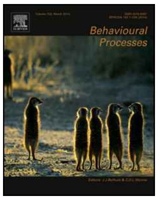
Behavioural Processes xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Use of incidentally encoded memory from a single experience in cats

Saho Takagi[a,*], Mana Tsuzuki[a], Hitomi Chijiiwa[a,e], Minori Arahori[a,e], Arii Watanabe[b,c], Atsuko Saito[b,d], Kazuo Fujita[a]

[a] *Department of Psychology, Graduate School of Letters, Kyoto University, Yoshida-honmachi, Sakyo, Kyoto 606-8501, Japan*
[b] *Graduate School of Arts and Sciences, The University of Tokyo, 3-8-1 Komaba, Meguro-ku, Tokyo 153-8902, Japan*
[c] *Department of Cognitive and Information Sciences, Faculty of Letters, Chiba University, 1-33 Yayoi-cho, Inage, Chiba 263-8522, Japan*
[d] *Department of Childhood Education, Musashino University, 41-1-20 Shinmachi, Nishitokyo-shi, Tokyo 202-8585, Japan*
[e] *Japan Society for the Promotion of Science, 5-3-1 Chiyoda, Tokyo 102-0083, Japan*

ARTICLE INFO

Article history:
Received 29 October 2016
Received in revised form
28 December 2016
Accepted 30 December 2016
Available online xxx

Keywords:
Incidental memory
Episodic memory
Cats
Felis catus

ABSTRACT

We examined whether cats could retrieve and utilize incidentally encoded information from a single past event in a simple food-exploration task previously used for dogs (Fujita et al., 2012). In Experiment 1, cats were led to four open, baited containers and allowed to eat from two of them (Exposure phase). After a 15-min delay during which the cats were absent and all containers were replaced with empty ones, the cats were unexpectedly returned to the room and allowed to explore the containers (Test phase). Although the cats' first choice of container to visit was random, they explored containers from which they had not previously eaten for longer than those from which they did previously eat. In the Exposure phase of Experiment 2, two containers held food, one held a nonedible object, and the fourth was empty. Cats were allowed to eat from one of them. In the post-delay Test phase, the cats first visited the remaining baited-uneaten container significantly more often than chance and they spent more time exploring this container. Because the cats' behavior in the Test phase cannot be explained by association of the container with a pleasant experience (eating), the results suggest that cats retrieved and utilized "what" and "where" information from an incidentally encoded memory from a single experience.

1. Introduction

We humans often consciously try to mentally reconstruct unique events we have experienced, and the resulting declarative memory of these events is called episodic memory (Tulving, 1972). Episodic memory has two important properties. First, it contains what happened, where it happened and when it happened in an integrated fashion ("WWW memory") (Tulving, 2002, 2005). The second property is its incidental nature; that is, the memory is not a result of active encoding at the time when the event occurred (Zentall et al., 2001). Although some researchers insist that episodic memory requires language and autonoetic consciousness and is unique to humans (Suddendorf and Corballis, 1997, 2007; Tulving, 2002), recent experiments suggest that many nonhuman animals also show "episodic-like memory" that includes at least one of the properties above.

Clayton and Dickinson (1998) first demonstrated that in the context of food caching, western scrub-jays (*Aphelocoma californica*) are able to remember "what, where, and when" of specific past events in an integrated fashion. Further demonstrations of WWW memory were subsequently reported in various nonhuman species including bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and orangutans (*Pongo pygmaeus*) (Martin-Ordas et al., 2010), rhesus macaques (*Macaca mulatta*) (Hoffman et al., 2009), black-capped chickadees (*Poecile atricapillus*) (Feeney et al., 2009), magpies (*Pica pica*) (Zinkivskay et al., 2009), rats (*Rattus norvegicus*) (Babb and Crystal, 2006; Roberts et al., 2008), mice (*Mus musculus*) (Dere et al., 2005), honeybees (*Apis mellifera* L.) (Pahl et al., 2007), and cuttlefish (*Sepia officinalis*) (Jozet-Alves et al., 2013).

Incidental encoding is more difficult to test in nonhumans, but it has also been examined in a few species, for example by means of an "unexpected question task". Tomonaga and Kaneko (2014) inserted occasional "recognition tests" among visual search trials, requiring chimpanzees to choose the stimulus they had just touched in the search task. Chimpanzees succeeded in these recognition tasks. Pigeons also successfully retrieved memory recently encoded for another task in an "unexpected question" (Zentall et al., 2001; Singer and Zentall, 2007). The literature thus suggests that several nonhuman species may be able to remember their immediately preceding behavior, which is probably still in working memory.

---

* Corresponding author.
E-mail address: takagi.saho.67x@st.kyoto-u.ac.jp (S. Takagi).

http://dx.doi.org/10.1016/j.beproc.2016.12.014
0376-6357/© 2017 Elsevier B.V. All rights reserved.

Retrieval of incidentally encoded memories after longer delays has been also reported in nonhuman animals. For instance, language-trained bottlenosed dolphins (*Tursiops truncatus*) successfully repeated their previous behavior when unexpectedly asked to do so (Mercado et al., 1998). A language-trained chimpanzee requested food they had seen hours before to trainers who did not know about it (Menzel, 1999). Rats chose a correct alley in an unexpected test that combined two tasks on which they were previously trained independently (Zhou et al., 2012). Although these demonstrations are impressive, the methods used are of limited value for comparative studies because of the need for intensive training.

Ferkin et al. (2008) showed that male meadow voles (*Microtus pennsylvanicus*) were able to recall a single past event associated with mate choice, in the absence of training. Male voles were exposed to two females in separate chambers. One chamber contained a day-20 pregnant female (24 h prepartum), and the other chamber contained a nonpregnant female. When males were returned to the same apparatus 24 h after this single exposure, they preferentially visited the side where they had previously encountered the day-20 pregnant female, who was now in postpartum estrus (PPE). The meadow voles' behavior satisfies both WWW and incidental properties, but as the behavior was species-specific and not applicable to other species, it may not be homologous to human episodic memory. To answer important comparative questions such as how widespread episodic memory is, procedures are required that enable direct behavioral comparisons across species.

Fujita et al. (2012) established a simple task that incorporates no training or species-specific behavior to examine whether animals retrieve and utilize incidentally encoded memory from a single previous experience. Dogs were led to four open, baited containers and allowed to eat from two of them (Exposure phase). After a walk outside for at least 10 min (Delay phase) during which the containers were replaced with new but identical ones, the dogs were unexpectedly returned to the experimental room and allowed to explore the containers (Test phase). Contrary to what would be predicted if they learned to associate specific containers with food, the dogs showed a strong tendency to visit the containers from which they had not eaten in the Exposure phase. In this context the dogs' behavior suggested retrieval of information from incidental memory formed during a single past experience.

Here we asked whether cats retrieve and utilize incidentally encoded "where" (Experiment 1) and "where + what" (Experiment 2) information, using the simple memory task originally used with dogs by Fujita et al. (2012). Recent studies have shown that cats can match dogs in various cognitive tests, including responding to human gestural cues (Miklósi et al., 2005), discriminating between human emotional expressions (Galvan and Vonk, 2015; Merola et al., 2014), and referring to human facial expressions in the presence of a frightening object (Merola et al., 2012a, 2012b, 2015). We were therefore interested in how cats would respond when tested using the "unexpected question" procedure to assess incidental memory.

In Experiment 1, cats were shown four open, baited containers and allowed to eat from two of them. In Experiment 2, the original procedure was repeated except that we used two containers each baited with a piece of food, one container with a nonedible item, and one empty container to examine whether cats retrieved "what" information as well as "where" information.

We made two predictions about how cats would behave in the Test phase. First, if cats behaved in accordance with operant learning, they should first revisit containers where they previously obtained rewards in the Exposure phase. Second, conversely, if cats retrieved and utilized memory incidentally encoded in the Exposure phase, they should first visit containers from which they had not previously eaten, or explore them more.

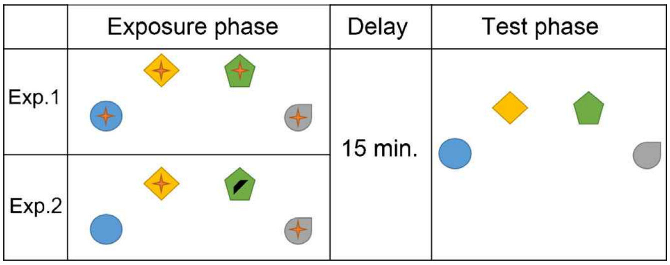


Fig. 1. The setup and the procedure of Experiments 1 and 2. In the Exposure phase, cats were directed to the four open containers. Stars represent the reward in both experiments, and the black trapezoid represents the neutral object in Experiment 2. All containers were baited in Experiment 1, and cats were allowed to eat from two of them. In Experiment 2, two containers had food, one had a neutral object, and the fourth was empty. Cats were exposed to all containers and were allowed to eat only one of the two rewards. After a delay of about 15-min the, test was conducted. In the Test phase, all containers were replaced with an identical set of containers to exclude any olfactory cues. Cats moved freely to explore the containers.

2. Experiment 1

2.1. Method

2.1.1. Subjects

Forty-nine domestic cats (*Felis catus*) (31 males and 18 females) participated, of which 28 were house cats and 21 were kept at three "cat cafés".[1] Their ages ranged from 3 months to 14 years (mean: 3.4 years, SD: 3.5). We recruited cats and owners of cat cafés through a personal acquaintance network. Each café had a separate room where we tested cats individually. In addition to approval from the institutional experimental committee (see paragraph on compliance with ethical standards), informed consent was obtained from all owners before the test. The cats were not deprived of any water or food during the study.

2.1.2. Apparatus

Two identical sets of four containers were used in each test, within-set containers varying in dimensions such as shape, size, and color. All containers were 12–20 cm in diameter, and 6–12 cm deep. Made of either plastic or clay, the containers were white, pink, green, or blue. We used four small pieces of each cat's favorite food (e.g., chicken breast strips, dried-bonito shavings) as rewards. The rewards were small enough for the cats to consume quickly. The cats' behavior during each test was recorded by a video camera (SONY, HDR-CX390, Japan).

2.1.3. Procedure

2.1.3.1. Exposure phase. The cats were individually tested in a separate room in a familiar place, either the owner's house or the cat café. The open containers were arranged in a fan shape with a radius of 1 m from a start point. The space between each adjacent container was 15 cm to 30 cm depending on the size of the room. All containers were baited in Experiment 1 (Fig. 1). When the set-up was ready, experimenter 1 (E1) asked the owner (O) or experimenter 2 (E2) to take the cat to the start point. Once the cat was there, E1 asked O or E2 to gently coax the cat to each container one by one in clockwise or counterclockwise order, direct the cat's attention to each one, and allow the cat to eat the reward found in two specified containers (see below). E1 also asked O or E2 to prevent the cat from eating the rewards that were in the other two

---

[1] A cat café is a place where visitors can interact with the resident cats.

Please cite this article in press as: Takagi, S., et al., Use of incidentally encoded memory from a single experience in cats. Behav. Process. (2016), http://dx.doi.org/10.1016/j.beproc.2016.12.014

containers. Thus, the cat saw and usually tried to eat all four rewards but was allowed to eat only two of them. After the cat visited all containers, E1 asked O or E2 to take the cat out of the test room. The Exposure phase took about 40 s. to complete. The containers the cat ate from are hereafter referred to as "baited-eaten" containers and those not eaten from are "baited-uneaten" containers. The combinations of the location of baited-eaten containers (six) and the visiting order (two: clockwise or counterclockwise) made a total of 12 possible Exposure phase sequences. Each cat received one trial of a randomly selected sequence.

2.1.3.2. Delay phase. The Delay phase lasted about 15 min (range: 12–23 min), which is thought to be beyond working memory capacity of cats for retaining such an episode (Fiset and Doré, 2006). E1 replaced the containers with the identical set in exactly the same layout, but to control for olfactory cues no food was placed in any container. During the Delay phase cats participated in various other experiments related to physical inference and social understanding, which conceivably interfered with their working memory for preceding events. Cats were able to move freely between these collateral tests but were not allowed to enter the original test room.

2.1.3.3. Test phase. Either O or E2 took the cat to the start point in front of the containers, and simply released it to explore freely. Experimenter 3 (E3), ignorant of the visiting sequence in the Exposure phase, recorded the cat's behavior on video. The trial ended when the cat (1) showed no further exploration of any container for 30 s, or (2) returned to the start point. We scored "no choice" when a cat explored no container for at least 3 min, and stopped recording. To prevent inadvertent cueing, E2 turned away immediately after releasing the cat at the start point. Both O and E3 refrained from making eye contact or responding to the cat in any way that might influence the cat's behavior.

2.1.4. Analysis

The videos of the Test phase were analyzed using Power Director 10 (Cyber Link, Taiwan) at a rate of 30 frames per sec. Cats failing to visit any containers in Test phase were excluded. We coded the first and second visits to a container along with the duration of exploration of each container. We defined the first visit as the container first explored by the cat. A coder, blind to the sequence, coded the visits by each cat and the total number of frames during which the cat explored each container. Exploration was defined as looking into or sniffing a container with no more than 5 cm (estimated) between container and cat's nose. To check inter-observer reliability, one of the authors, blind to the sequence, coded a randomly chosen 25% of the videos. The correlation between the two coders was excellent both for the order of visiting (Pearson's $r = 1$, $n = 20$, $p < 0.01$) and time spent exploring each container (Pearson's $r = 0.97$, $n = 20$, $p < 0.01$).

We pooled the data from house cats and café cats because there were no differences in any aspects. For first visits, we used a two-sided binomial test to assess whether the number of cats visiting a "baited-uneaten" container was different from chance level (1/2). We used paired *t*-tests to examine whether the duration of exploration was different between "baited-eaten" and "baited-uneaten" containers. We first included age and sex as fixed factors in a LMM. However, there was no significant effect of age in exploration patterns. As for sex, males explored baited-uneaten containers longer than baited-eaten ones, probably because of the difference in the number of subjects (29 males and 16 females). Therefore we excluded them as fixed factors. All statistical analyses were conducted with R version 3.2.0 (R Core Team, 2015). The alpha level was set at 0.05. Four cats were excluded from the analysis because they did not visit any container, leaving a total of 45 cats.

Table 1
The number of cats visiting each container in Experiment 1.

	First choice	Second choice
Baited-eaten	17	18
Baited-uneaten	28	20

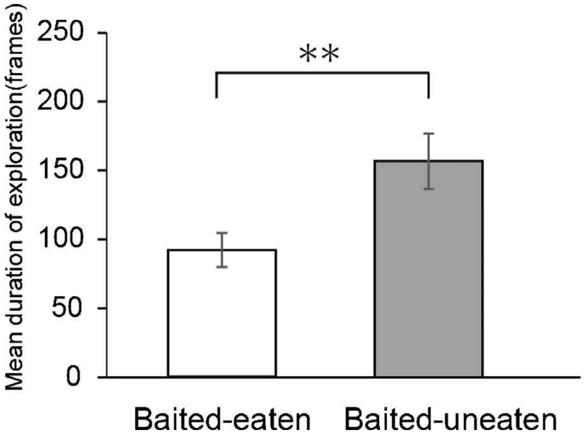


Fig. 2. Mean duration of exploration of the "Baited-eaten" and "Baited-uneaten" containers in Experiment 1(** $p < 0.01$).

3. Results and discussion

Seventeen of 45 cats visited one of the baited-eaten containers and 28 cats visited one of the baited-uneaten containers as their first choice in the Test phase (Table 1); this result was not significantly different from chance ($p = 0.135$, binomial test). There was no difference in the number of cats visiting the baited-eaten and baited-uneaten containers as their second choice. (Table 1). Twenty-five cats simply moved to an adjacent container from the one they visited first; ten revisited the same container, three visited the other containers, and seven left after the first visit.

The mean duration of exploration of baited-eaten and baited-uneaten containers was 91 and 156 frames, respectively (Fig. 2). This difference was statistically significant (paired *t*-test, $t(44) = 3.57$, $p < 0.01$).

Cats spent more time exploring baited-uneaten containers than baited-eaten containers. This result suggests that they spontaneously retrieved and used their memory of their previous experience, and it is consistent with our second prediction; the first prediction based on operant conditioning was not supported.

However, contrary to our second prediction, visiting baited-uneaten containers first was not a statistically significant trend. These results might be explained by individual differences in foraging strategies between cats, with some visiting a "baited-uneaten" container first ("win-shift strategy") and others approaching the "baited-eaten" container first ("win-stay strategy"). The former strategy is adaptive when food sources are dispersed (e.g., Olton and Schlosberg, 1978). However, we suspect that the latter strategy may be more typical of cats fed regularly from a specific container at a specific location. The fact that many cats probably switched from the latter strategy implies adaptive behavioral flexibility based on retrieval of an incidentally encoded memory.

Thus, cats in Experiment 1 seem to have retrieved "where" information from memory of an incidentally encoded previous experience. One may wonder which stimulus dimension was retrieved: the location of the container, its appearance, or both. However, we use "where" in the broad sense as the receptacle holding the target item. When people talk about episodic memory, "where" often denotes a place such as a museum, a park, or a theatre, places with different appearances. Our aim was discover

Please cite this article in press as: Takagi, S., et al., Use of incidentally encoded memory from a single experience in cats. Behav. Process. (2016), http://dx.doi.org/10.1016/j.beproc.2016.12.014

whether cats retrieve and utilize incidentally encoded information from a single past experience, not to identify the exact contents of what they retrieve.

Experiment 1 showed that cats spontaneously retrieved “where” memory of baited-uneaten containers in an unexpected situation. In Experiment 2, we asked whether cats could also retrieve “what” information from a single experience.

4. Experiment 2

4.1. Methods

4.1.1. Subjects

Fifty-eight domestic cats (34 males and 24 females) participated in Experiment 2. Thirty-three were house cats and 25 were kept at four cat cafés. Their ages ranged from 3 months to 15 years (mean: 4.7 years, SD: 3.9 years). Eight cats had participated in Experiment 1, which took place at least 5 months earlier.

4.1.2. Apparatus

As in Experiment 1, two identical sets of four open containers were prepared for each cat. Two pieces of each cat’s favorite food were used as rewards. We used a black hairpin (5 cm) as a neutral, nonedible object.

4.1.3. Procedure

4.1.3.1. Exposure phase. This phase was the same as in Experiment 1 except for two modifications (Fig. 1). First, E1 deposited one pieces of food in each of two containers and the neutral object in another container. The fourth container remained empty. Second, E1 asked O or E2 to allow the cat to eat one of the two food rewards. The combination of locations of allowed and prohibited rewards, neutral object, empty container (24) and visiting order (two: clockwise or counterclockwise) made 48 sequences in total. One sequence was randomly allotted to each cat.

4.1.3.2. Delay phase. This phase was exactly the same as in Experiment 1, and lasted about 15 min (range: 11–22 min).

4.1.3.3. Test phase. This phase was conducted exactly as in Experiment 1.

4.1.4. Analysis

For the first and second visits we used a two-sided binomial test to see if the number of cats visiting each container was different from chance (1/4). For duration of exploration, we used a repeated-measures ANOVA to examine whether duration of exploration was different among the containers. As there were no significant effects of either age or sex in exploration patterns, we excluded them as fixed factors. We conducted multiple comparisons using the Shaffer procedure. Fifteen cats were excluded from the analyses because they never visited the containers, leaving a total of 46 in the analyses.

To check inter-observer reliability, one author who was blind to the sequence coded a randomly chosen 25% of the videos. The correlation between the two coders was excellent both for order of visiting (Pearson’s $r = 1$, $n = 44$, $p < 0.01$) and time spent exploring the container (Pearson’s $r = 0.99$, $n = 44$, $p < 0.01$).

5. Results and discussion

Eighteen of 46 cats visited the baited-uneaten containers as their first choice, which was significantly above chance level (1/4) ($p = 0.03$, binomial test). Eleven, 8, and 9 cats first visited the baited-eaten, object, and empty containers, respectively (Table. 2). There was no difference in the number of cats visiting each container as their second choice. Twenty-nine cats simply moved to the container adjacent to the one they visited first, ten revisited the same container, two visited the other containers, and five approached no second container.

Table 2
The number of cats visiting each container in Experiment 2 (* $p < 0.05$).

	First choice	Second choice
Baited-eaten	11	12
Baited-uneaten	18*	12
Object	8	9
Empty	9	7
		*$p < 0.05$

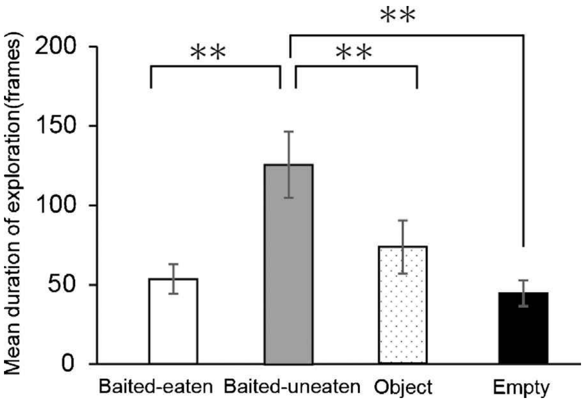


Fig. 3. Mean duration of exploration of the containers in Experiment 2 (** $p < 0.01$).

Cats explored the baited-uneaten container for longest of all containers, with a mean duration of 125 frames (Fig. 3), compared with 53, 73, and 43 frames for the baited-eaten, object, and empty container, respectively. The difference in duration of exploration of the four containers was significant (F (3, 132) = 9.52, $p < 0.01$). Post-hoc analyses revealed significant differences between baited-uneaten and baited-eaten containers (t (44) = 3.93, $p < 0.01$), baited-uneaten and object containers (t (44) = 3.06, $p < 0.01$), and baited-uneaten and empty containers (t (44) = 3.97, $p < 0.01$).

Cats visited first and spent more time exploring the only baited-uneaten container in the Test phase. This suggests that their incidental memory involves “what” as well as “where” information about previous experiences. This tendency again accords with our prediction based on incidentally encoded memory, and does not support the prediction based on an association between container and reward.

6. General discussion

We asked whether cats could retrieve and utilize memory incidentally encoded during a previous experience. In Experiment 1, cats spent more time exploring baited-uneaten containers in an unexpected test after eating two of four pieces of food, although their tendency to visit these containers first failed to reach significance. Their differential exploration shows that cats can retrieve incidentally encoded “where” information. In Experiment 2, we asked whether cats could retrieve not only “where” information but also “what” information from a single past event. Specifically, we used two containers each baited with a piece of food, one container with a nonedible item, and one empty container. In the unexpected test cats first visited and preferentially explored the only baited-uneaten container, suggesting that they retrieved and utilized incidentally encoded memory involving “what” as well as

Please cite this article in press as: Takagi, S., et al., Use of incidentally encoded memory from a single experience in cats. Behav. Process. (2016), http://dx.doi.org/10.1016/j.beproc.2016.12.014

"where" information in an integrated fashion. Therefore, our results demonstrate that cats may possess an incidental memory system, similar to dogs and humans.

We can rule out inadvertent cueing by experimenters or the owner as a possible explanation of these results. First, the experimenter who recorded the videos (E3) did not witness the Exposure phase and so was ignorant which containers were baited or uneaten. Second, although O and E2 who knew from which containers cats had previously eaten, O was asked to refrain from trying to influence the cat's behavior in any way (very few cats looked at the owner), and E2 turned away immediately after releasing the cat. We can also eliminate potential odor cues as a confounding factor, as the containers used in the Exposure phase were replaced with new, identical but empty ones during the Delay phase.

Interestingly, we found no behavioral differences between house cats and café cats, despite differences in the way the two groups are fed. The former regularly experience empty food containers after eating, whereas the latter rarely do because their food containers usually have more food than the cats can eat. In the case of dogs, how people interacted with them in daily life has been shown to affect their behavior. Fujita et al. (2012) tested two groups of dogs, in Japan and Germany. The Japanese dogs more reliably visited the baited-uneaten container than did German dogs, which the authors suggested might be due to a difference in how dogs were trained. Compared to Japanese, German owners tend to train dogs strictly to obey commands. In the Exposure phase German dogs might therefore have learned that the baited-uneaten container was prohibited. However, cats are less often trained to obey commands, at home or in cafes.

Despite slight differences between cats in this study and dogs in a previous study regarding first visit performances and effects of their daily routine, like dogs, cats were more likely to explore containers they did not previously eat from. The memory system incorporating this kind of incidentally encoded memory trace may be shared among carnivores, or more generally mammals (Mercado et al., 1998; Zhou et al., 2012). Future studies should investigate for how long the incidental memory system can retain information about a specific experience. The delay in this study was around 15 min; however, our casual impression is that cats may remember for much longer periods. Furthermore, whether cats integrate "when" information as well as "what" and "where" in their retrieval of incidental memory of past experiences is an important question for future research.

In closing, we note that the method used here could be valuable for comparative studies, as it requires no training and is simple to conduct. A clearer picture of how this kind of memory system has evolved and its distribution may emerge from testing species from a variety of ecological and phylogenetic backgrounds.

7. Conclusion

We demonstrated that cats have an ability to retrieve and utilize incidentally encoded "what" and "where" information from a single past experience.

Compliance with ethical standards

This study adhered to the ethical guidelines of Kyoto University, and was approved by the Animal Experiments Committee of the Graduate School of Letters, Kyoto University.

Competing interests

The authors declare no conflicts of interest.

Acknowledgments

This study was financially supported by the Grant-in-aid for Scientific Research (KAKENHI) Nos. 25240020, 26119514, 16H01505, and 16H06301 to K. Fujita from the Japan Society for the Promotion of Science (JSPS), No. 25118003 to A. Saito, No. JP16J08691 to H. Chijiiwa, and No. JP16J1034 to M. Arahori. The authors acknowledge with thanks all owners and cats who volunteered in this study. The authors also wish to thank James R. Anderson for editing the article.

References

Babb, S.J., Crystal, J.D., 2006. Episodic-like memory in the rat. Curr. Biol. 1, 1317–1321.
Clayton, N.S., Dickinson, A., 1998. Episodic-like memory during cache recovery by scrub jays. Nature 395, 272–274.
Dere, E., Huston, J.P., Silva, M.A.D.S., 2005. Episodic-like memory in mice: simultaneous assessment of object, place and temporal order memory. Brain Res. Protoc. 16, 10–19.
Feeney, M.C., Roberts, W.A., Sherry, D.F., 2009. Memory for what, where, and when in the black-capped chickadee (*Poecile atricapillus*). Anim. Cogn. 12, 767–777.
Ferkin, M.H., Combs, A., del Barco-Trillo, J., Pierce, A.A., Franklin, S., 2008. Meadow voles (*Microtus pennsylvanicus*) have the capacity to recall the what, where, and when of a single past event. Anim. Cogn. 11, 147–159.
Fiset, S., Doré, F.Y., 2006. Duration of cats' (*Felis catus*) working memory for disappearing objects. Anim. Cogn. 9, 62–70.
Fujita, K., Morisaki, A., Takaoka, A., Maeda, T., Hori, Y., 2012. Incidental memory in dogs (*Canis familiaris*): adaptive behavioral solution at an unexpected memory test. Anim. Cogn. 15, 1055–1063.
Galvan, M., Vonk, J., 2015. Man's other best friend: domestic cats (*F. silvestris catus*) and their discrimination of human emotion cues. Anim. Cogn. 19, 193–205.
Hoffman, M.L., Beran, M.J., Washburn, D.A., 2009. Memory for what, where, and when information in rhesus monkeys (*Macaca mulatta*). J. Exp. Psychol.: Anim. Behav. Process. 35, 143–152.
Jozet-Alves, C., Bertin, M., Clayton, N.S., 2013. Evidence of episodic-like memory in cuttlefish. Curr. Biol. 23, R1033–R1035.
Martin-Ordas, G., Haun, D., Colmenares, F., Call, J., 2010. Keeping track of time: evidence for episodic-like memory in great apes. Anim. Cogn. 13, 331–340.
Menzel, C.R., 1999. Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan troglodytes*) after extended delays. J. Comp. Psychol. 113, 426–434.
Mercado, E., Murray, S.O., Uyeyama, R.K., Pack, A.A., Herman, L.M., 1998. Memory for recent actions in the bottlenosed dolphin (*Tursiops truncatus*): repetition of arbitrary behaviors using an abstract rule. Anim. Learn. Behav. 26, 210–218.
Merola, I., Prato-Previde, E., Marshall-Pescini, S., 2012a. Social referencing in dog-owner dyads? Anim. Cogn. 15, 175–185.
Merola, I., Prato-Previde, E., Marshall-Pescini, S., 2012b. Dogs' social referencing towards owners and strangers. PLoS One 7, e47653.
Merola, I., Prato-Previde, E., Lazzaroni, M., Marshall-Pescini, S., 2014. Dogs' comprehension of referential emotional expressions: familiar people and familiar emotions are easier. Anim. Cogn. 17, 373–385.
Merola, I., Lazzaroni, M., Marshall-Pescini, S., Prato-Previde, E., 2015. Social referencing and cat–human communication. Anim. Cogn. 18, 639–648.
Miklósi, Á., Pongrácz, P., Lakatos, G., Topál, J., Csányi, V., 2005. A comparative study of the use of visual communicative signals in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. J. Comp. Psychol. 119, 179–186.
Olton, D.S., Schlosberg, P., 1978. Foodsearching strategies in young rats: winshift predominates over win-stay. J. Comp. Physiol. Psychol. 92, 609–618.
Pahl, M., Zhu, H., Pix, W., Tautz, J., Zhang, S., 2007. Circadian timed episodic-like memory-a bee knows what to do when, and also where. J. Exp. Biol. 210, 3559–3567.
Core Team, R., 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL : https://www.R-project.org/.
Roberts, W.A., Feeney, M.C., MacPherson, K., Petter, M., McMillan, N., Musolino, E., 2008. Episodic-like memory in rats: is it based on when or how long ago? Science 320, 113–115.
Singer, R.A., Zentall, T.R., 2007. Pigeons learn to answer the question "where did you just pick?" And can report peck location when unexpectedly asked. Learn. Behav. 35, 184–189.
Suddendorf, T., Corballis, M.C., 1997. Mental time travel and the evolution of the human mind. Genet. Soc. Gen. Psychol. Monogr. 123, 133–167.
Suddendorf, T., Corballis, M.C., 2007. The evolution of foresight: what is mental time travel, and is it unique to humans? Behav. Brain Sci. 30, 299–313.
Tomonaga, M., Kaneko, T., 2014. What did you choose just now? Chimpanzees' short-term retention of memories of their own behavior. PeerJ 2, e637.
Tulving, E., 1972. Episodic and semantic memory. In: Tulving, E., Donaldson, W. (Eds.), Organization of Memory. Academic Press, New York, pp. 382–403.
Tulving, E., 2002. Episodic memory: from mind to brain. Annu. Rev. Psychol. 53, 1–25.

Tulving, E., 2005. Episodic memory and autonoesis: uniquely human? In: Terrace, H.S., Metcalfe, J. (Eds.), The Missing Link in Cognition: Origins of Self-reflective Consciousness. Oxford University Press, pp. 3–56.

Zentall, T.R., Clement, T.S., Bhatt, R.S., Allen, J., 2001. Episodic-like memory in pigeons. Psychon. Bull. Rev. 8, 685–690.

Zhou, W., Hohmann, A.G., Crystal, J.D., 2012. Rats answer an unexpected question after incidental encoding. Curr. Biol. 22, 1149–1153.

Zinkivskay, A., Nazir, F., Smulders, T.V., 2009. What–where–when memory in magpies (Pica pica). Anim. Cogn. 12, 119–125.

Please cite this article in press as: Takagi, S., et al., Use of incidentally encoded memory from a single experience in cats. Behav. Process. (2016), http://dx.doi.org/10.1016/j.beproc.2016.12.014