RECOLLECTION OF WHAT-WHERE-WHICH MEMORY IN DEGUS (*OCTODON DEGUS*)

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To examine if a feature of episodic-like memory reported in rats is shared with other species, we investigated whether degus would form an integrated memory of object (what), place (where), and context (which). We used two E-shaped mazes with different contexts regarding the wall and the floor. Degus were entered into the middle arm and first explored the maze with two trial-unique objects placed at each end of the backbone of the E, with their location reversed between contexts. After being habituated to one of the objects in the holding cage, the degus re-explored the maze. Subjects explored the non-habituated object in these baseline trials. In the critical test, the objects were located at the end of the outer arms of the maze. Degus went into the arm where they expected the non-habituated object significantly more often than the other. This result suggests recollection of an integrated What-Where-Which memory.

Key words: Degus *Octodon degus*, Episodic-like memory, spontaneous object recognition, recollection, occasion setter

INTRODUCTION

Octodon degus

Degus (*Octodon degus*) are a diurnal, group-living hystricomorph rodent species commonly found in Chile (Woods & Boraker, 1975). Because of their social nature, they have received increasing attention in research on social behavior (e.g., Lacey & Ebensperger, 2008; Ebensperger & Hayes, 2016; Lee, 2004; Ardiles et al., 2013, for review). They are frequently used as an animal model in several topics including circadian rhythms (e.g., Lee, 2004), hippocampus function (e.g., Uekita & Okanoya, 2013), and Alzheimer disease (e.g., Ardiles et al., 2012, 2013; Rivera, Inestrosa, & Bozinovic, 2016).

However, non-social cognitive abilities of degus are in general poorly known, though some reports suggest both competence and limitations in several situations (e.g., tool

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use: Okanoya, Tokimoto, Kumazawa, Hihara, & Iriki, 2008; Kumazawa-Manita, Hama, Miyawaki, & Iriki, 2013; spatial cognition: Popović, Madrid, Rol, Caballero-Bleda, & Popović, 2010; Uekita & Okanoya, 2011; Kumazawa-Manita et al., 2013). Further studies of various non-social cognitive abilities in degus would be valuable; in view of their role as a model of Alzheimer disease, their memory processes may be especially worthy of attention. In this study, we investigated a kind of episodic memory in degus. As degus are becoming more popular as a companion animal, though not domesticated, information about memory might also be useful to owners of this species.

Mental time travel and episodic memory in nonhuman animals

Episodic memory is referred as the memory of one's private past experience; it is a part of declarative memory but distinguished from semantic memory (Tulving, 1972, 1983). It has recently been argued that episodic memory constitutes the retrospective part of mental time travel (MTT), combined with future planning as prospective MTT (Suddendorf & Corballis, 1997). Because it may include *conscious* recollection of past events, whether episodic memory (and furthermore MTT) is uniquely human or not has been a highly controversial topic for around two decades (Suddendorf & Busby, 2003; Suddendorf & Corballis, 2007; Suddendorf, Addis, & Corballis, 2009; Tulving, 2001, 2002, 2005), since Clayton and Dickinson (1998) demonstrated one of the key features of episodic memory in scrub jays. Various behavioral and observational criteria that do not require language or "autonoetic consciousness" (Tulving, 2002, 2005) were established in comparative cognitive research (reviewed by Allen & Fortin, 2013; Crystal, 2010; Feeney & Roberts, 2012; Raby & Clayton, 2012; Zentall, 2013, but see Suddendorf & Corballis, 2010).

One major criterion is whether animals can retrieve memories that integrate content (what), place (where), and temporal context (when) (Tulving, 1972). Behavior that matches this criterion is often called What-Where-When (WWW) or episodic-like memory (e.g., Clayton, Bussey, & Dickinson, 2003). Numerous studies have that various nonhuman species can satisfy this criterion, including birds (scrub jays: Clayton & Dickinson, 1998; magpies: Zinkivskay, Nazir, & Smulders, 2009; chickadees: Feeney, Roberts, & Sherry, 2009; pigeons: Skov-Rakette, Miller, & Shettleworth, 2006; Meyers-Manor, Overmier, Hatfield & Croswell, 2014; hummingbirds, González-Gómez, Bozinovic & Vásquez, 2011), rodents (rats: Babb & Crystal, 2006; Roberts et al., 2008; mice: Dere, Huston, & Silva, 2005; meadow voles: Ferkin, Combs, delBarco-Trillo, Pierce, & Franklin, 2008), primates (rhesus macaques: Hoffman, Beran, & Washburn, 2009; great apes: Martin-Ordas, Haun, Colmenares, & Call, 2010), and invertebrates (honeybees: Pahl, Zhu, Pix, Tautz, & Zhang, 2007; cuttlefish: Jozet-Alves, Bertin, & Clayton, 2013).

Another criterion, which could distinguish episodic from semantic memory, is the incidental nature of the encoded information (see Zentall, Clement, Bhatt, & Allen, 2001; Zentall, 2013), i.e., whether animals can recall what they encoded incidentally or unpurposefully when unexpectedly asked. Whether animals can correctly answer an unexpected question about their past has received relatively less attention, but several species have been studied including birds and mammals in both short-term (pigeons: Zentall et al., 2001; Singer & Zentall, 2007; Zentall, Singer, & Stagner, 2008; chimpanzees:

Tomonaga & Kaneko, 2014) and long-term memory task (rats: Zhou, Hohmann, & Crystal, 2012; dogs: Fujita, Morisaki, Takaoka, Maeda, & Hori, 2012).

From When to Which: Alternative definition in What-Where-When memory

Regarding the former nature of episodic memory, or What-Where-When memory, the precise characteristics of the “when” component has been a topic of debate in particular. In some studies, for example, “when” information was not as robustly retrieved in WWW tests as in Clayton and Dickinson (1998) (rats: Bird, Roberts, Abroms, Kit, & Crupi, 2003; rhesus macaques: Hampton, Hampstead, & Murray, 2005). Some propose that even if animals remember temporal information about an event, it is necessary to distinguish between “*how long ago*” and “*when*” the event happened. Based on radial-maze performances in rats, Roberts et al. (2008) suggested that the nature of temporal information that rats retrieve may be “*how long ago*” or the length of the duration, not “*when*” or a particular moment in the past. By contrast, Zhou and Crystal (2009) stated that animals (rats in this case) retrieve the specific time of day. The studies cited above, however, may not completely eliminate alternative non-episodic accounts (e.g., the relative strength of the memory trace or the possibility of semantic memory).

Eacott and colleagues proposed another view about “when” information. They suggested that “when” is replaceable with “which occasion,” or environmental context, as these two are functionally equivalent as an occasion setter in distinguishing a unique past event from others (Eacott & Easton, 2010, 2012, Easton & Eacott, 2008). With slight modification of the spontaneous object recognition task (Ennaceur & Delacour, 1988), they showed that rats formed an integrated memory of the object (what), its position (where), and its context (which) in two open fields with different contexts (Eacott & Norman, 2004). Because of the relative ease of experimental control, this task involving “which” has been successfully used as an alternative paradigm to test nonverbal episodic-like memory in various species including humans (Yukatan minipigs: Kouwenberg, Walsh, Morgan, & Martin, 2009; human children: Newcombe, Balcomb, Ferrara, Hansen, & Koski, 2014; hummingbirds: Jelbert, Hurly, Marshall, & Healy, 2014; zebrafish: Hamilton et al., 2016).

The studies above demonstrated *recognition* of WWW information. Eacott, Easton, and Zinkivskay (2005) showed that rats not only recognized, but *recalled* What-Where-Which information that they previously experienced (see also Dere, Huston, & Silva, 2007). Instead of an open field (Eacott & Norman, 2004), they used two E-shaped mazes with different contexts to conduct the same What-Where-Which object recognition task. Subjects always started to explore the maze from the middle arm of the E. In the critical test phase, objects were located at each end of side arm of the E, being non-visible at the choice point (i.e., the end of the middle arm). The subjects chose the arm containing the unfamiliar object in a particular context even when it was out of their sight. These results suggest that the rats’ performance was not explainable by non-episodic clues such as object familiarity or change detection derived from visual information at choice, but was more likely to result from recollection of the rat’s past experience. In addition, recall was impaired but recognition (direct exploration of the same object when visible) was intact in rats with fornix lesions, suggesting different neural mechanisms underlying these memory

processes (Easton, Zinkivskay, & Eacott, 2009).

To our knowledge, no studies have tested other species with this E-maze paradigm. Here we report that degus also show recollection of What-Where-Which memory in a task similar to those used by Eacott et al. (2005). Previous studies (e.g., Uekita & Okanoya, 2011; Ardiles et al., 2012) have shown that degus preferentially explore novel or unfamiliar objects, as do rats and other rodents. Therefore, we predicted that in the same task as Eacott et al. (2005) degus would preferentially re-explore relatively non-habituated objects that were not presented in their holding cage after the first exploration. Our behavioral measures included (1) direction of the first turn (into the arm with the habituated or non-habituated object) before the objects became visible, and (2) the duration of exploration of each object in context. The former was a direct index of recall memory because no visual information about the objects is available at choice. The latter was to confirm validity of the task as novelty exploration.

METHODS

Subjects

Eight adult degus, 4 males (Pazu, Jill, Gri, and Mao) and 4 females (Lara, Iyo, Iris, and Meg), all between 1 and 3 years old, participated in the experiment (see details in Table 1). Seven subjects were housed individually or in pairs in polycarbonate cages (26 cm (W) $\times$ 42 cm (L) $\times$ 20 cm (H)). One subject, Iris, was housed in a group of 4 in a transparent acrylic vivarium (80 cm (W) $\times$ 50 cm (L) $\times$ 40 cm (H)) with two wooden nests, two running wheels, two food cups and a water bottle. Wood shavings served as bedding for all degus. No housemate degus participated. Food (Brisky degu pellet, oriental yeast RC4, carrots, and timothy hay) and water were available *ad libitum*. The housing room was kept at $22 \pm 1^\circ\text{C}$ and illuminated on a 12:12 light-dark cycle (lights on at 5:00). All subjects had participated in several behavioral experiments unrelated to the present study, investigating vocal learning, olfactory discrimination and so on.

The care and use of degus adhered to the guidelines of the Graduate School of Letters, Kyoto University, and the experiment was conducted with the approval of the Animal Experiment Committee of the same school.

Apparatus (Fig. 1)

We used two E-shaped mazes (37 cm (W) $\times$ 60 cm (L) $\times$ 30 cm (H)), made of corrugated plastic cardboard, similar to the one used in Eacott, et al. (2005). The mazes were covered with a clear acrylic panel to prevent subjects from jumping out. These mazes were the same size and shape, whereas the color of wall and floor, and the materials of floor were different to create different contexts; one was white with a smooth floor, the other was gray with a wire mesh-covered floor (henceforth referred to as “white” and “gray” contexts, respectively). We video-recorded the behavior of subjects in the maze from above.

Pairs of various small objects were placed in the mazes. The objects were made of plastic, metal, ceramic, glass, wood, or hard gum. We glued a white square plate (8 $\times$ 8 cm, made of corrugated plastic cardboard) to the bottom of the object. We used 50 sets of two different object pairs in total. We changed the objects every day; that is, the objects were trial-unique. To show the objects to degus in the holding cage (described below), we prepared duplicates of each set.

We prepared a plastic box (45 cm (W) $\times$ 30 cm (L) $\times$ 35 cm (H)) for each individual. This was used as a holding cage in which the degus waited for their turn in the experimental room. Wood shavings were used as a floor covering.

Procedure

The procedure consisted of 5 (or 6) phases in total. Habituation and Pretest trials 1 to 3 involved pretesting or habituation to the experimental environment. Four subjects (Gri, Mao, Iris and Meg) received additional experience in Pretest trials 3, whereas the other four (Pazu, Jill, Lara, and Iyo) did not (see Table 1).

Fig. 1. *Top:* a schematic view of the apparatus with different contexts. *Bottom:* the floor of each apparatus. The floor was covered with wire mesh in the gray apparatus, not in the white. See Text for details.

The Recognition Test was to confirm the validity of the experimental setup before the critical Recall Test. The subjects were always released from the end of the middle arm of the E maze. We cleaned the mazes with wet and dry tissue papers to erase odors before every trial.

Habituation to the mazes (2 days) We first habituated subjects to each maze for 2 days. On the first day, subjects explored one of the mazes for 30 min and on next day they explored the other. No objects were placed in the mazes during habituation. The order of experiencing the mazes was counterbalanced among subjects.

Pretest trials 1 (2 days) We placed objects in each maze. This phase was for the degus to learn that the positions of objects in the same context on each day were stable. On the first day, subjects first explored one maze in which two different objects were located at either end of the backbone of the maze, for 5 min. Then after spending 5 min in their holding cage, they were returned to the same maze for another 5 min. This procedure was then repeated for the other maze. Identical objects were used for both mazes but their placements were reversed. This entire procedure was repeated on the second day with a new set of objects and with the order of the mazes reversed (e.g., Day 1: white-white-gray-gray, Day 2: gray-gray-white-white, with the delay in the holding cage inserted between the explorations in each maze). The context that each degu experienced first was counterbalanced among subjects.

Pretest trials 2 (2 days) These trials were for the degus to learn the stability of the object positions in the same context on a given day irrespective of the order of exploration of the different-context mazes. Subjects experienced the sequence of exploration in the two contexts, but the exploration in the second context was inserted between the two explorations of the same context. On Day 1, subjects first explored one maze with objects for 3 min. Then, after 3 min in the holding cage, they explored the other maze for 3 min. Finally, the subjects re-explored the first maze. On Day 2, the subjects experienced the entire sequence in the reversed order (e.g., gray-white-gray after white-gray-white context with inserted delay). The order of the sequence was counterbalanced among subjects.

Pretest trials 3 (2 days; 4 subjects only) In these trials, the basic procedure was the same as in Pretest trials 2, but for re-exploration we moved the objects to the end of each arm at the end of the backbone of the E maze, to allow the subjects to habituate to this novel arrangement before the subsequent Recall test, which was given to 4 of the 8 degus. For this reason, we conducted these trials between the Recognition Test and the Recall Test.

Recognition Test (8 days; Fig. 2a) We conducted the Recognition Test, a standard object-in-place test,

Fig. 2. Examples of a trial in test phases. **a:** Recognition Test. The letters A (A') and B (B') represent habituated and non-habituated objects, respectively. **b:** Recall Test and Probe Test. The dotted line shown in the final exploration in the white context is the assumed line for the behavioral criterion of the choice (when subjects go through the line, we deemed it as their choice). The order of the context sequence (white-gray-white in this figure) was counterbalanced among subjects, and reversed every trial. See text for details.

as a baseline to compare performance with those in the subsequent Recall Test. Subjects explored in the same sequence as in Pretest trials 2, with the exception of the second delay period in the holding cage. First, the duration of the second delay was 8 min rather than 3 min. Second, the subjects were exposed to one of the objects (of the duplicated set) in their holding cage. The exploration time in each maze and the duration of the first delay remained at 3 min. The entire sequence was given once per day and the subjects were tested for 8 days in total. The order of the sequence was reversed each day, and counterbalanced among subjects. Due to exposure to one of the objects in the holding cage (habituation), the other object should be more novel to the degus compared to the habituated object. It was therefore predicted that subjects would preferentially explore the non-habituated object more than the habituated one in the final exploration period.

Recall Test (32 days) and Probe Test (4 days; Fig. 2b) This phase was almost the same as the Recognition Test, but the objects were moved to the end of each arm for re-exploration in the maze the degus first encountered. First, subjects explored one maze with objects at either end of its backbone for 3 min. Then after the first 3-min delay in the holding cage, the subjects explored the other maze having the same objects located in the reversed positions for 3 min. In the second delay after the second exploration, subjects were exposed to one of the objects in their holding cage for 8 min. Finally, the subjects re-explored the first maze with the objects moved to the end of each arm for 3 min. Importantly, the objects were not visible from the middle point of the backbone. We repeated this sequence for 32 days, 1 trial per day. The order of the sequence was reversed each day (e.g., gray-white-gray after white-gray-white), and counterbalanced among subjects.

The probe trials were conducted in the first context after every 8th test trial. In probe trials no objects were placed in the maze, so that any possibility of olfactory cues was eliminated.

Data Analysis

We analyzed the data from the Recognition Test and the Recall Test including probe trials. First, we recorded the direction of the subjects' first turn from the start arm in the final exploration period of each trial. We defined a turn as the snout poking beyond the assumed line from which the objects were visible from the center arm (see Fig. 2b). We compared the mean proportion of first turns to chance level (50%) using a one-sample t-test. The first turn in the Recall Test was the principal measure, because it suggests recall, not recognition, of the location of the objects by means of the integrated What (object)-Where (left/right)-Which (context) memory.

Second, we measured the duration of exploration of each object from the video recording at a rate of 30 frames per sec, using Power Director 9 software (Cyberlink). We defined exploration as touching the object with the snout or forepaw, biting or sniffing. We excluded other behaviors near the object such as just climbing or running around. To reduce the effect of variability over time and to extract earlier responses, we analyzed duration data in 1-min units (e.g., Dix & Aggleton, 1999). We used two-way repeated-measures analysis of variance (ANOVA) with object type (habituated, non-habituated) and test interval (0–1, 1–2, and 2–3 min) as within-subject variables. If the interaction was significant, we conducted post-hoc tests using Shaffer’s multiple comparisons procedure. Because the assumption of sphericity was not met, we applied Greenhouse-Geisser correction.

In the Probe Test, we only recorded the first turn, similar to that used in the analysis of the Recognition Test and the Recall Test. Because there was no object in the E-maze, we recorded a turn if the degu turned to the arm that might be expected to have the habituated or non-habituated object.

As there was no difference in the behavior of degus that received Pretest trials 3 or not, we collapsed the data from the two groups. All statistical analyses were run in R version 3.2.3. (R Development Core Team, 2015).

RESULTS

Recognition Test (Fig. 3)

Choice at the first turn Fig. 3a shows the proportion of first turns to the arm with the non-habituated object in the Recognition Test. Most subjects turned first to the arm with the non-habituated object in more than half of the trials; the mean proportion (67.2%) was significantly higher than chance (50%) (one-sample t-test, $t(7) = 5.23, p < 0.01$).

Duration of exploration Fig. 3b shows the mean duration of exploration of non-habituated and habituated objects in the Recognition Test. A two-way ANOVA revealed a

Table 1. A summary of subject information and individual performances.

Individual information					Results (1st turn to non-habituated object; chance = 50%)		
name	sex	age in month	housing	Participation in Pretest trials 3	Recognition test (8 trials)	Recall test (32 trials)	Probe test (4 trials)
Pazu	m	13	paired	No	4	17	2
Jill	m	18	single	No	6	16	2
Lara	f	17	paired	No	6	17	2
Iyo	f	21	single	No	6	20	4
Gri	m	35	single	Yes	5	20	3
Mao	m	28	single	Yes	5	17	3
Iris	f	32	group	Yes	6	17	1
Meg	f	28	single	Yes	5	19	2

Note. Letters (m or f) in sex column stand for male or female, respectively. The numbers in age column stand for age in months at the beginning of the experiment. The results columns show the number of the trials that each individual turned first to the arm having (or expected to hold) the non-habituated object.

Fig. 3. Results of the Recognition Test. **a:** Mean proportion (+SE) of the first turns to the arm having the non-habituated object. The dotted line indicates the chance level (50%). **b:** Mean (+SE) exploration time (sec.) to the non-habituated / habituated objects in the 3 minutes of the Recognition Test. **: $p < 0.01$.

significant main effect of test interval ($F(2, 14) = 10.15$, $p < 0.01$). A post-hoc analysis revealed that exploration of the objects was longest in the first interval (0–1 min.). The main effect of object type was marginally significant ($F(1, 7) = 4.52$, $p < 0.1$). In addition, there was a significant interaction of object type and test interval ($F(1.11, 7.76) = 9.04$, $p < 0.05$). A post hoc analysis revealed that exploration of non-habituated objects was significantly longer than habituated ones during the first interval (0–1min: $F(1, 7) = 23.63$, $p < 0.01$; 1–2 min $F(1, 7) = 2.88$, $p > 0.1$, n.s.; 2–3 min $F(1, 7) = 2.99$, $p > 0.1$, n.s.). Multiple comparison analysis revealed that exploration of the non-habituated object was significantly longer in the first (0–1min.) than the subsequent two intervals (first-second: $t(7) = 6.28$, $p < 0.01$; first-third: $t(7) = 3.43$, $p < 0.05$), whereas the exploration of the habituated object was significantly longer in the first (0–1 min.) than the third (2–3 min.) interval ($t(7) = 3.50$, $p < 0.05$).

Recall Test (Fig. 4)

As described above, we pooled the data of the subjects who did and did not participate in additional Pretest trials 3, because the difference between the mean proportion of first turns of these two groups was not significant (two-sample t-test, $t(6) = -0.65$, $p > 0.1$, n.s.).

Choice at the first turn Fig. 4a shows the proportion of first turns to the arm with the non-habituated object in the Recall Test. As in the Recognition Test, all subjects turned first to the arm with the non-habituated object in most trials. The mean proportion of choices for the side with the non-habituated object (55.9%) was significantly higher than chance (50%; one-sample t-test, $t(7) = 3.42$, $p < 0.05$).

Duration of exploration Fig. 4b shows the mean duration of exploration of non-

Fig. 4. Results of the Recall Test. **a:** Mean proportion (+SE) of the first turns to the arm having the non-habituated object. The dotted line indicates chance level (50%). **b:** Mean (+SE) exploration time (sec.) to the non-habituated / habituated objects in the 3 minutes of the Recall Test.
*: $p < 0.05$; ***: $p < 0.001$.

habituated and habituated objects in the Recall Test. A two-way ANOVA revealed significant main effects of object type ($F(1, 7) = 10.33, p < 0.05$) and test interval ($F(1.21, 8.5) = 18.44, p < 0.01$). A post hoc analysis revealed that exploration of the objects was longest in the first interval (0–1 min.). In addition, there was a significant interaction of object type and test interval ($F(1.23, 8.6) = 10.66, p < 0.01$). A post hoc analysis revealed that exploration of non-habituated object was significantly longer than for habituated objects during the first interval (0–1 min: $F(1, 7) = 34.04, p < 0.001$; 1–2 min $F(1, 7) = 0.77, p > 0.1$, n.s.; 2–3 min $F(1, 7) = 5.09, p < 0.1$). Multiple comparison analysis revealed similar results to those in the Recognition Test: exploration of the non-habituated object was significantly longer in the first (0–1 min.) than the subsequent two intervals (first-second: $t(7) = 6.55, p < 0.01$; first-third: $t(7) = 5.33, p < 0.01$), whereas the exploration of habituated objects was significantly longer in the first (0–1 min.) than the third (2–3 min.) interval ($t(7) = 5.35, p < 0.01$).

Probe Test (Fig. 5)

Choice at the first turn Fig. 5 shows the proportion of first turns to the arm expected to have the non-habituated object in the Probe Test. The choice for the side with the non-habituated object appeared higher than chance but did not reach statistical significance, probably due to small N. (one-sample t-test, $t(7) = 1.16, p > 0.1$, n.s.).

Fig. 5. Mean proportion (+SE) of the first turns to the arm that is expected to hold the non-habituated object in the Probe Test. The dotted line indicates chance level (50%).

DISCUSSION

The present study demonstrated that degus, like rats, showed integrated memory of “what (object)”, “where (place)”, and “which (context)” information from previous exploration experiences. In the critical Recall Test, degus preferentially turned to the arm in which the non-habituated object was located at the end depending on the context. Because the objects were not visible from the turning point, their turn was unlikely to reflect familiarity of each object based on direct visual information. Instead, the degus appear to have decided in which direction to turn by recalling the memory encoded from their previous exploration. This result suggests degus’ recollection of memory that integrates what, where, and which from their previous experience.

The validity of the present procedure is confirmed by the increased time spent in exploration of non-habituated compared with habituated objects in both the Recognition Test and the Recall Test. In both tests it was found that the subjects preferentially explored non-habituated objects overall, especially in the first minute. These results are consistent with previous studies of degus that used the novelty exploration paradigm (Uekita & Okanoya, 2011; Ardiles et al., 2012). This increased exploration suggests degus’ recognition of What-Where-Which memory similar to that shown in open field studies in rats (Eacott & Norman, 2004) and other species (Kouwenberg et al., 2009; Jelbert et al., 2014; Hamilton et al., 2016).

It should be noted that there was a slight difference in the procedure between this experiment and that by Eacott et al. (2005): in the latter the objects were located at the end of the side arm throughout the trial in the test phase, whereas in our study the objects were translocated from the corner to the end in the re-exploration in the first context (see Dere et al., 2007; Easton & Eacott, 2008; Easton et al., 2009). Thus, the precise location of the

non-habituated object at the choice was different. However, because the main spatial component (i.e., left or right) of the Where information was maintained throughout the trial, this difference should not affect recollection of the animal's What-Where-Which memory.

The results of the Probe Test failed to replicate Eacott et al. (2005); unlike rats, the degus' choice of the arm that might be expected to hold the non-habituated object failed to reach statistical significance. One possible reason for this may be the small number of trials (4 trials per subject, see also Table 1). Because first-turn performance in the E-maze task tends to be generally low (around 60%, see also Eacott et al., 2005 for comparable performance in rats), this limitation of trial number is a likely cause of the non-significant result. Easton and Eacott (2008) explain the reason for the relatively low performance being that the paradigm relies on spontaneous exploration and therefore may include animals' innate object preferences. Thus, more probe trials may be required in future similar investigations. A closer replication of Eacott et al. (2005) might be valuable for clarifying the relative performances of rats and degus in this paradigm.

Does this paradigm satisfy the other feature for episodic memory?

As described in the Introduction, there are two major behavioral criteria for episodic memory in nonhumans: 1) integration of WWW information (Tulving, 1972), and 2) incidental encoding (e.g., Zentall et al., 2001). To our knowledge, cases satisfying both criteria are extremely rare. One exception concerns male meadow voles that revisited the location where they found a pregnant female who would go into postpartum estrus in 24 hours, depending upon passage of time (Ferkin et al., 2008). However, this behavior is more likely to be a hardwired reproductive strategy than based on episodic memory homologous to ours. Thus, to construct a plausible picture of the evolution of episodic memory, behavioral tests using species-general behaviors are required (Fujita et al., 2012).

Although our study examined the WWW nature of memory in degus, it may also involve the second feature, incidental encoding. In our procedure, objects were trial-unique and so the memory for the objects should also have been trial-unique. Importantly, the degus were never trained to retrieve memory of previously experienced objects at any stage of the experiment. Thus their choice of arm where they expected to find relatively unfamiliar objects might satisfy both criteria of episodic memory. However, exploration of novel objects may be inherently rewarding for the animals. Repeated exploration in the same environments might result in memorizing the location of the objects found there. But as there is not yet any behavioral paradigm that perfectly satisfies both criteria, further tests on this task with diverse species appear worthwhile.

The task used here, replacing "when" to "which" in WWW memory, might have various advantages. Temporal information, or "when," is replaceable by the environmental contexts, because both have the same function as an occasion setter that helps distinguishing one past event from others (Eacott & Easton, 2010, 2012, Easton & Eacott, 2008). In what-where-when paradigms, it is difficult to eliminate the possibility of non-episodic accounts such as processes based on memory strength or conditional discrimination, regardless of whether it is "how long ago" or "time of day" (Roberts et al., 2008; Zhou & Crystal, 2009).

Given these difficulties, what-where-which paradigms are easier to conduct, and might be used as a valid replacement for what-where-when memory tests.

Implications for future research

Our research is the first replication of the paradigm used for rats (Eacott et al., 2005) in a different species. We obtained basically the same results in degus, which implies that the ability to recall What-Where-Which episodic-like memories may be shared among rodents. It could be informative to use the same task not only with other rodents but also various species that show novelty preferences (Blaser & Heyser, 2015). Alternatively, by replacing objects with food rewards, for example, other species could be tested, as long as they show specific satiety.

One important component that animals naturally encode episodically might be social characteristics. We studied memory in degus, a social rodent (Lacey & Ebensperger, 2008; Ebensperger & Hayes, 2016). Although our degus showed episodic-like memory for nonsocial objects, it is conceivable that they could do likewise for social information such as individual recognition (Villavicencio, Márquez, Quispe, & Vásquez, 2009). Only a few studies have assessed episodic-like memory involving social factors in nonhuman animals (cleaner wrasses: Salwiczek & Bshary, 2011; chickadees: Wiechers, 2012; meadow voles: Ferkin et al., 2008; gorillas: Schwartz, Colon, Sanchez, Rodriguez, & Evans, 2002). As another application of the current experimental paradigm, if we use social cues such as conspecifics or their olfactory, auditory, or visual stimuli instead of nonsocial objects, highly social animals like degus may show superior “*Who-Where-Which*” memory recollection than nonsocial animals, such as hamsters. Because degus live socially (Lacey & Ebensperger, 2008), remembering past experience in such an integrated manner may be adaptive for their social life.

It might also be interesting to investigate the effect of aging on episodic-like memory in degus, as they have received much interest as a model of Alzheimer’s disease (e.g., Ardiles et al., 2012). Although our subjects were relatively young (aged less than 3 years, see Table 1), older degus may show impairments in recognition or recollection of episodic-like memory.

To summarize, we examined the ability of degus to recall the integrated memory of what (object), where (place), and which (context) in a modified object recognition task. In the critical Recall Test phase, degus preferentially chose the arm in which a non-habituated object was located at the end of the outer arm of E-maze. As the objects were not visible at choice, our results suggest that degus have abilities not only to recognize but also to recall their What-Where-Which memory. With this useful experimental paradigm, further comparative research should investigate species diversity, and the evolution of episodic memory in nonhumans.

REFERENCES

- Allen, T. A., & Fortin, N. J. 2013. The evolution of episodic memory. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 10379–10386.
- Ardiles, A., Ewer, J., Acosta, M. L., Kirkwood, A., Martinez, A., Ebensperger, L., . . . Palacios, A. G. 2013.

- Octodon degus* (Molina 1782): A model in comparative biology and biomedicine. *Cold Spring Harbor Protocols*, **2013**(4), 312–318.
- Ardiles, Á. O., Tapia-Rojas, C. C., Mandal, M., Alexandre, F., Kirkwood, A., Inestrosa, N. C., & Palacios, A. G. 2012. Postsynaptic dysfunction is associated with spatial and object recognition memory loss in a natural model of Alzheimer's disease. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 13835–13840.
- Babb, S. J., & Crystal, J. D. 2006. Episodic-like memory in the rat. *Current Biology*, **16**, 1317–1321.
- Bird, L. R., Roberts, W. A., Abroms, B., Kit, K. A., & Crupi, C. 2003. Spatial memory for food hidden by rats (*Rattus norvegicus*) on the radial maze: Studies of memory for where, what, and when. *Journal of Comparative Psychology*, **117**, 176–187.
- Blaser, R., & Heyser, C. 2015. Spontaneous object recognition: A promising approach to the comparative study of memory. *Frontiers in Behavioral Neuroscience*, **9**, 183.
- Clayton, N. S., Bussey, T. J., & Dickinson, A. 2003. Can animals recall the past and plan for the future? *Nature Reviews Neuroscience*, **4**, 685–691.
- Clayton, N. S., & Dickinson, A. 1998. Episodic-like memory during cache recovery by scrub jays. *Nature*, **395**, 272–274.
- Crystal, J. D. 2010. Episodic-like memory in animals. *Behavioural Brain Research*, **215**, 235–243.
- 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 Research Protocols*, **16**, 10–19.
- Dere, E., Huston, J. P., & Silva, M. A. D. S. 2007. The pharmacology, neuroanatomy and neurogenetics of one-trial object recognition in rodents. *Neuroscience & Biobehavioral Reviews*, **31**, 673–704.
- Dix, S. L., & Aggleton, J. P. 1999. Extending the spontaneous preference test of recognition: Evidence of object-location and object-context recognition. *Behavioural Brain Research*, **99**, 191–200.
- Eacott, M. J., & Easton, A. 2010. Episodic memory in animals: Remembering which occasion. *Neuropsychologia*, **48**, 2273–2280.
- Eacott, M. J., & Easton, A. 2012. Remembering the past and thinking about the future: Is it really about time? *Learning and Motivation*, **43**, 200–208.
- Eacott, M. J., Easton, A., & Zinkivskay, A. 2005. Recollection in an episodic-like memory task in the rat. *Learning & Memory*, **12**, 221–223.
- Eacott, M. J., & Norman, G. 2004. Integrated memory for object, place, and context in rats: A possible model of episodic-like memory? *The Journal of Neuroscience*, **24**, 1948–1953.
- Easton, A., & Eacott, M. J. 2008. A new working definition of episodic memory: Replacing “when” with “which”. In E. Dere, A. Easton, L. Nadel, & J. P. Huston (Eds.), *Handbook of episodic memory* (vol. 18, pp. 185–196). Amsterdam, Netherlands: Elsevier.
- Easton, A., Zinkivskay, A., & Eacott, M. J. 2009. Recollection is impaired, but familiarity remains intact in rats with lesions of the fornix. *Hippocampus*, **19**, 837–843.
- Ebensperger, L. A., & Hayes, L. D. (Eds.) 2016. *Sociobiology of caviomorph rodents: An integrative approach*. West Sussex, United Kingdom: John Wiley & Sons.
- Ennaceur, A., & Delacour, J. 1988. A new one-trial test for neurobiological studies of memory in rats. 1: Behavioral data. *Behavioural Brain Research*, **31**, 47–59.
- Feeney, M. C., & Roberts, W. A. 2012. Comparative mental time travel: Is there a cognitive divide between humans and animals in episodic memory and planning? In J. Vonk & T. K. Shackelford (Eds.), *The oxford handbook of comparative evolutionary psychology* (pp. 236–260). New York, NY: Oxford University Press.
- Feeney, M. C., Roberts, W. A., & Sherry, D. F. 2009. Memory for what, where, and when in the black-capped chickadee (*Parus atricapillus*). *Animal Cognition*, **12**, 767–777.
- Ferkin, M. H., Combs, A., delBarco-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. *Animal Cognition*, **11**, 147–159.
- 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. *Animal Cognition*, **15**, 1055–1063.
- González-Gómez, P. L., Bozinovic, F., & Vásquez, R. A. 2011. Elements of episodic-like memory in free-living hummingbirds, energetic consequences. *Animal Behaviour*, **81**, 1257–1262.
- Hamilton, T. J., Myggland, A., Duperreault, E., May, Z., Gallup, J., Powell, R. A., . . . Digweed, S. M. 2016. Episodic-like memory in zebrafish. *Animal Cognition*, **19**, 1071–1079.

- Hampton, R. R., Hampstead, B. M., & Murray, E. A. 2005. Rhesus monkeys (*Macaca mulatta*) demonstrate robust memory for what and where, but not when, in an open-field test of memory. *Learning and Motivation*, **36**, 245–259.
- Hoffman, M. L., Beran, M. J., & Washburn, D. A. 2009. Memory for “what”, “where”, and “when” information in rhesus monkeys (*Macaca mulatta*). *Journal of Experimental Psychology: Animal Behavior Processes*, **35**, 143–152.
- Jelbert, S. A., Hurly, T. A., Marshall, R. E., & Healy, S. D. 2014. Wild, free-living hummingbirds can learn what happened, where and in which context. *Animal Behaviour*, **89**, 185–189.
- Jozet-Alves, C., Bertin, M., & Clayton, N. S. 2013. Evidence of episodic-like memory in cuttlefish. *Current Biology*, **23**, R1033–R1035.
- Kouwenberg, A. L., Walsh, C. J., Morgan, B. E., & Martin, G. M. 2009. Episodic-like memory in crossbred Yucatan minipigs (*Sus scrofa*). *Applied Animal Behaviour Science*, **117**, 165–172.
- Kumazawa-Manita, N., Hama, H., Miyawaki, A., & Iriki, A. 2013. Tool use specific adult neurogenesis and synaptogenesis in rodent (*Octodon degus*) hippocampus. *PLoS ONE*, **8**, e58649.
- Lacey, E. A., & Ebensperger, L. A. 2008. Social structure in octodontid and ctenomyid rodents. In J. O. Wolff & P. W. Sherman (Eds.), *Rodent societies: An ecological and evolutionary perspective* (pp. 403–415). Chicago, IL: University of Chicago Press.
- Lee, T. M. 2004. *Octodon degus*: A diurnal, social, and long-lived rodent. *ILAR Journal*, **45**, 14–24.
- Martin-Ordas, G., Haun, D., Colmenares, F., & Call, J. 2010. Keeping track of time: Evidence for episodic-like memory in great apes. *Animal Cognition*, **13**, 331–340.
- Meyers-Manor, J. E., Overmier, J. B., Hatfield, D. W., & Croswell, J. 2014. Not so bird-brained: Pigeons show what-where-when memory both as time of day and how long ago. *Journal of Experimental Psychology: Animal Learning and Cognition*, **40**, 225–240.
- Newcombe, N. S., Balcomb, F., Ferrara, K., Hansen, M., & Koski, J. 2014. Two rooms, two representations? Episodic-like memory in toddlers and preschoolers. *Developmental Science*, **17**, 743–756.
- Okanoya, K., Tokimoto, N., Kumazawa, N., Hihara, S., & Iriki, A. 2008. Tool-use training in a species of rodent: The emergence of an optimal motor strategy and functional understanding. *PLoS ONE*, **3**, e1860.
- 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. *Journal of Experimental Biology*, **210**, 3559–3567.
- Popović, N., Madrid, J. A., Rol, M. Á., Caballero-Bleda, M., & Popović, M. 2010. Barnes maze performance of *Octodon degus* is gender dependent. *Behavioural Brain Research*, **212**, 159–167.
- R Development Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Raby, C. R., & Clayton, N. S. 2012. Episodic memory and planning. In J. Vonk & T. K. Shackelford (Eds.), *The oxford handbook of comparative evolutionary psychology* (pp. 217–235). New York, NY: Oxford University Press.
- Rivera, D. S., Inestrosa, N. C., & Bozinovic, F. 2016. On cognitive ecology and the environmental factors that promote Alzheimer disease: Lessons from *Octodon degus* (Rodentia: Octodontidae). *Biological Research*, **49**, 1.
- 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.
- Salwiczek, L. H., & Bshary, R. 2011. Cleaner wrasses keep track of the ‘when’ and ‘what’ in a foraging task. *Ethology*, **117**, 939–948.
- Schwartz, B. L., Colon, M. R., Sanchez, I. C., Rodriguez, I., & Evans, S. 2002. Single-trial learning of “what” and “who” information in a gorilla (*Gorilla gorilla gorilla*): Implications for episodic memory. *Animal Cognition*, **5**, 85–90.
- Singer, R. A., & Zentall, T. R. 2007. Pigeons learn to answer the question “where did you just peck?” and can report peck location when unexpectedly asked. *Learning & Behavior*, **35**, 184–189.
- Skov-Rakette, S. I., Miller, N. Y., & Shettleworth, S. J. 2006. What-where-when memory in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, **32**, 345–358.
- Suddendorf, T., Addis, D. R., & Corballis, M. C. 2009. Mental time travel and the shaping of the human mind. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 1317–1324.
- Suddendorf, T., & Busby, J. 2003. Mental time travel in animals? *Trends in Cognitive Sciences*, **7**, 391–396.
- Suddendorf, T., & Corballis, M. C. 1997. Mental time travel and the evolution of the human mind. *Genetic, Social, and General Psychology Monographs*, **123**, 133–167.

- Suddendorf, T., & Corballis, M. C. 2007. The evolution of foresight: What is mental time travel, and is it unique to humans? *Behavioral and Brain Sciences*, **30**, 299–313.
- Suddendorf, T., & Corballis, M. C. 2010. Behavioural evidence for mental time travel in nonhuman animals. *Behavioural Brain Research*, **215**, 292–298.
- Tomonaga, M., & Kaneko, T. 2014. What did you choose just now? Chimpanzees' short-term retention of memories of their own behavior. *PeerJ*, **2**, e637. doi: 10.7717/peerj.637
- Tulving E. 1972. Episodic and semantic memory. In E. Tulving & W. Donaldson (Eds.), *Organization of memory* (pp. 382–403). New York, NY: Academic Press.
- Tulving, E. 1983. *Elements of episodic memory*. New York, NY: Oxford University Press.
- Tulving, E. 2001. Episodic memory and common sense: How far apart? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **356**, 1505–1515.
- Tulving, E. 2002. Episodic memory: From mind to brain. *Annual Review of Psychology*, **53**, 1–25.
- Tulving, E. 2005. Episodic memory and autonoesis: Uniquely human? In H. S. Terrace & J. Metcalfe (Eds.), *The missing link in cognition: Origins of self-reflective consciousness* (pp. 3–56). New York, NY: Oxford University Press.
- Uekita, T., & Okanoya, K. 2011. Hippocampus lesions induced deficits in social and spatial recognition in *Octodon degus*. *Behavioural Brain Research*, **219**, 302–309.
- Uekita, T., & Okanoya, K. 2013. Gesshirui degu no kaiba kinou: Shakai ninchi to kukan ninchi [The function of hippocampus on *Octodon degus*: Social and spatial recognition]. *Japanese Psychological Review*, **56**, 295–309.
- Villavicencio, C. P., Márquez, I. N., Quispe, R., & Vásquez, R. A. 2009. Familiarity and phenotypic similarity influence kin discrimination in the social rodent *Octodon degus*. *Animal Behaviour*, **78**, 377–384.
- Wiechers, A. A. 2012. Social episodic-like memory in the black-capped chickadee (*Poecile atricapillus*). *Electronic Thesis and Dissertation Repository*, Paper 726. Retrieved from <http://ir.lib.uwo.ca/etd/726>
- Woods, C. A., & Boraker, D. K. 1975. *Octodon degus*. *Mammalian Species*, **67**, 1–5.
- Zentall, T. R. 2013. Animals represent the past and the future. *Evolutionary Psychology*, **11**, 573–590.
- Zentall, T. R., Clement, T. S., Bhatt, R. S., & Allen, J. 2001. Episodic-like memory in pigeons. *Psychonomic Bulletin & Review*, **8**, 685–690.
- Zentall, T. R., Singer, R. A., & Stagner, J. P. 2008. Episodic-like memory: Pigeons can report location pecked when unexpectedly asked. *Behavioural Processes*, **79**, 93–98.
- Zhou, W., & Crystal, J. D. 2009. Evidence for remembering when events occurred in a rodent model of episodic memory. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 9525–9529.
- Zhou, W., Hohmann, A. G., & Crystal, J. D. 2012. Rats answer an unexpected question after incidental encoding. *Current Biology*, **22**, 1149–1153.
- Zinkivskay, A., Nazir, F., & Smulders, T. V. 2009. What-where-when memory in magpies (*Pica pica*). *Animal Cognition*, **12**, 119–125.

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