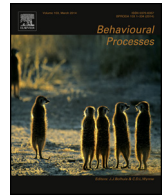




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Use of incidentally encoded memory from a single experience in cats

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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.

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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 autoeotic 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.

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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 Expo-

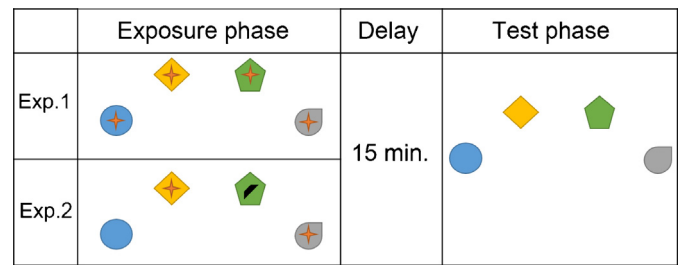


Fig. 1. The setup and the procedure of Experiments 1 and 2. In the Exposure phase, cats were directed to the four open containers. Stars represent the reward in both experiments, and the black trapezoid represents the neutral object in Experiment 2. All containers were baited in Experiment 1, and cats 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.

sure phase, they should first visit containers from which they had not previously eaten, or explore them more.

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.

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