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Title
Recall of others' actions after incidental encoding reveals episodic-like memory in dogs

Authors and affiliation
Claudia Fugazza[1,2,*], Ákos Pogány[2], Ádám Miklósi[1,2]
[1] *MTA-ELTE Comparative Ethology Research Group, Budapest, Hungary*
[2] *Department of Ethology, Eötvös Loránd University, Budapest, Hungary*
[*]Correspondence: claudia.happydog@gmail.com

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 h) 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.

Keywords:
Episodic memory, dogs, imitation, unexpected recall test, incidental encoding, Do as I Do.

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 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. As at present no experimental procedure exists to assess directly 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, thus 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 behaviours 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 hypothesised 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 imitation success to 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 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 Information). 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 has 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 in Supplemental Information). 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 6 different trials, dogs were always required to perform a simple training exercise: lying down ('Lie down training' in Supplemental Information). 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 nor tested) actions by unexpectedly commanding them to imitate instead of lying down (Supplemental Information, video). Dogs were tested with the 'Do it!' command only if they lied down spontaneously after the demonstration, suggesting with their behaviour 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 minute and 1 hour, in random order of the delays and the demonstrated actions. The tests were video recorded and later behaviourally 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, thus 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 in 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 a mere assumption that the test was unexpected [5, 9-13]. In contrast, we experimentally modified dogs' expectation and searched for behavioural 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 5 of 6 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 towards 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 analysed duration of looking in Tweedie Generalized Linear Mixed Models (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 h [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). Besides 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 Information).

Imitation success (binary response variable) was analysed using binomial Generalized Linear Mixed Models (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 h [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 successfully than when it was expected), and imitation success decreased fast (i.e., less 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 h retention interval when recalling was unexpected (this study) with results of our previous studies with similar conditions (also, with 1 min and 1 h 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 h delay [15]. In addition, imitation success with expected recall was more than two-fold compared to when recall was unexpected (binomial GLM of imitation success after 1 h retention intervals, expected recall [from 15] vs. unexpected recall [this study]: 83.3% vs. 35.3%; $\chi^2_1 = 7.0$, $P = 0.008$, $B \pm SE$ for expectedness $= 2.22 \pm 0.93$).

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 unlikely resulted in using explicit memory in the unexpected tests. The same cues were used also 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' expectation 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 behavioural 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), therefore, we relied on the assumption that the lie down training resulted in dogs not to encode explicitly 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 Information for more details on this analysis). This supports that the dogs could imitate the owner's 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.

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 behavioural 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. (2013) [5] tested chimpanzees and orangutans on their ability to recall the location of tools that they used previously to retrieve food. This study showed 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. (1998) [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 active on the actions and 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 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 behaviourally 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.

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TABLES

Table 1

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 between levels of test condition (fixed factor) and statistical significance are given from the binomial Generalized Linear Mixed Model. Dogs were repeatedly tested in three test conditions: in baseline (expected imitation test), and after 1 min and 1 h retention intervals (unexpected imitation tests), separately.

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 h (unexpected)	-3.51 ± 1.27	-2.77	0.006

Table 2

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

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 hour unexpected	5	0	5	1	1	5

FIGURE LEGEND

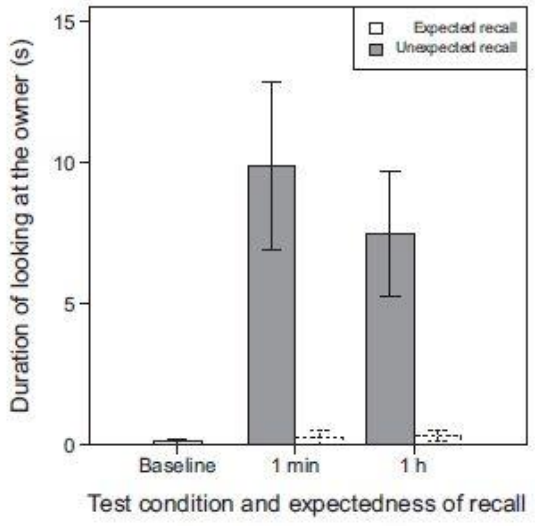

Figure 1.
Duration of looking at the owner in Do as I Do tests of dogs after expected (white bars) or unexpected (grey bars) 'Do it!' commands were given. Bars with continuous lines represent data from the present study and bars with dashed lines represent data from two previous studies with similar conditions but expected recall (1 minute retention time with lie down distraction before imitation [14]; 1 hour retention time [15]) See also Violation of expectation: dogs look longer at the owner if the test is unexpected in Supplemental Information.

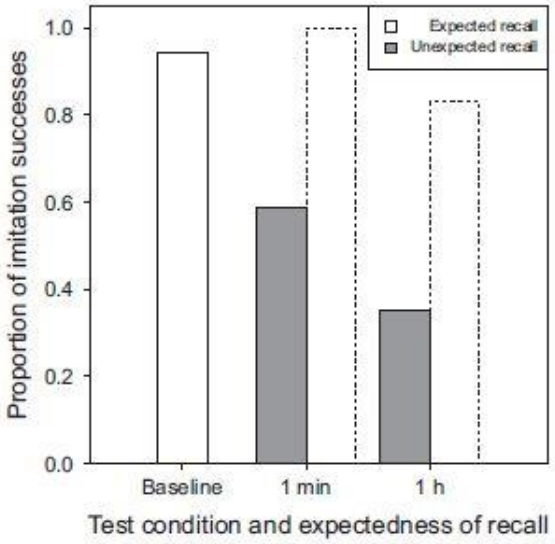

Figure 2.
Proportion of imitation successes in Do as I Do tests of dogs. Continuous bars show repeated tests of N = 17 dogs in the three experimental conditions of the present study. The white bar represents the proportion of dogs that successfully imitated after completing the Do as I Do training, i.e. in a baseline condition in which the command to imitate was expected. The grey bars represent the proportion of dogs that imitated after completing also 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 minute and 1 hour retention intervals, separately. Dashed bars represent proportion of imitation success in previous studies with similar conditions and identical delays but expected imitation test (1 minute with lie down distraction before imitation [14]; 1 hour [15]).