration and recall (half a day or one day after demonstration in certain tests). Due to experimental considerations, therefore, we used a relatively small sample size and a repeated measures design. Twenty-four adult pet dogs of various breeds participated in this study with their owners. Before the study began, all subjects were trained by their owners with the 'Do as I Do' method to match their behaviour to actions that were demonstrated by a human (Fugazza and Miklósi 2014a).

$N = 12$ dogs were assigned to each of control ('immediate recall') and manipulated ('delayed recall') groups, randomly. Age of the dogs varied from 1 to 10 years (mean $\pm$ SD age in immediate and delayed recall groups: 4.8 ± 3.6 and 6.3 ± 2.1 years, respectively). The immediate recall group included three Border Collies, one Rottweiler, two Labrador Retriever, three Czechoslovakian Wolfdogs and three mixed breed. The delayed recall group included three Border Collies, one Galgo, one Labrador Retriever, one Golden Retriever, one Jack Russell Terrier, two poodles, one Shetland Shepherd and two mixed breed.

Preliminary training

The preliminary Do as I Do training and the experimental procedure we used are necessary to test dogs' imitative abilities and memory of others' actions because the subjects learn that they are required to imitate as precisely as possible, allowing the researcher to test them without incurring in other methodological, attentional and/or motivational confounding factors. This procedure relies on imitation, an ability of dogs that is within their natural cognitive skills (Miller et al. 2009; Range et al. 2011; Topál et al. 2006).

The preliminary Do as I Do training is based on Topál et al. (2006) and Fugazza and Miklósi (2014b), and it involves two steps. First, dogs are trained through operant conditioning techniques to match their behaviour to three familiar actions demonstrated by their owners on command 'Do it!'. Second, this command is generalized to three other familiar actions, after which the 'Do it!' command can be used as a training rule to imitate any demonstrated novel task. Owners learned to train their dogs during seminars held by CF (for more details on the training procedure see also Fugazza and Miklósi 2014a).

As a criterion for participation in the experiment, dogs had to pass a test of being able to display at least six familiar actions (i.e. actions already trained with other techniques) on the 'Do it!' command during a 10-trial session in which the six actions are shown by a novel demonstrator in a randomized order, imitating those correctly in at least eight trials out of ten (Fugazza and Miklósi 2014b). In order to make dogs familiar with the testing procedure, before testing, dogs were also trained to wait for a short interval (approximately 30 s) after the demonstration, before the command to imitate was given (Fugazza and Miklósi 2014a).

Experimental procedure

In each test, four objects were displayed (a box, a lid, a tube and a helmet; Table 1), and these four objects were kept the same for all dogs in all tests. Based on the two-action procedure (Akins and Zentall 1996), for each object, two actions of similar difficulty (A and B) were defined, but only one of these actions was ever demonstrated to a given dog. Action A or action B was randomly assigned to a given dog for an object, so that half of the dogs received action A and half of them action B as demonstration for any of the four objects. If a particular dog had been previously trained on an action that was similar to either action A or B, we assigned the other action to this subject (see Table 1 for details) to avoid previous training experience confounding our results. The two object-related actions (A and B) were chosen to represent tasks of similar difficulty (simple interactions with objects), and similar performance across the various actions confirmed this (see "Results"). Therefore, the only difference between the two experimental groups was the length of the retention interval between demonstration and recall for a given test.

Each dog participated in four tests except for one dog in the delayed recall group that was tested only three times because the owner could not bring the dog back for testing after the retention interval. In the first test, an action was demonstrated on the box, in the second on the lid, in the

Table 1 Description of objects used for testing

Objects	Action A	Action B
Box: a plastic box placed upside down (i.e. with the open end facing the ground)	The owner climbs on top of the box with his feet, first stepping on it with one foot then with the other ($N_{IR} = 6$; $N_{DR} = 6$)	The owner puts both hands on the box ($N_{IR} = 6$; $N_{DR} = 6$)
	The dog climbs on top of the box with all four legs, first with the front paws then with the hind legs	The dog puts both front paws on the box
Lid: a plastic lid hanging at the height of the dog's shoulder from a string attached to a horizontal pole	The owner swings the lid using one hand (it is required that the lid moves, without any height requirement) ($N_{IR} = 3$; $N_{DR} = 4$)	The owner swings the lid using his nose ($N_{IR} = 9$; $N_{DR} = 8$)
	The dog swings the lid using one front paw (it is required that the lid moves, without any height requirement)	The dog swings the lid using his nose
Tube: a cartoon tube placed horizontally on the ground	The owner touches the tube with one hand ($N_{IR} = 6$; $N_{DR} = 3$)	The owner walks past the tube so that both feet pass on the other side of the tube ($N_{IR} = 6$; $N_{DR} = 8$)
	The dog touches the tube with one front paw	The dog walks past the tube so that all four paws pass on the other side of the tube
Helmet: a motorcycle helmet placed on the ground	The owner walks around the helmet ($N_{IR} = 7$; $N_{DR} = 5$)	The owner touches the helmet with one hand ($N_{IR} = 5$; $N_{DR} = 7$)
	The dog walks around the helmet	The dog touches the helmet with one front paw

For each object, we provide the description of action A and action B that the human demonstrator performed, and the expected behaviour by the dog in case of successful imitation (two-action procedure). We also provide number of dogs to which each action was demonstrated ('N_{IR}' refers to immediate recall, whereas 'N_{DR}' refers to delayed recall group)

third on the tube and in the fourth on the helmet (see Table 1). This order was kept fixed in both immediate recall and delayed recall group for two reasons. First, although a complete randomization would have allowed us to separately investigate the effect of test action and delay, we were interested only in the latter. Second, by keeping a fixed order of test actions, we decreased the factors in our statistical models and increased the chance for finding possible differences between experimental groups.

Before a test started, the four objects were randomly positioned in the testing area, as represented in Fig. 1. To exclude the influence of potentially confounding olfactory cues, the owner of the dog helped to carry all four objects to the predetermined positions, so that he/she left his/her traces of odour on every object. In this way, we could exclude the possibility that dogs were guided to the object used for the demonstration and that recalling was facilitated exclusively by olfactory cues.

In the beginning of a test, the owner made the dog stay in the centre point of the test area (i.e. equal distances from the four objects), using commands known by the dog. Then the owner demonstrated once the assigned object-related action (for a description of the objects and actions see Table 1). Following the demonstration, dogs in the immediate recall group were immediately commanded by the 'Do it!' command from the owner. For dogs in the delayed recall group, retention intervals of various durations (1, 2, 12 and 24 h) elapsed before the command was given. In the delayed recall group, during the delays of 1 and 2 h, the owner was led to a designated area where the dog could stay with him/her, either on a leash or in his/her crate. During 12- and 24-h delays, the owner and the dog went home overnight and were allowed to engage in their regular daily activities. When the scheduled retention interval elapsed, they returned to their predetermined position in the testing area and the dog was commanded to imitate.

In order to avoid any possible Clever Hans effect on the dogs' performance, owners were asked to look straight ahead and keep their eyes closed while giving the 'Do it!' command (Fugazza and Miklósi 2014a).

Data collection and analysis

Video recordings of the dogs' behaviour following the 'Do it!' command were used to observe whether they matched the demonstrated action. Videos of the first action performed by the dogs immediately after the 'Do it!' command were shown in a randomized order to a coder who was blind with regard to the demonstrations. The coder was asked to assess whether the dog performed action A, action B or any other actions (see "Results").

The response of a dog was considered as matching the demonstrated action if the dog performed an action similar to the one demonstrated by the owner, using a matching body part—e.g. if the human touched an object with one

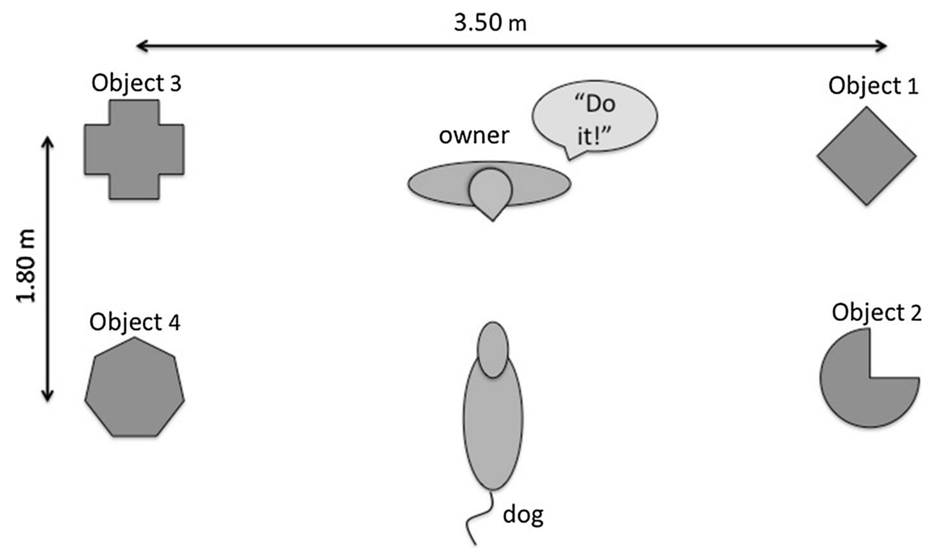

Fig. 1 Experimental set-up of deferred imitation tests. Before demonstration and when the 'Do it!' command is given by the owner, the owner and the dog face each other in a predetermined position in the centre of four objects, one of them on which an action is demonstrated

hand, the dog touched it with one of its front paws, while a nose touch on the object by the human was matched by a nose touch by the dog. If the owner used two hands to interact with the object, a matching action from the dog was also with both front paws. Table 1 provides detailed information on what is considered a matched action for each demonstrated action. If, however, the dog performed any other than the demonstrated action (including action A when action B was demonstrated, an action that was not in the repertoire or no action at all) or the dog interacted first with another object, action matching was considered unsuccessful.

We used the R statistical environment (v. 3.1.1, R Development Core Team 2014) to analyse our data. We carried out two analyses to investigate the underlying process (imitation) that is responsible for action matching and the effect of increasing retention time on imitation success.

First, we followed the analysis of the two-action procedure described by Akins and Zentall (1996), but adapted it to our experimental design and the single binary response variable we had for each test. In this analysis, we focused on the tests in which dogs performed action A or B (76 of 95 tests) and introduced a new variable ('action A') which was coded 1 if the action performed by the dog was A and 0 if the performed action was B. Action A (binary response variable) was then analysed in a binomial generalized linear mixed model with demonstrated action as an explanatory variable (factor with two levels: A or B) and dog name as a random term. If action matching was due to imitation [as opposed to other alternative processes such as stimulus enhancement or goal emulation, (Zentall 2006)], we expected demonstrated action to explain whether action A or B was performed by the dog.

For the second analysis that included all tests of the dogs (95 tests: 24 dogs have been tested on four objects each, except for one dog with three objects only, see "Materials and methods"), imitation success was coded either 1 when the dog matched action (i.e. the dog performed action A when action A was demonstrated and action B when action B was demonstrated, on the object used by the demonstrator) or 0 when the dog did not match action (e.g. the dog performed any other action (including action B) than action A, or performed no action at all, when action A was demonstrated). Imitation success (binary response variable) was then analysed using binomial generalized linear mixed models (GLMM, R package 'lme4', Bates et al. 2014) with experimental group (factor with two levels) and test (factor with four levels) as fixed effects and dog name as a random term. If delay between demonstration and recall has an effect on imitation success, this should be reflected in a significant experimental group x test interaction; therefore, the latter two-way interaction term was included in the model. Initial models included action (factor with two levels, A or B), but were excluded after confirming no effect in our analysis. The effects of explanatory variables were analysed by likelihood ratio test.

Results

Action matching and imitation

Dogs performed action A or B in 76 of 95 tests (i.e. in 80 % of all tests; for a full description on dogs' responses, see Table 2). Action A and action B were demonstrated in 32 and 44 of these tests, respectively, and in all but 2 of these 76 tests, the dogs performed the same action (A or B)

Table 2 Description of dogs' responses after the 'Do it!' command in all tests

Tests in which dogs performed action A when action A was demonstrated	31
Tests in which dogs performed action B when action B was demonstrated	43
Tests in which dogs performed action A when action B was demonstrated	1
Tests in which dogs performed action B when action A was demonstrated	1
Tests in which dogs approached the object manipulated by the demonstrator but did not perform any of the demonstrated actions	4
Tests in which dogs performed the demonstrated action on a different object	1
Tests in which dogs did not approach any object and did not perform any of the demonstrated actions	10
Tests in which dogs performed an action which was among the demonstrated ones but not on the object used by the demonstrator	3
Tests in which dogs approached the object and performed an action among the ones demonstrated in other tests	1

We provide the number of tests in which dogs performed the described actions

as the one that had been demonstrated to them (i.e. in 97.4 % of 76 tests). This has been confirmed by our statistical analysis, in which demonstrated action explained almost all variation in performed action (GLMM, action: $\chi^2 = 84.49$, $df = 1$, $P < 0.0001$). Therefore, we found solid evidence that action matching was due to imitation, rather than alternative processes resulting in similar outcomes (Zentall 2006).

The effect of retention time on imitation success

Imitation success (calculated as the mean ± SE of per cent action matching over the four tests of dogs) was 77.8 ± 4.6 %. Imitation success did not differ between dogs with immediate and delayed recall (immediate vs. delayed recall groups, mean ± SE per cent success: 83.3 ± 5.6 % vs. 72.2 ± 7.2 %; GLMM, experimental group x test interaction: $\chi^2 = 4.15$, $df = 3$, $P = 0.246$; Fig. 2). The type of action (A or B) had no effect on imitation success ($\chi^2 = 0$, $df = 1$, $P = 0.997$) and was excluded from the final model.

When focusing our analysis on the delayed group only, we also did not find a significant effect of delay on imitation success (GLMM, test: $\chi^2 = 1.51$, $df = 3$, $P = 0.680$), although apart from the first test, dogs' imitation success in the delayed recall group tended to decrease compared to their peers in the immediate recall group (Fig. 2).

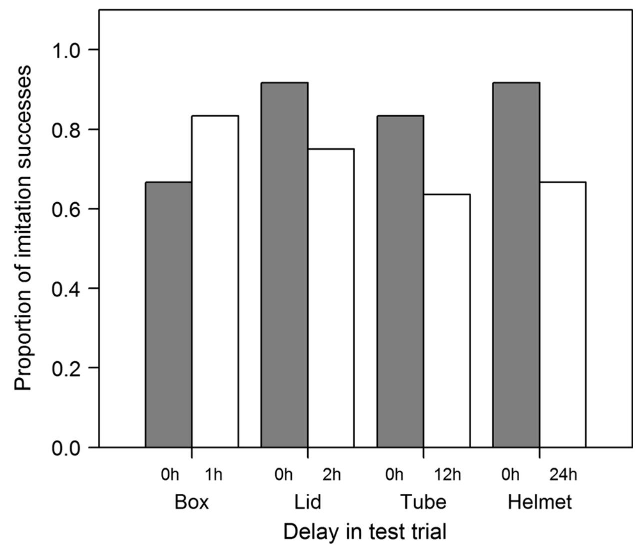

Fig. 2 Proportion of successful imitations in Do as I Do tests of pet dogs. Dogs in immediate recall group (*grey bars*, $N = 12$) and delayed recall group (*white bars*, $N = 12$ in all tests except the 12-h delay in which one dog could not participate in the test) were repeatedly tested with four objects/actions and bars with the same colour represent the proportion of the same 12 individuals which successfully imitated the action on the given object. In the delayed recall group, dogs were commanded to imitate after 1, 2, 12 and 24 h following demonstration

Discussion

This study provides evidence that dogs possess long-term declarative memory of others' actions. Dogs were able to imitate the demonstrated actions after delays ranging from 1 to 24 h, and their success rate was similar to that of dogs that were required to imitate immediately.

Such ability to imitate after long delays without motor practice on the actions during the retention interval broadly supports the presence of declarative memory in dogs. While declarative memory in animals has been studied using different methods, including testing for an ability to establish cognitive maps (Singer and Zentall 2007) and investigating the capacity to remember the what, where and when of an event (Clayton and Dickinson 1998), to our knowledge, this is the first time that declarative memory of imitative actions is demonstrated in non-human animals after such long delays.

Dogs' success in imitating the actions in terms of body movements cannot be explained by stimulus enhancement (Thorpe 1963) or goal emulation (Tomasello 1990) because dogs did not only match the objects used during the demonstration, but also match action A or B (in accord with the two-action procedure) and with their body part corresponding to that of the demonstrator. Thus, their stored representation goes beyond encoding the features of the object or the location of demonstration unlike in delayed matching-to-sample paradigms (Dumas 1998). Because deferred imitation relies on declarative memory, dogs' deferred imitation after long delays provides evidence for enduring representation of the actions performed on the object, i.e. long-term memory for imitative actions.

It is likely that in our study, the target object used during demonstration functioned as retrieval cue that facilitated recalling the actions that were performed on it (Herbert and Hayne 2000; Learmonth 2004). Separating dogs' ability to recall demonstrations of body movements independently from objects (i.e. testing for capability to imitate non-object-related actions after a delay) is an interesting aim for a potential follow-up study. Chimpanzees trained for imitation have been shown to be able to copy also arbitrary actions without target objects, such as hand signs and facial expressions (Custance et al. 1995; Hayes and Hayes 1952). An orang-utan trained with the Do as I Do method also showed some limited ability to imitate body movements, with higher imitation success for gross body areas and lower success for smaller body parts (Call 2001). To our knowledge, however, primates' ability to copy body movements after a delay has not been tested.

Although we did not find a significant difference between imitation successes of dogs in the two groups, subjects in the immediate recall group tended to perform better than subjects in the delayed recall group across all tests but the first. Admittedly, our sample size was limited due to experimental considerations, so we acknowledge that a larger sample size could have detected a weaker group effect. This suggests that dogs' recall might be hindered by longer delays, and an intriguing task for further studies may be to map dogs' performance after more than 24 h retention time.

The subjects of our study were pet dogs that had received a specific training aimed at teaching them the 'imitation rule' (Do as I Do training), which is needed to test imitation for the methodological reasons explained above. Previous experience with this training revealed that all well-socialized pet dogs can be trained with this method (Fugazza and Miklósi 2014b), suggesting that the results reported here can be generalized to family pet dogs in general.

In sum, by using the Do as I Do paradigm combined with the two-action procedure, our study demonstrates presence of long-term declarative memory for imitative actions in family dogs. We did not find a significant drop in imitation success within the range of 24 h, leaving to future studies the intriguing task to find the limit of dogs' memory of others' actions and the role of the presence of the target objects used during demonstration in dogs' recall.

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Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest with their sponsors.

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