Brief Communication

Recollection in an episodic-like memory task in the rat

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Episodic memory in humans is the conscious recollection of a past event. Animal models of episodic-like memory assess the memory for “what” happened, “where” it happened, and either “when” it happened, or in “which” context it happened, although recollection on such tasks is often difficult to measure. Here we present the first evidence of successful recollection of a past event in a rat in a task which is easily performed, requires little training, and is easily adaptable for other commonly used laboratory species.

Episodic memory in humans involves the conscious recollection of a unique past event that was personally experienced (Tulving 1983). Although this type of memory is impaired in human amnesia (Scoville and Milner 1957; Delay and Brion 1969; Zola-Morgan et al. 1986; Vargha-Khadem et al. 1997), understanding the neural basis of this type of memory has proved problematic. In part, this is due to the lack of experimental tasks for laboratory animals that model episodic memory. This difficulty in developing a task of episodic memory in nonhuman animals arises due to the requirement for episodic memory to involve conscious recollection of the experience (Tulving 1983). Such conscious recollection is extremely difficult to demonstrate without the use of language.

A number of researchers, then, have taken an alternative approach to developing tasks of episodic memory in animals. An alternative definition of episodic memory exists in Tulving's description of a memory that “receives and stores information about temporally dated episodes or events, and temporal-spatial relations between them.” (Tulving 1983). Using this definition of episodic memory, one can begin to develop tasks that examine the memory for events by demonstrating memory for an object (what), its location (where), and when it happened. Such “what-where-when” memory does not require evidence of either conscious recollection or awareness (and as such is often referred to as episodic-like memory), and can be successfully demonstrated in birds. Clayton and Dickinson (1998) allowed scrub jays to cache two types of food. One (wax worms) was preferred but perishable, and the other (peanuts) was less preferred but not perishable. These foodstuffs were cached in a number of spatial locations in the presence of a unique visual context. The scrub jays were then returned to the apparatus after a short delay or a long delay. Following a short delay the birds preferred to recover the wax worms. However, after the longer delay the birds preferred to recover the peanuts. By recovering the preferred food stuff at intervals when it had not perished, and the less-preferred foodstuff after intervals in which the wax worms would have perished, the birds demonstrated memory for which food they cached (what), and where and when they cached it.

Although the work of Clayton and Dickinson demonstrated episodic-like memory in birds, this task relies on the natural food-caching behavior of scrub jays. Therefore, the task is not readily adapted to more commonly used laboratory animals (such as rats or monkeys), which would be essential in order to

explore the neural mechanisms of this type of memory. Indeed, attempts to use procedures similar to that used by Clayton and Dickinson in rats (Bird et al. 2003) and monkeys (Hampton et al. 2005) appear to show that in this task both species have good memory for “what” and “where” but poor memory for “when.” Rats are able to track time (Ferster and Skinner 1957; Ergorul and Eichenbaum 2004), but it appears that memory for “when” in episodic-like tasks has not yet been successfully demonstrated. However, in humans the memory for the timing of events is also poor, and can in fact be dissociated from episodic memory (Friedman 1993). It has been proposed that in episodic memory, “when” serves only as an occasion setter to distinguish one experience from another similar experience (Eacott and Norman 2004). Therefore, episodic-like memory in animals may be defined as “what-where-which” (Eacott and Norman 2004; Eacott and Gaffan 2005) where “which” is any occasion setter that defines the experience as unique. A memory of “when” an event occurred can therefore be considered as a temporal form of the occasion setting “which.”

Using this broader definition of episodic-like memory in animals leads to tasks in which memory can be assessed for objects in particular locations within a context. In monkeys and rats, scene memory has been considered a measure of episodic-like memory (Gaffan 1994; Simpson et al. 1998). In this task the animal learns about the location of a specific object within a unique background scene. This task is known to be reliant on the fornix (Gaffan 1994) and diencephalic structures anatomically related to the hippocampus (anterior thalamus and mamillary bodies, Parker and Gaffan 1997a,b), which are also important for episodic memory in humans (Delay and Brion 1969; Zola-Morgan et al. 1986; Vargha-Khadem et al. 1997; Aggleton and Brown 1999). Indeed, this task is also impaired in patients with fornix damage and episodic memory impairments (Aggleton et al. 2000), indicating that scene memory taxes the mechanisms of episodic memory. However, scene learning requires reinforcement of learning and lengthy pretraining (Gaffan 1994; Simpson et al. 1998).

An alternative task was recently developed (Eacott and Norman 2004) that relies upon rats' innate preference for novel items (Ennaceur and Delacour 1988). The task takes place in an open field apparatus in which the floor and wall coverings (context), objects, and their locations can be manipulated by the experimenter. Rats are initially exposed to two objects within a particular context presented in the open field. In a second exposure, the same two objects are presented in opposite positions within a different context in the same open field. In a test phase, animals are placed back in the open field with one of the previous

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Figure 1. Outline of E-maze apparatus. (A) E-maze with black context present and objects (A and B) visible from the start arm (S). (B) E-maze with mesh context present and objects visible from the start arm and in positions opposite to those in A. (C) E-maze with black context present and objects not visible from the start arm (S). (D) E-maze with mesh context present, objects not visible from start arm, and in positions opposite to those in C.

contexts present but now with two copies of just one of the objects previously experienced. One of these objects is now in a location not previously associated with that context for that object. Because of the rat's innate novelty preference, the rat explores this novel object-location-context (what-where-which) combination more than the familiar combination. This task requires only habituation to the apparatus, can be adapted easily for other species, and is sensitive to lesions of the fornix (Eacott and Norman 2004), and therefore provides a useful episodic-like memory task.

However, both scene learning (Gaffan 1994) and the task used by Eacott and Norman (2004) can be solved by familiarity of the objects seen. In contrast, human memory relies on both familiarity and recollection processes (Yonelinas 2001), and episodic memory itself relies typically on recollection of the past experience (Tulving 1983). Recent evidence suggests that rats do use both familiarity- and recollection-based processes when recognizing odors (Fortin et al. 2004), but to date no task has successfully demonstrated recollection in an episodic-like memory task in a species other than birds. Here we demonstrate such a task based on a modification of Eacott and Norman's (2004) novelty-based task.

Sixteen Dark Agouti rats (Bantin and Kingman) housed in diurnal conditions with ad libitum access to food and water were habituated to a wooden E-maze (60 cm long $\times$ 37 cm wide $\times$ 21 cm high, with three arms, each 15 cm wide $\times$ 21 cm long). The inside of the E-maze was either smooth and black or covered in wire mesh to provide different visual and tactile contexts. Animals ran one trial a day, and the objects used were trial-unique (no object was presented for more than one day in an animal's experience). Objects were junk objects including bottles, jars, small toys, and combinations of objects.

In phase 1 of pretraining, animals received two 30-min habituation sessions with each context. In phase 2, the animals subsequently received two trials (one with each context) in which they were placed in the maze for a period of 5 min with two objects present at either end of the backbone of the maze (Fig. 1A). The animals were allowed to explore the objects before being transferred to a separate holding cage for a further 5-min period. Finally, the animals were returned to the maze for another 5 min with the same context and objects present in the same locations, in order to learn that within a day the location of objects was stable within a given context.

In phase 3 of pretraining, animals were placed in the E-maze with one context present and two objects visible (Fig. 1A; objects

changed from session to session) for a period of 3 min before being transferred to a holding cage for 3 min. The animals were then returned to the maze for 3 min, but in the presence of the other context, and with the objects in opposite locations (Fig. 1B), before being removed to the holding cage for a further 3 min. Finally, animals were returned to the E-maze for a 3-min period in the presence of one of the earlier contexts (counterbalanced for order of presentation), allowing the animals to learn that within a day the location of objects remained stable within a given context, even with multiple events.

Stage 4 of pretraining comprised eight trials run as above, but now the animals were held in the holding cage for 8 min between exposure to the second context and returning to the maze for the final time. During this period in the holding cage, animals were allowed to explore a copy of one of the objects presented in the maze, allowing the animals to habituate to this object. On returning to the E-maze the animals' behavior was monitored to determine which object they explored first. Animals typically explored the object to which they had not been habituated in the holding cage, in accordance with their innate preference for novelty (Ennaceur and Delacour 1988). This allowed a measure of the animals' object preference, with animals turning towards the novel (nonhabituated) object on average 64.8% of the time, which is significantly above the level expected by chance ($t[15] = 3.721$, $P < 0.001$, one-tailed).

The experimental stage of the task consisted of 16 trials run as above, but now objects in the E-maze were out of sight of the animal, being placed in the outside arms of the maze (Fig. 1C,D). When the objects are visible on emerging from the startbox (as in the stage described above), a preference for the nonhabituated object can be based on familiarity alone. However, because in this stage the objects were not visible to the rat emerging from the start box, the rat had to *recollect* the prior experience in this context in order to seek out the relatively novel object; the task cannot be solved by familiarity. Performance at this stage was measured by scoring left and right turns from videos of animals in the maze, with turns being measured as snout over a line marked on the Perspex roof of the maze that was matched to the line of sight needed to see the object in the arm of the maze.

The rats turned towards the nonhabituated object on average 65.2% of the time (s.d. 10.9), which is significantly above the level expected by chance ($t[15] = 5.57$, $P < 0.0001$, one-tailed; Fig. 2). In addition, each rat had two probe trials (one after trial

Figure 2. Mean percentage of turns towards the nonhabituated object (demonstrating recollection of the past event) in trials with objects present (left) and on probe trials with no objects present (right). For trials on which objects were present, average performance of individual animals is shown by $\bullet$.

8 and one after trial 16) in which no objects were present in the test phase, thus controlling for any extraneous cues that might be guiding the animals' behavior. In this condition, too, rats made a significantly greater number of turns towards the nonhabituated object than would be expected by chance (mean = 68.75%, s.d. = 40.31, $t[15] = 1.86$, $P < 0.05$, one-tailed; Fig. 2).

Although the animals chose the nonhabituated object more than would be expected by chance, it is true that the mean percentage of responses to the nonhabituated object was relatively low (65.2%). It is worth noting that the mean percentage of responses to the nonhabituated object in stage 4 of pretraining was of a similar level (64.8%). At this stage of pretraining the objects were visible to the animal on leaving the start arm, and therefore performance at this stage can be taken as a measure of the strength of object preference in the animals. As the level of correct responding was similar in stage 4 of pretraining and in the experimental stage, it appears not that memory performance at the experimental stage is weak, but rather that memory performance at the experimental stage reflects the strength of the animals' object preference. It is possible that with different periods for the habituation it would be possible to establish a stronger object preference, and hence a stronger memory in the experimental stage.

By selecting the nonhabituated object when it is out of sight, the animals demonstrate recollection of the object (what) and the location it is in (where) that is dependent upon the context (which). As discussed above, "what-where-which" memory can be considered to be episodic-like in animals (Eacott and Norman 2004). The "which" in this experiment is an occasion setter which discriminates between similar experiences (the locations of the same objects in different locations). This makes the present experiment similar to another successful task of episodic-like memory in animals in which "when" discriminates similar events (Clayton and Dickinson 1998). Moreover, because the preference for the nonhabituated object is gained after the exposure to the original event, and either object may be preferred depending on the object used at habituation, the memory demonstrated here, like episodic memory in humans, is flexible. Also, in contrast to some other tasks of episodic-like memory in animals (e.g., Gaffan 1994; Eacott and Norman 2004; Ergorul and Eichenbaum 2004), the present task can only be solved using recollection of past experiences, as the objects are not visible to provide familiarity cues to the rats. It should be noted that we make no claims as to the rats' awareness of the past event in performing the task. Rather we make the claim that the rats cannot make familiarity judgments and therefore are likely to rely on mechanisms similar to those of recall in humans (Fortin et al. 2004).

Finally, the experiment we report does not rely on reward or substantial pretraining. The task is also easily adapted to different laboratories and to different species. We believe, therefore, that this is the first demonstration of recollection in an episodic-like memory task that can be widely used in a variety of species to investigate the mechanisms of such learning.

References

- Aggleton, J.P. and Brown, M.W. 1999. Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behav. Brain Sci.* **22**: 425–444.
- Aggleton, J.P., McMackin, D., Carpenter, K., Hornak, J., Kapur, N., Halpin, S., Wiles, C.M., Kamel, H., Brennan, P., Carton, S. et al. 2000. Differential cognitive effects of colloid cysts in the third ventricle that spare or compromise the fornix. *Brain* **123**: 800–815.
- Bird, L.R., Roberts, W.A., Abroms, B., Kit, K.A., and Crupi, C. 2003. Spatial memory for food hidden by rats (*Rattus norvegicus*) on the radial maze: Studies of memory for where, what, and when. *J. Comp. Psychol.* **117**: 176–187.
- Clayton, N.S. and Dickinson, A. 1998. Episodic-like memory during cache recovery by scrub jays. *Nature* **395**: 272–274.
- Delay, J. and Brion, S. 1969. *Le syndrome de Korsakoff*. Masson, Paris.
- Eacott, M.J. and Gaffan, E.A. 2005. The roles of perirhinal cortex, postrhinal cortex and the fornix in memory for objects, contexts and events in the rat. *Quart. J. Exp. Psychol. B* (in press).
- Eacott, M.J. and Norman, G. 2004. Integrated memory for object, place, and context in rats: A possible model of episodic-like memory? *J. Neurosci.* **24**: 1948–1953.
- Ennaceur, A. and Delacour, J. 1988. A new one-trial test for neurobiological studies of memory in rats. 1: Behavioral data. *Behav. Brain Res.* **31**: 47–59.
- Ergorul, C. and Eichenbaum, H. 2004. The hippocampus and memory for "what," "where," and "when." *Learn. Mem.* **11**: 397–405.
- Ferster, C.B. and Skinner, B.F. 1957. Schedules of reinforcement. Appleton-Century-Crofts, New York.
- Fortin, N.J., Wright, S.P., and Eichenbaum, H. 2004. Recollection-like memory retrieval in rats is dependent on the hippocampus. *Nature* **431**: 188–190.
- Friedman, W.J. 1993. Memory for the time of past events. *Psychol. Bull.* **113**: 44–66.
- Gaffan, D. 1994. Scene-specific memory for objects: A model of episodic memory impairment in monkeys with fornix transection. *J. Cog. Neurosci.* **6**: 305–320.
- Hampton, R.R., Hampstead, B.M., and 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. *Learn. Motiv.* (in press).
- Parker, A. and Gaffan, D. 1997a. The effect of anterior thalamic and cingulate cortex lesions on object-in-place memory in monkeys. *Neuropsychologia* **35**: 1093–1102.
- . 1997b. Mamillary body lesions in monkeys impair object-in-place memory: Functional unity of the fornix-mamillary system. *J. Cog. Neurosci.* **9**: 512–521.
- Scoville, W.B. and Milner, B. 1957. Loss of recent memory after bilateral hippocampal lesions. *J. Neurochem.* **20**: 11–21.
- Simpson, E.L., Gaffan, E.A., and Eacott, M.J. 1998. Rats' object-in-place encoding and the effect of fornix transection. *Psychobiol.* **26**: 190–204.
- Tulving, E. 1983. *Elements of episodic memory*. Clarendon Press, Oxford, UK.
- Vargha-Khadem, F., Gadian, D.G., Watkins, K.E., Connelly, A., Van Paesschen, W., and Mishkin, M. 1997. Differential effects of early hippocampal pathology on episodic and semantic memory. *Science* **277**: 376–380.
- Yonelinas, A.P. 2001. Components of episodic memory: The contribution of recollection and familiarity. *Phil. Trans. Royal Soc. B Bio. Sci.* **356**: 1363–1374.
- Zola-Morgan, S., Squire, L.R., and Amaral, D.G. 1986. Human amnesia and the medial temporal region: Enduring memory impairment following a bilateral lesion limited to field CA1 of the hippocampus. *J. Neurosci.* **6**: 2950–2967.

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