Report

Current Biology

# Recall of Others' Actions after Incidental Encoding Reveals Episodic-like Memory in Dogs

## Highlights

- Episodic-like memory of others' actions was tested in dogs
- Dogs were trained to imitate human actions with the Do as I Do method
- Dogs could recall the owners' actions when unexpectedly requested to imitate
- Memory of owners' actions decreased faster with increased test delay

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## In Brief

Fugazza et al. investigated dogs' ability to recall human actions in unexpected episodic memory tests. Dogs trained to imitate with the Do as I Do method were tested on their memory of previously demonstrated human actions when they did not expect the memory test. Dogs could imitate, although their memory decayed faster with increased delay.

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# Recall of Others' Actions after Incidental Encoding Reveals Episodic-like Memory in Dogs

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## SUMMARY

**The existence of episodic memory in non-human animals is a debated topic that has been investigated using different methodologies that reflect diverse theoretical approaches to its definition. A fundamental feature of episodic memory is recalling after incidental encoding, which can be assessed if the recall test is unexpected [1]. We used a modified version of the "Do as I Do" method [2], relying on dogs' ability to imitate human actions, to test whether dogs can rely on episodic memory when recalling others' actions from the past. Dogs were first trained to imitate human actions on command. Next, they were trained to perform a simple training exercise (lying down), irrespective of the previously demonstrated action. This way, we substituted their expectation to be required to imitate with the expectation to be required to lie down. We then tested whether dogs recalled the demonstrated actions by unexpectedly giving them the command to imitate, instead of lying down. Dogs were tested with a short (1 min) and a long (1 hr) retention interval. They were able to recall the demonstrated actions after both intervals; however, their performance declined more with time compared to conditions in which imitation was expected. These findings show that dogs recall past events as complex as human actions even if they do not expect the memory test, providing evidence for episodic-like memory. Dogs offer an ideal model to study episodic memory in non-human species, and this methodological approach allows investigating memory of complex, context-rich events.**

## RESULTS AND DISCUSSION

Episodic memory has been defined as memory of personal events and specific episodes in one's life, and it is thought to be linked to self-awareness [e.g., 3, 4]. Whether non-human animals possess some forms of episodic memory is a controversial topic, and it is difficult to design experimental procedures to assess self-awareness unambiguously. Therefore, this form of memory in non-human animals is referred to as "episodic-like memory." The diversity of methods to investigate episodic-like memory reflects the controversies regarding its definition [5–8]; however, recent approaches seem to agree that the recalling of an event relies on episodic memory when encoding of such event was incidental [9–13]. Incidental encoding occurs when information is stored without knowing that it has to be remembered or that it will be important later [9]. This requisite ensures that the subject cannot rely on learned rules (semantic memory) to succeed in the subsequent memory test. Because, at present, no experimental procedure exists to directly assess the type of encoding (i.e., a subjective state), a crucial criterion of studies focusing on episodic-like memory is that the recall test should be unexpected [1]. Unexpectedness of the test ensures that there is no specific motivation for explicit encoding, so incidental encoding can be reasonably assumed.

To explore the ability of dogs to recall past events when there was no expectation of the recall test, we used an innovative methodology: a modified version of the "Do as I Do" paradigm, relying on dogs' ability to imitate human actions after a delay [14, 15]. Our aim was to test dogs' episodic-like memory of past events (i.e., human actions) that are richer in content and more complex than what was tested in the majority of previous studies [e.g., 7, 9, 16, 17]. In most of these studies, laboratory animals were tested on memory of simple events, such as object exploration or feedings. Although these findings provide important advances for the study of episodic memory, real-life events are far more complex and richer in content. Particularly, from a pet dog's perspective, the actions of humans are arbitrary behaviors that are always potentially different and can be performed on many different objects and in many different contexts. Episodic-like memory of such context-rich events was not tested previously in non-human species, except for chimpanzees and orangutans [5]; thus, it is not known whether this ability evolved only in primates or is a more widespread trait.

Here, we investigate whether dogs can rely on episodic-like memory to recall context-rich events from the past. We hypothesized that dogs can rely on episodic-like-memory to recall and imitate incidentally encoded actions performed by their owners, and we tested two predictions. First, we expected dogs to be able to imitate incidentally encoded actions when the imitation test was unexpected, albeit less successfully compared to their baseline imitation success when recall is expected. Second, we predicted that imitation success would decrease significantly with longer retention intervals, as memory appears to decay faster when encoding is incidental as opposed to when it is intentional [7, 18, 19]. Before testing, pet dogs were trained in two

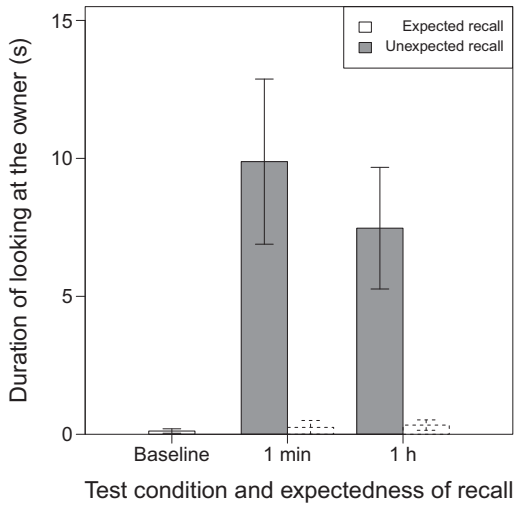


**Figure 1. Duration of Looking at Owner**

Duration of looking at the owner in Do as I Do tests of dogs after expected (white bars) or unexpected (gray bars) "Do it!" commands were given. Bars with continuous lines represent data from the present study; bars with dashed lines represent data from two previous studies with similar conditions but expected recall (1 min retention time with "Lie down" distraction before imitation[14]; 1 hr retention time[15]).

See also "Violation of expectation: dogs look longer at the owner if the test is unexpected" in Supplemental Experimental Procedures.

stages; the first stage has been independent of this study, as we enrolled dogs that were previously trained by their owners with the regular Do as I Do training to imitate human actions on command "Do it!" [2, 14] (for more details, see "Do as I Do training" in Supplemental Experimental Procedures). At the beginning of this study, the dogs' baseline imitation success was assessed with the two-action method [20] in an expected imitation test ("baseline imitation" henceforth). Every dog had been exposed once to the demonstration of one of two possible novel (not trained) actions on an object (e.g., climb on a chair or touch the chair with paws; see Table S1). After the demonstration, the owner gave the "Do it!" command. Dogs were then free to perform any action, including other actions than those chosen for the tests.

To ensure that the subsequent imitation test was unexpected, after the baseline test, dogs underwent a second stage of training in which they were not required to imitate anymore. Instead, after the owners' demonstration of various actions in sessions of six different trials, dogs were always required to perform a simple training exercise: lying down ("Lie down training" in Supplemental Experimental Procedures). The aim of this training was to substitute the dogs' expectation of the imitation command with the expectation of a "Lie down" command. After the successful "Lie down" training, we tested dogs' memory of unfamiliar (previously not trained or tested) actions by unexpectedly commanding them to imitate instead of lying down (Movie S1). Dogs were tested with the "Do it!" command only if they lied down spontaneously after the demonstration, suggesting with their behavior that they expected a lie down command (all dogs lied down spontaneously).

Dogs were not allowed to motor practice the demonstrated actions; they could only observe them during the demonstration. We tested each dog in two imitation tests: after retention intervals (i.e., time between demonstration and the "Do it!" command to imitate) of 1 min and 1 hr, in random order of the delays and the demonstrated actions. The tests were video recorded and later behaviorally coded for statistical analysis. It is reasonable to assume that in these tests, a successful imitation of the previously demonstrated action was possible only if dogs encoded the action incidentally, because the imitation test was unexpected, so there was no motivation for the dogs to encode them explicitly. Therefore, our method complies with the requirements for testing episodic memory (recall of an incidentally encoded event assessed by an unexpected recall test).

The unexpectedness of the test is a critical and at the same time challenging issue because it is difficult to assess the mental state of non-verbal subjects (i.e., acquire information about their expectations). Previous studies relied on the mere assumption that the test was unexpected [5, 9–13]. In contrast, we experimentally modified dogs' expectations and searched for behavioral evidence for this. First, we ensured that the dogs expected to receive the "Lie down" command—and not the imitation command—by training all dogs until they spontaneously lied down after they had seen the demonstrated actions in at least five of six trials in two consecutive training sessions. In the unexpected tests, all dogs lied down spontaneously after the demonstrated actions, indicating that they expected a "Lie down" command, not an imitation command. Second, we relied on the well-established violation of expectation paradigm [e.g., 21, 22] that has also been successfully used in dogs [23–25]. This paradigm predicts a longer duration of looking toward the source of violation of expectation; therefore, we expected longer duration of looking at the owner who issued the "Do it!" command when this was unexpected as opposed to when it was expected. Because of the excess of zeros in the expected imitation tests (due to dogs that did not look at the owner after the "Do it!" command was given), we analyzed duration of looking in Tweedie Generalized Linear Mixed Models (GLMMs; package "cplm" [26] in R statistical environment, v. 3.2.3 [27]), with dog ID as random term and test condition as fixed effect (factor with three levels: baseline [expected imitation test], 1 min [unexpected imitation test], and 1 hr [unexpected imitation test]). Dogs looked significantly longer at the owner in the two conditions with unexpected imitation test than in the baseline condition with expected imitation test (likelihood ratio test of Tweedie GLMMs with and without test condition as fixed factor: $\chi^2_2 = 25.45$, $p < 0.001$; Figure 1). Other than expectedness, longer duration of looking may be explained by between-group differences in retention times and the effect of distraction by the "Lie down" command. Therefore, we excluded these alternative explanations in further analyses comparing the duration of looking in the present study with that of previous studies with identical delays but expected imitation tests (Figure 1 and "Violation of expectation" analysis in Supplemental Experimental Procedures).

Imitation success (binary response variable) was analyzed using binomial GLMMs (R package "lme4" [27]), with dog ID as random term and test condition as fixed effect (factor with three levels: baseline [expected imitation test], 1 min [unexpected imitation test], and 1 hr [unexpected imitation test]). In support of both of our predictions, we found that dogs were able to imitate when the imitation test was unexpected (although less

**Table 1. Imitation Success**

| Effects of Test Condition | Parameter Estimate ± SE | z | p |
|---|---|---|---|
| Intercept (baseline, expected) | 2.87 ± 1.11 | 2.59 | 0.010 |
| Baseline (expected) → 1 min (unexpected) | −2.50 ± 1.19 | −2.10 | 0.036 |
| Baseline (expected) → 1 hr (unexpected) | −3.51 ± 1.27 | −2.77 | 0.006 |

Imitation success (binary response variable) in Do as I Do tests of dogs (N = 17) based on whether recalling is expected and the length of retention interval. Parameter estimates with standard error (SE) between levels of test condition (fixed factor) and statistical significance are given from the binomial GLMM. Dogs were repeatedly tested in three test conditions: in baseline (expected imitation test) and after 1 min and 1 hr retention intervals (unexpected imitation tests), separately.

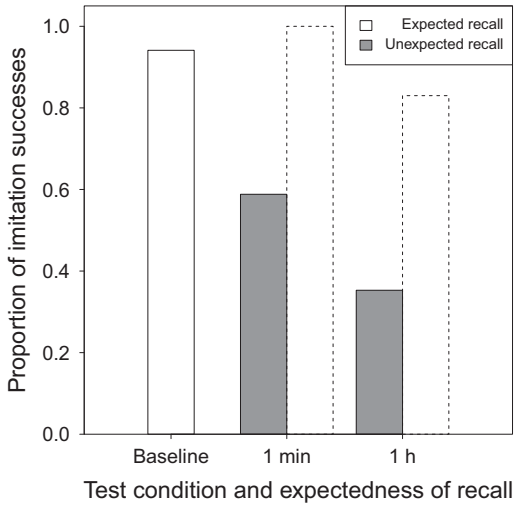


**Figure 2. Imitation Success**

Proportion of imitation successes in Do as I Do tests of dogs. Continuous bars show repeated tests of N = 17 dogs in the three experimental conditions of the present study. The white bar represents the proportion of dogs that successfully imitated after completing the Do as I Do training, i.e., in a baseline condition in which the command to imitate was expected. The gray bars represent the proportion of dogs that imitated after also completing the second training aimed at modifying their expectation ("Lie down" training). In the latter two test conditions, the command to imitate was unexpected and was given after 1 min and 1 hr retention intervals, separately. Dashed bars represent proportion of imitation success in previous studies with similar conditions and identical delays but expected imitation test (1 min with "Lie down" distraction before imitation[14]; 1 hr[15]).

successfully than when it was expected), and imitation success decreased quickly (i.e., fewer subjects imitated) with increasing retention interval (GLMM of imitation success, effect of test condition: $\chi^2_2 = 14.7$, $p < 0.001$; Table 1; Figure 2). A more rapid decay of dogs' memory as a result of incidental encoding was apparent when we compared imitation success after 1 min and 1 hr retention interval when recalling was unexpected (this study) with results of our previous studies, with similar conditions (also with 1 min and 1 hr retention intervals) but when the imitation test was expected [14, 15] (Figure 2). When the recall test was expected, imitation success of dogs was not significantly different between immediate recall and recall after 1 hr delay [15]. In addition, imitation success with expected recall was more than 2-fold compared to when recall was unexpected (binomial GLM of imitation success after 1 hr retention intervals, expected recall [from 15] versus unexpected recall [this study]: 83.3% versus 35.3%; $\chi^2_1 = 7.0$, $p = 0.008$, regression coefficient [B ± SE] for expectedness = 2.22 ± 0.93).

We argue that the difference in memory decay between this study and the previous one with identical delay [15] further corroborates that the dogs relied on an episodic-like memory in the present study, as this type of memory is proposed to decay faster with time than other types of long-term memory [18, 19]. In the case of expected imitation tests, dogs may have encoded the owners' demonstrated actions explicitly because, as a result of previous training, they expected to be required to imitate. This implies that dogs might have used semantic memory to succeed in the deferred imitation task. In contrast, in the present study dogs were tested in the deferred imitation test only after assuring that their expectation of the future action required from them was different from the demonstrated action. Despite this, our results suggest that dogs could encode the demonstrated actions incidentally, although less successfully compared to the baseline.

Ostensive signals used by the owners to prevent dogs from moving during the demonstrations ("Stay and pay attention" command) may have increased the dogs' attention, but this is unlikely to have resulted in using explicit memory in the unexpected tests. The same cues were also used during the "Lie down" training, in which dogs specifically learned that the owner's subsequent actions were irrelevant. In addition, this command is commonly used in everyday life situations with pet dogs, whenever owners want to prevent their dogs from interfering with their activities. Following the concept of incidental encoding (not knowing that the information will be important later [1, 9]), we experimentally modified dogs' expectations so that recalling the previously demonstrated actions was unexpectedly required. Although we provided multiple, independent experimental evidence for unexpectedness of recall (spontaneous lying down at the beginning of the test and behavioral signs of violation of expectation when unexpectedly required to imitate), we acknowledge that ensuring incidental encoding by direct evidence is problematic because it concerns the inner state of the subjects. Such direct and exclusive evidence seems extremely challenging to provide (if not impossible), so we relied on the assumption that the "Lie down" training resulted in dogs not explicitly encoding the demonstrated actions because these were irrelevant for the subsequent task. A steeper decrease in imitation success, albeit as an indirect evidence, strongly supports that we succeeded in this [18, 19].

Importantly, by using the two-action procedure in which two actions (A or B) are demonstrated on an object, our study provides evidence that the underlying process resulting in dogs' reproduction of the demonstrated actions was deferred imitation (in 94.3% of all the tests when dogs performed action A or B, it was in correspondence with the demonstrated actions; Table 2; see Supplemental Experimental Procedures for more details on this analysis). This supports the notion that the dogs could imitate owners' actions that were incidentally encoded without being presented with samples of those at the time of recall and without motor practicing during the retention interval.

**Table 2. Imitation Analysis**

| Test Condition and Retention Interval | Demonstrated A | | | Demonstrated B | | |
|---|---|---|---|---|---|---|
| | Performed A | Performed B | Performed Other | Performed A | Performed B | Performed Other |
| Baseline imitation | 9 | 0 | 1 | 0 | 7 | 0 |
| 1 min unexpected | 5 | 1 | 2 | 0 | 6 | 3 |
| 1 hr unexpected | 5 | 0 | 5 | 1 | 1 | 5 |

Number of dogs that performed action A, action B, or any other actions based on the demonstrated action in the various conditions of the Do as I Do test.

Testing for deferred imitation is a widely used approach to investigate the development of cognitive abilities in human infants [e.g., 28] and chimpanzees [29, 30]. These studies, however, were not specifically designed to investigate episodic memory, and it cannot be determined whether encoding of the demonstrations was incidental. Incidental encoding may also occur in cases of latent learning [31], although it has to be confirmed. Important advances about recall of incidentally acquired information were recently made by authors applying methods that rely on the unexpectedness of the recall test [9–13]. Zentall et al. [11] argued that in order to investigate episodic-like memory in non-verbal species, it is possible to teach them to use a trained behavioral response to "answer" a question about a past event (e.g., "Did you peck or not?"). Then the subjects can be "asked" this question unexpectedly, to assess whether they can remember the event. Using this method, the authors provided evidence that pigeons recall a simple species-specific action (pecking) and its location [12] after short delays. Zhou et al. [9] revealed that rats could not solve an unexpected memory task when the CA3 region of their hippocampus was inactivated, suggesting that this brain region is involved when recalling from memory is unexpected. Martin-Ordas et al. [5] tested chimpanzees and orangutans on their ability to recall the location of tools that they used previously to retrieve food. This study showed the ability to recall tool locations for long delays—even 3 years—after having used them. Although this suggests that some non-human species may recall events with a more complex nature than those tested in previous studies, the role of previous motor practice cannot be completely excluded due to the fact that those subjects performed the actions before testing. Mercado et al. [32] tested dolphins on their ability to reproduce the action they had just performed. Although, given the short delay, the subjects could have relied on their working memory, this methodological approach has the potential to test episodic-like memory for complex past events (one's own actions) if subjects are prevented from keeping their mind actively on the actions so that the unexpectedness of the test can be ensured.

Our study makes an important advance in the study of episodic-like memory for multiple reasons. To our knowledge, this is the first time that a non-human species shows evidence of being able to recall complex events (i.e., others' actions) without motor practicing on them during the retention interval—thus relying on a mental representation of the action that has been formed during incidental encoding, as assessed by an unexpected test. Note that in most previous studies of episodic-like memory, subjects participated in sample trials in which the same stimuli were presented as in test trials [e.g., 16, 17]. Our experimental procedure ensured that even if dogs were presented at the time of the test with the same objects that were used at the time of encoding, the specific actions performed by the demonstrator could only be imitated if dogs recalled a mental representation that was formed during encoding.

This modified version of the Do as I Do method has the potential to be applicable to a variety of species; the list of species in which the Do as I Do method has been used successfully includes dolphins (*Tursiops truncatus*) [33], parrots (*Psittaciformes*) [34], and killer whales (*Orcinus orca*) [35].

Moreover, to our knowledge this is the first study that experimentally addressed and behaviorally confirmed unexpectedness of the recall test. We believe that our research approach of modified expectation combined with the violation of expectation paradigm can be adapted to various experimental designs.

In conclusion, by using a modified version of the Do as I Do method, we found evidence that dogs can remember events as complex as human actions after incidental encoding, as assessed by an unexpected memory test, without motor practicing the actions during the retention interval and without being presented at the time of the memory test with the same samples presented when encoding took place. This is the first evidence of episodic-like memory of others' actions in a non-human species, and it is the first report of this type of memory in dogs. We suggest that dogs might provide a new non-human animal model to study the complexity of incidental encoding of context-rich events, especially because of their evolutionary and developmental advantage to live in human social groups.

## SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, one table, and one movie and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.09.057.

A video abstract is available at http://dx.doi.org/10.1016/j.cub.2016.09.057#mmc4.

## AUTHOR CONTRIBUTIONS

The study was conceived by C.F., A.P., and A.M. The experiments were run by C.F.; A.P. analyzed the data. The article was drafted by C.F. and revised by A.P and A.M. All authors gave final approval for publication and agree to be held accountable for this work.

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## Supplemental Information

# Recall of Others' Actions after Incidental Encoding Reveals Episodic-like Memory in Dogs

**Claudia Fugazza, Ákos Pogány, and Ádám Miklósi**

**TABLE S1 (related to Table 2).** Objects and actions used according to the two action procedure in the baseline imitation test and in the two unexpected imitation tests. Objects and actions were randomly chosen for each dog for the baseline test. Then they were randomly chosen for the subsequent two episodic-like memory tests, but excluding the actions already demonstrated in the previous test(s). Thus each dog was tested only once for imitation of one possible action on each object. We include the description of the two actions (A and B) used as human demonstrations (two-action procedure) and description of the expected corresponding dog behaviour.

| | **Action A** | | **Action B** | |
|---|---|---|---|---|
| **Object** | **Human** | **Dog** | **Human** | **Dog** |
| Bucket | Demonstrator looks inside the bucket | Dog looks inside the bucket | Demonstrator walks around the bucket | Dog walks around the bucket |
| Umbrella | Demonstrator touches the opened umbrella with nose | Dog touches the opened umbrella with nose | Demonstrator touches the opened umbrella with one hand | Dog touches the opened umbrella with a front paw |
| Chair | Demonstrator puts his/her hands on the chair | Dog puts both front paws on the chair | Demonstrator steps up on the chair | Dog climbs on the chair with all four legs |

## SUPPLEMENTAL EXPERIMENTAL PROCEDURE

### Subjects

The subjects were N = 17 adult companion dogs (6 males and 11 females) of various breeds and mixed breed, whose owners volunteered to participate in this study. All the dogs had been previously trained with the Do as I Do method by their owners, as described below. Of the 17 dogs, 13 had participated in previous studies using the Do as I Do method; all the dogs involved in the study received the same training (see below).

### Do as I Do training

The training protocol had been explained to all owners by the experimenter (CF) before the study began. This training included two phases:

Phase 1: Dogs were trained to match their behaviour to 3 demonstrated familiar actions on command 'Do it!' through operant conditioning methods. Once the dogs reached approximately 80 % imitation success in two consecutive sessions of approximately 6 trials each, they progressed to the second training phase.

Phase 2: Dogs were trained to match their behaviour to 6 demonstrated familiar actions on command 'Do it!'. Each owner decided what actions to demonstrate, based on what the dogs were already well-trained to perform. During training, owners used food or access to favourite toys as a reward for correct performance. After completing this training (i.e. approximately 80 % imitation success in two consecutive sessions) dogs were able to reproduce novel actions on command 'Do it!' [S1, S2], even with a long delay (retention interval) between demonstration and the 'Do it!' command [S3, S4].

After completing the Do as I Do training, dogs were tested in the baseline imitation test (see below) and progressed to the Lie down training (see below).

### Baseline (expected) imitation test

The aim of the baseline test was to assess dogs' imitation success of the novel object-related actions when recalling is expected. The owner and the dog stood in front of each other in the middle of 6

objects (an opened umbrella, a bucket, a chair, a cone, an agility hurdle and a tissue), laid on the floor in a circle, 2 m from them.
The owner asked the dog to stay and pay attention, using cues known by the dog.
Next the owner demonstrated one of two possible actions randomly chosen of 6 actions/3 objects (see Supplemental Table S1), while the other objects were there to provide distraction and possibility for the dogs to perform actions other than the demonstrated ones.
After the demonstration, the owner went back to his start position in front of the dog and gave the command to imitate ('Do it!'), while he/she was looking straightforward and was not moving. If the dog did not perform an action within 10 seconds, a second 'Do it!' command was given. All, but one dog imitated successfully.

**Lie down training**
The aim of the Lie down training was to substitute the dogs' expectation to receive a command to imitate with the expectation of receiving a command to lie down. In this training phase the setup was identical to the one used for the Baseline test, except for the owner and the dog standing on a blue carpet that was placed in the middle of the objects. The carpet was used to facilitate teaching dogs that when they were on the blue carpet, they were never required to imitate and were always requested to lie down following their owners' demonstrated actions.
The owner asked the dog to stay on the blue carpet and to pay attention, using cues known by the dog.
Next the owner demonstrated an action on one of the 6 objects. Different objects/actions were demonstrated in each trial, including the actions used in the tests.
The owner went back to his/her start position in front of the dog and gave the command to lie down using cues known by the dog. This procedure was repeated in 6-trial training sessions, with at least 10-minute breaks between them.
From the 19$^{th}$ trial on (start of training session four), after the demonstrations, the owner returned to his/her start position and waited 5 seconds while looking straightforward, before giving the command to lie down.
The training continued until the dog spontaneously lied down following the owner's demonstrations (once the owner returned to the blue carpet and looked straightforward), in at least 5 out of 6 trials in two consecutive sessions.
Dogs lied down spontaneously after 4.3 ± 1.5 (mean ± SD; range: 2-8) training sessions consisting of 6 different demonstrated actions each.

**Unexpected imitation test**
The setup was identical to the one used for the Lie down training.
The owner asked the dog to stay on the blue carpet and to pay attention, using cues known by the dog.
Next the owner demonstrated one of two possible actions randomly chosen of 6 actions / 3 objects, excluding those already demonstrated in the previous test(s) (Supplemental Table S1).
After the predetermined retention interval, the owner went back to his/her start position in front of the dog, waited for 5 seconds looking straightforward and, as soon as the dog spontaneously lied down, the owner gave the command to imitate ('Do it!') always looking straightforward. If the dog did not move from the blue carpet for 10 seconds after the 'Do it!' command, the owner repeated it again. If the dog did not perform any action within 10 seconds from the last command, imitation was considered as unsuccessful.
During the retention interval of 1 minute the owner and the dog stayed behind an opaque screen to prevent dogs from watching the objects. During the retention interval of 1 hour, the owner put the dog in his/her car or in a familiar kennel. This was also intended to prevent dogs from keeping their mind active on the demonstration by looking at the target object.

**Action matching and imitation**

To investigate the underlying process that resulted in 'imitation success' in our experiment, we used the well-established two-action method already used in dogs and other species [S4-S6]. The first object-related actions performed by the dogs after the 'Do it!' command were shortly described (e.g. 'touches umbrella with nose') by a coder who was blind with regard to the demonstration, based on the video recordings of the tests. Later these short behavioural descriptions were used to establish whether the dog performed the demonstrated action (actions A and B were pre-defined, see Table S1 above). The performed action was considered as matching the demonstrated one when both were either action A or action B. Furthermore, the dog had to use the corresponding body part for performing a similar body movement as the demonstrator, considering the species-specific differences between the them ('functional imitation', e.g. if the demonstrator touched an object with one hand, the dog touched the same object with one of its front paws, while a nose touch on the object by the demonstrator was matched by a nose touch by the dog; Table S1).

**Action matching due to imitation**

To analyse the underlying process of action matching in our study, we followed our previously described method [S4, S5]; a statistical analysis that is an adaptation of the original approach described by Akins and Zentall [S6]. We refrained from comparing imitation success of dogs to chance level because we do not have 'priors' to calculate the probability for action A or B by chance for three reasons:

1) In our test, it was not taken for granted that dogs would perform *any* action at all. Indeed, one of the possible responses of the dogs was no action at all: dogs in 5 of 51 tests did not do any actions and this decreases the hypothetical chance level;

2) Dogs could interact with the demonstrated object in many ways. Therefore, it is impossible to set an a priori probability for spontaneous actions (that is, no imitation) that includes many more actions besides only action A or B;

3) 50% would be an artificial chance level also because only we (experimenters) knew that the action demonstrated to the dog on a given object was randomly selected from two (action A or B). A given dog has seen, therefore, only one of the actions. Thus this is different from the situation in which the subject has to select from two possible demonstrations. This is probably most illuminating if we imagine that instead of 2 actions (A or B), we would have selected from 20 possible actions (but as in our experiment, we would have always shown only one to a given dog, so everything kept the same from the dogs' perspective). Chance level based on this fallacious logic should then decrease to 5%, making it very likely to find a significant effect, but clearly, the experiment (as well as dogs' reactions) would be the same as in our experiment.

In our analysis first, we focused only on the cases in which the dog performed action A or action B (i.e. excluded those tests in which the dogs performed any other actions or no actions at all), resulting in 35 of 51 tests (68.6%) included. For these tests, we introduced a new binary variable ('action A') which was coded 1 if the action performed by the dog was action A, and 0, if the performed action was action B (irrespective of the demonstrated action). This binary response variable was then analysed in a binomial Generalized Linear Mixed Model (GLMM, R package 'lme4', [S7]) with demonstrated action (factor with two levels: A or B) as an explanatory variable and dog ID as a random term. A significant effect of demonstrated action in this analysis indicates that imitation (rather than such alternative processes as stimulus enhancement or goal emulation, [S8]) is behind action matching.

From the 35 tests in which dogs performed action A or action B, 33 times (94.3%) this was in correspondence with the demonstrated action (GLMM, demonstrated action: $\chi^2_1 = 33.2$, $P < 0.0001$). Our analysis corroborated, therefore, that whenever dogs matched the demonstrated actions, it was due to imitation.

**Violation of expectation: dogs look longer at the owner if the test is unexpected**

To assess whether the imitation test was unexpected for the dogs we applied the violation of expectation paradigm, predicting increased duration of looking at the owner who issued the unexpected imitation command when the recall test is unexpected, as compared to when it is expected [S9-S11]. As reported in the manuscript, our analyses confirmed this, however, longer duration of looking could be explained by (1) between-group differences in retention times and also (2) by the distracting effect of lying down. Therefore, we carried out further between-study analyses to exclude these two alternative explanations:

*The effect of different retention times*

To address this alternative explanation, we compared duration of looking at the owner in a previous study [S4] vs. in this study, in both cases with deferred imitation after retention times of 1 h. Our results confirmed that unexpectedness of the 'Do it!' command, rather than retention time explains longer duration of looking at the owner in the present study (LRT of Tweedie GLMMs of duration of looking with and without study as fixed factor: $\chi^2_1 = 34.28$, $P < 0.001$; Figure 1 in the manuscript). This result supports that in the present study dogs did not expect to be required to imitate.

*Distracting effect of lying down*

Both in the within-study and in the above between-study comparisons, test conditions were different also in that the unexpected conditions always included dogs being required to lie down before being required to imitate, whereas no lying down was required in the baseline test of the present study, when the imitation command was expected.

In one of our previous experiments [S3], we required dogs to lie down as a mere distraction before giving them the command to imitate. In this case no preliminary training was carried out to teach dogs to expect a lie down command thus the imitation test was still expected. In order to exclude that lying down only acted as a mere distraction in the present study, we compared duration of looking at the owner who issued the (unexpected) 'Do it!' command in the present study with the duration of looking at the owner in the previous study [S3]. We used data from these two experiments with similar test conditions (1 min retention time and lying down), so any difference between duration of looking at the owner is driven by expectedness of recall.

We found longer duration of looking at the owner in the present study compared to the previous one (LRT of Tweedie GLMMs of duration of looking with and without study as fixed factor: $\chi^2_1 = 7.54$, $P = 0.006$; Figure 1 in the manuscript). Dogs imitated immediately after receiving the 'Do it!' command in the previous study, even if distracted by the preceding lie down command, but looked much longer at the owner when they received the unexpected command for imitation in this study. This analysis further corroborates that unexpectedness, rather than other possible distracting effects of lying down, is responsible for between-group differences in our present study.

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