Episodic memory: what can animals remember about their past?

Daniel Griffiths, Anthony Dickinson and Nicola Clayton

The question of whether episodic memory, the ability to recall unique, personal experiences, is restricted to humans is a matter of current controversy. Recent work on food-storing jays suggests that several features of episodic memory may not be as exclusive to humans as previously thought. In this review we outline the critical features of episodic memory in humans, its relationship to declarative memory, and recent results revealing that jays can learn to perform a task that depends on certain features of episodic memory and can thus be considered 'episodic-like'. Finally, we compare this avian performance with a contemporary definition of human episodic memory and consider the implications for studies of hippocampal function and animal cognition.

D. Griffiths and N. Clayton are at the Section of Neurobiology, Physiology and Behavior, University of California Davis, One Shield's Avenue, Davis, CA 95616, USA.

tel: +1 530 754 9184
fax: +1 530 752 5582
e-mail: dpgriffiths@ ucdavis.edu, nsclayton@ucdavis. edu
A. Dickinson is at the Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge, UK CB2 3EB.

tel: +44 1223 333577
fax: +44 1223 333564
e-mail: ad15@cus. cam.ac.uk

The encoding and storage of memories concerned with unique, personal experiences and their subsequent recall has long been the subject of intensive investigation in humans. This type of memory is referred to as episodic memory[1] to distinguish it from other forms of remembering, such as memories for facts about the world that may or may not have not been acquired through personal experiences[2]. According to Tulving's classical definition, episodic memory 'receives and stores information about temporally dated episodes or events, and temporal–spatial relationships among these events'[1]. Thus, episodic memory provides information about the 'what' and 'when' of events ('temporally dated experiences') and about 'where' they happened ('temporal–spatial relations'). Some researchers have stated that the storage and subsequent recall of this episodic information is beyond the memory capabilities of non-human animals[3,4]. However, recent work on memory for cache sites in food-storing jays provides a working model for testing episodic-like memory in animals[5].

Categories of human memory

Memory in humans can be subdivided into several categories. Historically, the most gross distinction is between declarative and non-declarative memory[1–4,6,7]. Non-declarative memory is characterized by its inaccessibility to conscious recall and is demonstrated by phenomena such as priming, motor learning of skills and simple forms of classical conditioning[6,7]. Tulving and Markowitsch[4] offer a comprehensive description of declarative memory, the essence of which is that it supports the retrieval of information that can be characterized in propositional form (i.e. it can be described symbolically) and has truth value. This information can be used to guide inferences and generalizations, both to support reasoning and to control behaviour, but the behavioural expression of the retrieved information is optional rather than obligatory.

Declarative memory has been further subdivided into episodic and semantic components. There is some disagreement as to the nature of this division and the relationship between these two memory systems, both in terms of function and the neural structures involved. It is generally agreed, however, that episodic memory is concerned with the conscious recall of specific past experiences, whereas semantic memory involves the storage and retrieval of factual knowledge about the world. The difference is often referred to in terms of remembering versus knowing: episodic memory is concerned with remembering specific personal experiences, whereas semantic memory mediates what one knows about the world[2]. Remembering getting soaked in the London rain last Tuesday is an example of episodic memory, but knowing that it often rains in England is an example of semantic memory because it need not be acquired as a result of a personal experience of getting wet.

Both episodic and semantic forms of declarative memory are thought to depend on the medial temporal lobe (MTL) and diencephalic structures (i.e. thalamic nuclei) of the brain[7,8]. It is here that there is disagreement as to the contributions of brain areas within these structures to episodic and semantic memory, based on evidence from case studies on human amnesics with varying brain pathologies. A number of authors[9–11] have suggested that the anterograde amnesia observed in patients with MTL damage is a result of disruption of declarative memory as a whole, with semantic and episodic memory being equally impaired. According to this theory, the size of the

---

Table 1. Episodic and declarative memory: defining features

Declarative memory (episodic and semantic common features)	Episodic memory: unique features
• Large, complex and highly structured, with fast encoding operations • Can receive factual information through different sensory modalities and internally generated sources • Stored informataion is representational (isomorphic with what is in the world) and propositional (can be described symbolically) • Information has truth value, can be accessed and expressed flexibly, and can be used as a basis for inferences • Processing is highly sensitive to context • System is cognitive (as opposed to behavioural): information can be 'thought about' • Behavioural expression of retrieval products is optional rather than obligatory • System interacts closely with other brain/behaviour systems, such as language, emotion, affect and reasoning • Dependent on MTL and diencephalic structures such as the thalamic nuclei	• Concerned with conscious recollection of specific past experiences • Oriented, at the time of retrieval, to the past • Accompanied by 'autonoetic' consciousness, which enables 'remembering' (relating to personal experience) as opposed to 'knowing' • Embedded relationship with semantic ('knowing') memory: episodic remembering always implies semantic knowing, whereas knowing does not imply remembering • Development occurs later than semantic abilities in children • More vulnerable to a number of brain pathologies and aging • Dependent on frontal lobes in a way that declarative memory is not: episodic retrieval is associated with changes in regional cerebral blood flow in right prefrontal cortex, which is rarely caused by semantic recall • Unique to humans?

(Adapted from Ref. 4.)

---

impairment is proportional to the extent of the damage to the MTL.

A similar declarative theory has been proposed by Eichenbaum and co-workers[12–14] in which declarative memory is divided into learning facts and remembering experiences, but different parts of the MTL are proposed to support different aspects of these memories. Those authors suggest that cortical systems encode individual, non-relational representations which the hippocampus subsequently organizes to create flexibly accessible relational representations, thus allowing inferential relationships between representations to be used in novel situations. Furthermore, the 'parahippocampal' region (entorhinal, perirhinal and parahippocampal cortices) is implicated in collating several streams of cortical input and allowing temporally extended representations. According to Eichenbaum[14] the hippocampus underpins the ability to distinguish between unique episodes and to integrate information extracted from these episodes within semantic knowledge. Thus, he suggests that episodic and declarative (semantic) memory are not alternative types of memory, but two benefits of a system in which the hippocampus supports the networking of cortical memories.

Tulving and Markowitsch[4] have developed a different framework for declarative memory. Their 'episodic theory' suggests that episodic and semantic memory are still two subsystems of declarative memory, but rather than existing as parallel subsystems as outlined above, their relationship is one of embeddedness. Semantic knowledge can be acquired with an impairment of episodic memory capabilities, but episodic memory cannot exist without semantic knowledge. Episodic memory is thus an extension of semantic knowledge: the context of when and where the information was acquired is combined with the semantic knowledge that was

gained on that occasion[3]. Damage to the semantic system would therefore impair both semantic and episodic memory, whereas damage to the episodic system would result in an impairment of episodic memory acquisition but not necessarily of the semantic system.

Support for this theory comes from the recent results by Vargha-Khadem *et al.*[15], who reported a case study of three amnesic patients who had average or near-average intelligence and could learn facts, but were unable to remember events that had happened previously, that is, they had semantic, but not episodic memory. All three of the patients had well-defined damage to the hippocampus, but not the surrounding area. This lead the authors, and Tulving and Markowitsch[4], to suggest that the hippocampus mediates the acquisition of episodic memory, and the parahippocampal region supports the acquisition of semantic knowledge. Eichenbaum[14] interpreted these results in terms of declarative theory, proposing that the deficit was not necessarily due to the inability to process purely episodic information in the way Vargha-Khadem suggested, but rather that it was a case of the subjects being incapable of processing complex declarative material that was only encountered once, a function that depends critically on the hippocampus.

The issue of defining and distinguishing declarative, semantic and episodic memory therefore remains unresolved at present. Tulving and Markowitsch[4] have suggested that these terms of reference should be restructured: they propose that 'declarative memory' should be defined in terms of the common features of episodic and semantic memory, and that 'episodic memory' should refer to those properties that 'declarative' memory does not possess (see Table 1). To quote Tulving and Markowitsch[4]: 'Another advantage of the proposed characterisation of declarative memory is that

it allows us to reserve the category of semantic memory to language-related declarative memory operations, in keeping with its original definition[1]. Everybody knows that language can greatly facilitate the operations of most memory systems, including declarative and episodic, but because language is not necessary for declarative memory, the terminological distinction helps to clarify matters'.

When presenting the new definition of 'episodic memory', Tulving and Markowitsch[4] state that it possesses features that no other memory system has (Table 1). An episodic memory system makes it possible to remember specific past experiences, and is the only form of memory in which retrieval is oriented to the past. They also state that episodic memory is accompanied by a special kind of consciousness, which they term 'autonoetic' consciousness. This is different from the 'noetic' consciousness that is involved with the retrieval of declarative information. Such a distinction is based on the fact that human subjects can distinguish between recalling past personal experience and remembering an impersonal declarative fact. Because of this, the two types of consciousness can be defined operationally in terms of remembering and knowing: remembering a specific event requires autonoetic consciousness, whereas knowing a fact is noetic in nature. This feature, in combination with the others outlined above (see Table 1), led Tulving and Markowitsch[4] to claim that episodic memory, as defined by these features, is not present in animals other than humans.

Animal studies of memory

To date, most of the learning and memory experiments on animals have not distinguished episodic from other forms of declarative memory: until recently there was little or no evidence that animals could recall a specific past experience and respond appropriately, nor was there any reason to believe that they would need such a memory system in the types of laboratory tasks on which they were tested. Many researchers have suggested, however, that animals are capable of declarative memory. For example, Tulving and Markowitsch[4] state that animals 'possess well-developed knowledge of the world (declarative memory systems), and are capable of acquiring vast amounts of flexibly expressible information'. In terms of empirical evidence, there are a number of laboratory experiments describing declarative memory, particularly in primates[16,17]. Perhaps the most compelling examples of this ability come from studies of the deployment of general knowledge in complex reasoning by great apes[18]. Even the humble rodent can perform declarative memory tasks such as goal-directed behaviour[19] and inferential learning in an odour-discrimination task[20].

Do animals have episodic memory?

Tulving and Markowitsch[4] define episodic memory, at least in part, in terms of the conscious experience of recollection. This definition presents an insurmountable barrier to demonstrating this form of memory in animals because there are simply no agreed behavioural markers of conscious experience. Other attempts to define episodic memory without reference to consciousness do not resolve this problem. Morris and Frey[21] asserted that to show event memory (a synonym for episodic memory), an experiment needs to prove

the presence of recollective experience. More formally, 'The task should distinguish between changes in behaviour that occur because an animal remembers some prior event and changes that merely happen because some prior event has occurred'. This definition, however, again lacks an agreed behavioural measure of the experience of recollection.

This dilemma can be resolved to some degree by using the classic definition of episodic memory when referring to animals: in his original definition, Tulving[1] identified episodic recall as the retrieval of information about 'where' a unique event or episode took place, 'what' occurred during the episode, and 'when' the episode happened. The merit of this definition is that the simultaneous retrieval and integration of information about these three features of a single, unique experience may be demonstrated behaviourally in animals.

Although there are many laboratory procedures for investigating memory for discrete past episodes, these tasks require the animal to retrieve information about only a single feature of the episode (see Table 2). For example, monkeys can be trained to choose between two complex objects on the basis of whether they are the same as (delayed matching-to-sample, DMS) or different from (delayed non-matching-to-sample or oddity, DNMS) an object they were shown some time previously at the start of the trial. The monkey might have recalled episodically the events at the start of the trial. A simpler explanation, however, is that the monkey learned to choose or avoid the most familiar object.

In many studies that appear to demonstrate episodic-like recall in animals, the results observed can be more simply explained in terms of familiarity. There is a distinct difference between the feeling that a stimulus is familiar and an episodic recollection of where and when it has been seen before[22,23]. For example, a face can appear highly familiar without any recall of where and when one has previously met its owner. By only requiring the monkeys to recognize a stimulus, but not recollect where and when it was previously seen, these matching tasks are most readily solved by familiarity rather than episodic recall, and, indeed, the fact that monkeys learned more rapidly when novel objects are used supports this account[24].

The experiments outlined in Table 2 suggest that these laboratory tasks can be explained in terms other than episodic recall. A different approach is to consider examples in nature when an animal might benefit from the capacity to remember the 'what, where and when' of individual past episodes. One potential example is the ability of brood parasitic species, such as cowbirds, to keep track of the current status of hosts' nests in which they lay their eggs, so that they can later return to the correct nest site at the appropriate time[25,26]. Another candidate for episodic recall by animals is the recovery of caches by food storing birds and mammals[27]. Many species scatter hoard food throughout their winter territories when food is abundant only to retrieve them days, weeks and even months later when food is scarce. A wealth of evidence from both the field and the laboratory shows that memory plays a role in cache retrieval[28]. In terms of purely behavioural criteria for episodic memory, the animal must be able to encode the information based on a single, personal experience that occurred in the past,

Table 2. Potential demonstrations of episodic memory in animals and their alternative explanations

Study	Potential demonstrations of episodic memory	Alternative, non-episodic account
Olton and Samuelson[39]	Rats recovered food from the arms of a radial maze. Once the site was emptied, they did not return to that arm again. Rats remembered visiting specific sites, and what they did there.	This result could be explained by a rule for avoiding familiar arms or, even more simply, a rule for avoiding the most recently-visited arm.
Gaffan[37]	Monkeys learned to choose between two complex visual scenes on the basis of whether one of them contained a specific object at a particular location within the scene. This task appears to require retrieval of both spatial ('where') and object ('what') information.	The discrimination was learned over many trials. There is no reason to believe that, on any given trial, the monkey's choice was controlled by the episodic recall of its choices and their outcomes on previous trials. The animals might have remembered the more general declarative information that a particular what–where configuration is associated with a reward.
Mishkin and Delacour[24]	Monkeys were trained to choose between two complex objects on the basis of whether they are the same as (delayed matching-to-sample, DMS), or different from (delayed non-matching-to-sample, DNMS), an object they were shown at the start of the trial. Monkeys recalled episodically the events at the start of the trial.	This result can be explained in terms of familiarity: the monkeys might simply have learned to choose (DMS) or avoid (DNMS) the most familiar object.
Steele and Morris[36]	Rats were trained on a delayed match-to-platform (DMP) task, with 4 trials per day. The position of platform on trial 1 changed each day, but remained in the same position for the remaining 3 trials that day. Rats recalled the experience of getting out of water on trial 1, and this enabled them to escape faster on the remaining trials that day. They remembered where the platform was, what happened (escape from water) and when (the position of the platform on any given day).	The rats might have learned to approach the most familiar location without any recollection that their visits to this location happened more recently than those on the first trial of the previous day. Rats might simply have learned over the days of training that they can escape if they approach the most familiar location on each trial.

and then accurately recall the information about what happened, where and when, at a later date.
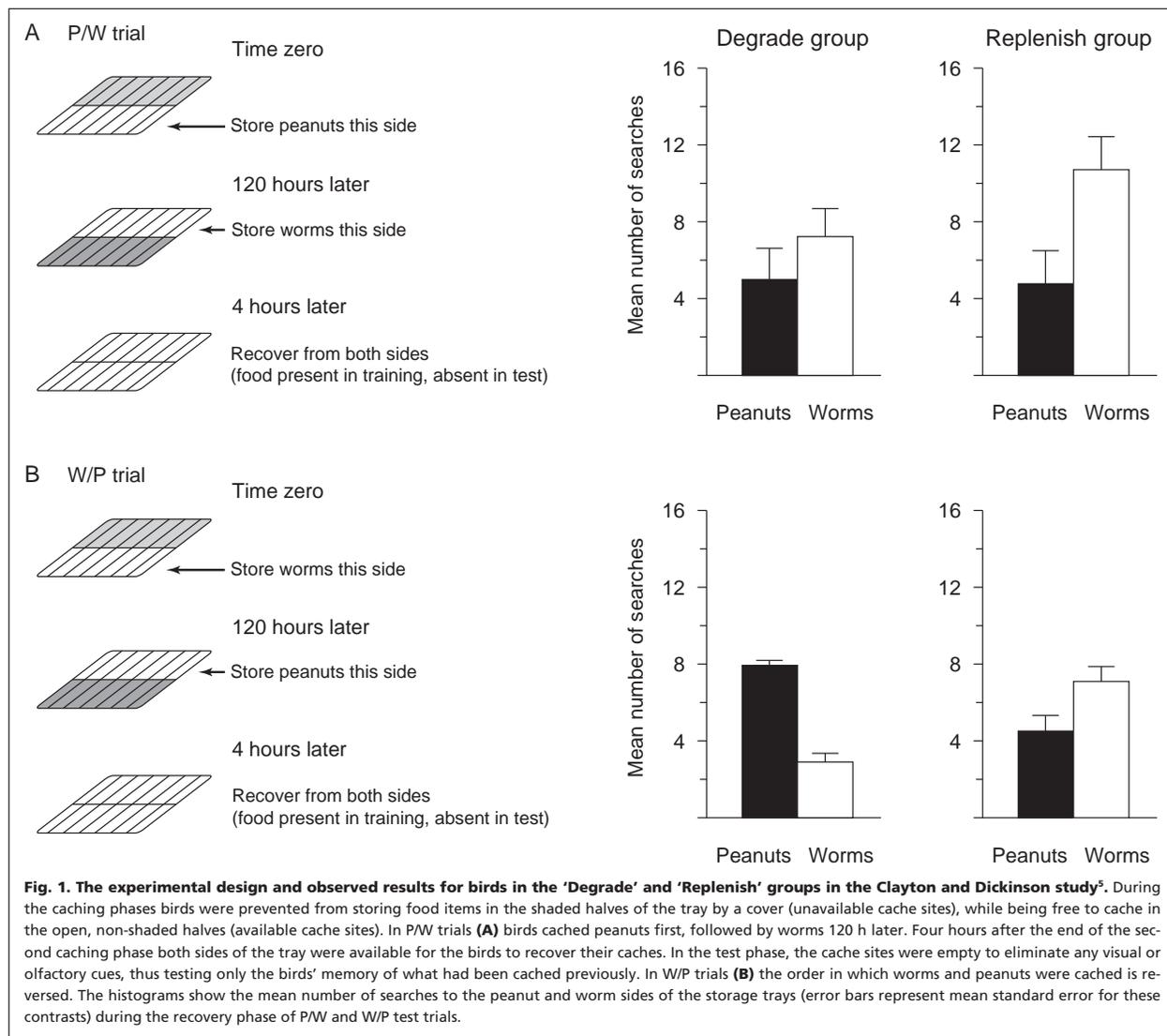
In birds, a number of features of food recovery suggest that episodic processes might play a role in the recovery of caches. Firstly, information guiding recovery is based on a single past experience of when that bird stored the food, suggesting that these birds remember information about a specific personal experience that occurred at one point in time in the past. Secondly, in terms of accuracy of memory, the retrieval pattern in at least some species reflects precise information about the spatial location of the cache[29,30]. Thirdly, birds can recall not only the location of their caches but also their contents[31–33]. In addition, many food-storing species cache insects and other perishable items in addition to seeds[27]. For example, European jays (*Garrulus glandarius*) cache perishable food at a lower frequency than non-perishable food and recover it more quickly[34]. It therefore may be adaptive for these species to encode and recall information about when a particular food item was cached, as well as what type of food was cached and where.

Jays can remember 'what, where and when'
Clayton and Dickinson[5] used the food-caching and recovery paradigm to examine whether or not scrub jays (*Aphelocoma coerulescens*) are capable of episodic-like memory, by testing their ability to remember what, where and when they have cached a particular foodstuff, based on a trial-unique experience of caching (Fig. 1). The birds were allowed to cache perishable wax worms (Fig. 2) and non-perishable peanuts, and recover these items either after a short (4 h) or long (124 h) retention interval. Jays prefer wax worms to peanuts, so when given a choice between the two food types they would preferentially recover and eat worms. One group ('Degrade' or 'D' group) was given training trials in which wax worms that had been stored for 124 h had rotted and become inedible, but were still edible if recovered after only 4 h. In a second group ('Replenish' or 'R' group), the wax worms were replaced by fresh ones before the birds were allowed to recover, so worms were edible at both long and short intervals. Stored peanuts do not spoil and thus were equally edible after 4 h and 124 h.

During training trials, birds could rely on the sight and smell of their caches as cues about where to search during cache recovery. To test whether or not jays could remember what, where and when the worms and peanuts had been cached in the absence of these cues, each individual received a pair of test trials in which all food items were removed prior to the recovery phase of each test trial and fresh sand (the storing substrate) was placed in the tray. If jays can remember what and where they stored the food items, those in the 'D' group would be expected to attempt to recover worms after a short interval but peanuts after the longer

Fig. 1. The experimental design and observed results for birds in the 'Degrade' and 'Replenish' groups in the Clayton and Dickinson study[5]. During the caching phases birds were prevented from storing food items in the shaded halves of the tray by a cover (unavailable cache sites), while being free to cache in the open, non-shaded halves (available cache sites). In P/W trials **(A)** birds cached peanuts first, followed by worms 120 h later. Four hours after the end of the second caching phase both sides of the tray were available for the birds to recover their caches. In the test phase, the cache sites were empty to eliminate any visual or olfactory cues, thus testing only the birds' memory of what had been cached previously. In W/P trials **(B)** the order in which worms and peanuts were cached is reversed. The histograms show the mean number of searches to the peanut and worm sides of the storage trays (error bars represent mean standard error for these contrasts) during the recovery phase of P/W and W/P test trials.

interval because the worms would have decayed and become unpalatable. The birds that had the fresh worms available at both intervals ('R' group) should preferentially search for the worms at both intervals, because they never experienced the effect of time on the palatability of the worm caches.

As predicted, on test trials, birds in the 'D' group reversed their preference from worms to peanuts at the long interval, but 'R' group birds preferred the worms at both intervals (Fig. 1). These results demonstrated that the peanut preference shown by the 'D' group was not simply due to differential forgetting of worm caches, and that the preference to search for worms 4 h after caching and for peanuts 124 h after worm caching does not reflect a genetic predisposition because this strategy was adopted only by birds in the 'D' group, which had the opportunity to learn that worms decay over time.

In terms of evidence for episodic-like memory, the critical result was the reversal of cache recovery preference. The switch in preference from worms to peanuts after the long interval required the birds to recognize a particular cache

site in terms of both its contents and the relative time that had elapsed between caching and recovery. This result can only be explained by recall of information about 'what' items (peanuts and worms) were cached, 'where' each type of item was stored and 'when' (4 h or 124 h) the worms were cached. Furthermore, the information was acquired as a result of a single, trial-unique experience.

Having demonstrated that jays can remember what type of food they have cached, and when as well as where that particular caching event took place, Clayton and Dickinson[33] showed that jays can also remember specific past experiences that occurred during cache recovery. The birds could remember not only which sites had been depleted by cache recovery but also which of two different types of food item had been recovered. Clayton and Dickinson[33] showed that scrub jays encode information about the type of food they store in cache sites, and that the birds can update their memory of whether or not a caching location currently contains a food item following recovery, in a way that cannot be explained in terms of the familiarity of the location. Finally, the birds were capable of

integrating information about the content of a cache site at recovery with information about the specific location of the cache.

Is episodic-like memory in jays an analogue of human episodic memory?

The results of these experiments show that jays remember what, where, and when a particular caching event occurred, and on re-encountering the contextual surroundings in which they had previously cached food, they know to direct a different behaviour – cache recovery. Furthermore, jays can differentiate between memories of caching and recovering, and update their information about the current status of a cache based on whether or not they had recovered the food that they had cached prior to the recovery test.

These results fulfil most of the criteria for episodic memory but the one major absence is that there is no evidence that the birds are using autonoetic consciousness in their recall of past events; as previously mentioned, this is probably untestable in animals because this form of consciousness has no obvious manifestation in non-linguistic behaviour. It is this feature that presently makes 'episodic' memory a uniquely human phenomenon, and probably always will.

Tulving and Markowitsch[4] argue that whilst it is impossible to prove the absence of episodic memory in animals because a universal negative cannot be disproved, it is equally difficult to demonstrate a difference between declarative (semantic) and episodic memory in non-human animals. In this context, the above results, and indeed many demonstrations of episodic memory, can be considered in the declarative terms suggested by Eichenbaum[14]. Consider a situation like the food-storing experiment above: the birds remember a series of facts about an object (the food item), a place (where they stored it), a time (how long it was since they stored the item) and an action (caching versus cache recovery) that allows them subsequently to recall that information and execute the appropriate behaviour. Each of these items could be considered individually as a semantic fact, because on their own they would not allow the recall of the specific episode of caching a food item. When all these facts are integrated, the animal would possess sufficient information to isolate what was cached and what was recovered, where and how long ago: functionally, the animal has enough information to recall the episode of caching a specific item. There are many well-documented examples of animals judging time[35], remembering spatial locations[36], recognizing objects[37], remembering context[38] and performing goal-directed actions[19] individually, so it seems that these factors can indeed be considered as declarative in nature.

This in turn raises the question of how much an animal (or indeed a person) has to show that it has learned about a specific event in order to suggest that it can recall that particular episode, and not just a series of semantic facts. If the birds were tested on some aspect of the experiment that was not relevant to the task at hand, for example, if they could not discriminate between the colour of sand used in the test and a novel colour, would this mean that the task is not a demonstration of episodic memory because the individuals

Fig. 2. Photograph of a scrub jay (*Aphelocoma coerulescens*) about to cache a wax worm. The birds cached both worms and peanuts in plastic ice-cube trays, which comprised a 2 × 7 array of cube moulds filled with sand, each of which was a potential cache site. The trays were attached to a wooden board and were surrounded by a visuospatially distinct structure made of Lego® bricks (see Refs 5,33 for more details). Different trays were used on every trial, and were placed in the birds' home cage at the time of caching and recovery.

did not remember all aspects of the caching episode? Therefore, the question becomes one of asking how much information about an event an animal needs to remember for a memory to be classed as episodic as opposed to the summation of a series of semantic facts.

The results of the food-storing study can be used to support a declarative theory of episodic memory; the only reason, however, that the results do not fit within Tulving and Markowitsch's[4] theory of episodic memory is that there is no evidence of the involvement of autonoetic consciousness. As the question of animal consciousness in episodic recall is seemingly an unanswerable one, the assertion that episodic memory is unique to humans cannot be refuted, and animal examples of episodic memory will continue to be considered as analogues of human episodic memory at best[4,17]. Nonetheless, the experiments of Clayton and Dickinson[5] have demonstrated that there are naturally occurring situations where an animal's ability to recall specific past events is of vital importance to its survival: if the

Outstanding questions

- Does the Clayton and Dickinson study[5] provide a model system to bridge the gap between animal and human theories of episodic memory?
- Can mammalian food-storers perform a similar episodic task adapted for their own natural histories?
- Can current mammalian laboratory tasks used on rats and monkeys (e.g. delayed match-to-sample or -place) be adapted to demonstrate unequivocally an ability to recall the 'what, where and when' of a specific event, or does the animal's behaviour need to have an adaptive 'requirement' for this type of recall, as in the food-storing example?
- To what extent is the hippocampus involved in the ability to recall episodic-like information? Previous studies suggest it is likely to be heavily involved in the 'what' and 'where', but is it involved in integrating the 'when' information?
- Which brain area is needed to encode temporal information?
- Some animals avoid the problems of perishability that jays have (e.g. grey squirrels, who excise the cotyledon from acorns to prevent them from germinating and thus spoiling as a food source). Are they less capable of performing a 'what, where, and when' memory task because they have taken a different route to solve the problem?

absence of behavioural indices of autonoetic consciousness means that this type of memory falls short of episodic memory in its strictest definition, then it should at least be considered distinct from other demonstrations of declarative memory in animals, and therefore deserving of its description of 'episodic-like'.

References

1 Tulving, E. (1972) Episodic and semantic memory, in *Organisation of Memory* (Tulving, E. and Donaldson, W., eds), pp. 381–403, Academic Press

2 Tulving, E. (1983) *Elements of Episodic Memory*, Clarendon Press

3 Tulving, E. (1995) Organization of memory: quo vadis?, in *The Cognitive Neurosciences* (Gazzaniga, M.S., ed.), pp. 839–847, MIT Press

4 Tulving, E. and Markowitsch, H.J. (1998) Episodic and declarative memory: role of the hippocampus *Hippocampus* 8, 198–204

5 Clayton, N.S. and Dickinson, A.D. (1998) Episodic-like memory during cache recovery by scrub jays *Nature* 395, 272–274

6 Schacter, D.L., Chiu, C.Y. and Ochsner, K.N. (1993) Implicit memory: a selective review *Annu. Rev. Neurosci.* 16, 159–182

7 Squire, L.R., Knowlton, B. and Musen, G. (1993) The structure and organization of memory *Annu. Rev. Psychol.* 44, 453–496

8 Shimamura, A.P. and Squire, L.R. (1987) A neuropsychological study of fact memory and source amnesia *J. Exp. Psych. Learn. Mem. Cognit.* 13, 464–473

9 Squire, L.R. and Knowlton, B. (1995) Memory, hippocampus and brain systems, in *The Cognitive Neurosciences* (Gazzaniga, M.S., ed.), pp. 825–837, MIT Press

10 Squire, L.R. and Zola, S.M. (1996) Structure and function of declarative and non-declarative memory systems *Proc. Natl. Acad. Sci. U. S. A.* 93, 13515–13522

11 Cohen, N.J., Poldrack, R.A. and Eichenbaum, H. (1997) Memory for items and memory relations in the procedural/declarative memory framework *Memory* 5, 131–178

12 Eichenbaum, H., Otto, T. and Cohen, N.J. (1994) Two functional components of the hippocampal memory system *Behav. Brain Sci.* 17, 449–518

13 Eichenbaum, H. *et al.* (1996) Functional organisation of the hippocampal memory system *Proc. Natl. Acad. Sci. U. S. A.* 93, 13500–13507

14 Eichenbaum, H. (1997) How does the brain organise memories? *Science* 277, 330–332

15 Vargha-Khadem, F. *et al.* (1997) Differential effects of early hippocampal pathology on episodic and semantic memory *Science* 277, 376–380

16 Zola-Morgan, S., Squire, L.R. and Ramus, S. (1995) Severity of memory impairment in monkeys as a function of locus and extent of damage within the medial temporal lobe memory system *Hippocampus* 5, 235–239

17 Gaffan, D. (1992) Amnesia for complex naturalistic scenes and for objects following fornix transection in the rhesus monkey *Eur. J. Neurosci.* 4, 381–388

18 Gillan, D.J., Premack, D. and Woodruff, G. (1981) Reasoning in the chimpanzee: I. Analogical reasoning *J. Exp. Psychol. Anim. Behav. Process.* 7, 1–17

19 Dickinson, A. (1980) *Contemporary Animal Learning Theory*, Cambridge University Press

20 Dusek, J.A. and Eichenbaum, H. (1997) The hippocampus and memory for orderly stimulus relations *Proc. Natl. Acad. Sci. U. S. A.* 94, 7109–7114

21 Morris, R.G.M. and Frey, U. (1997) Hippocampal synaptic plasticity: role in spatial learning or the automatic recording of attended experience? *Philos. Trans. R. Soc. Lond. Ser. B* 352, 1489–1503

22 Aggleton, J.P. and Brown, M.W. Episodic memory, amnesia and the hippocampal–anterior-thalamic axis *Behav. Brain Sci.* (in press)

23 Mandler, G. (1980) Recognising: the judgement of previous experience *Psychol. Rev.* 87, 252–271

24 Mishkin, M. and Delacour, J. (1975) An analysis of short-term visual memory in the monkey *J. Exp. Psych.: Anim. Behav. Proc.* 1, 326–334

25 Reboreda, J.C., Clayton, N.S. and Kacelnik, A. (1996) Species and sex differences in hippocampus size between parasitic and non-parasitic cowbirds *NeuroReport* 7, 505–508

26 Clayton, N.S., Reboreda, J.C. and Kacelnik, A. (1997) Seasonal changes of hippocampal volume in parasitic cowbirds *Behav. Process.* 41, 237–243

27 Vander Wall, S.B. (1990) *Food Hoarding in Animals*, University of Chicago Press

28 Shettleworth, S.J. (1995) Memory in food-storing birds: from the field to the Skinner box, in *Behavioural Brain Research in Naturalistic and Semi-Naturalistic Settings* (Alleva, E., Fasolo, H-P. and Nadel, L., eds), pp. 158–179, Kluwer Academic Publishers

29 Balda, R.P. and Kamil, A.C. (1992) Long-term spatial memory in Clark's nutcrackers (*Nucifraga columbiana*) *Anim. Behav.* 44, 761–769

30 Healy, S.D. and Suhonen, J. (1996) Memory for locations of stored food in willow tits and marsh tits *Behavior* 133, 71–80

31 Sherry, D.F. (1982) Food storage, memory and marsh tits *Anim. Behav.* 30, 631–633

32 Sherry, D.F. (1986) Food storage by black-capped chickadees: memory for the location of contents of caches *Anim. Behav.* 32, 451–464

33 Clayton, N.S. and Dickinson, A.D. Memory for the content of caches by scrub jays *J. Exp. Psychol. Anim. Behav. Process.* (in press)

34 Clayton, N.S., Mellor, R. and Jackson, A. (1996) Seasonal patterns of food storing in the European jay (*Garrulus glandarius*) *Ibis* 138, 250–255

35 Biebach, H., Gordjin, M. and Krebs, J.R. (1989) Time-and-place learning by garden warblers (*Sylvia borin*) *Anim. Behav.* 37, 353–360

36 Steele, R.J. and Morris, R.G.M. Delay-dependent impairment of a hippocampal-dependent matching to place task with chronic and intrahippocampal infusion of the NMDA antagonist D-AP5 *Hippocampus* (in press)

37 Gaffan, D. (1994) Scene-specific memory for objects: a model of episodic memory impairments in monkeys with fornix transection *J. Cogn. Neurosci.* 6, 305–320

38 Kim, J.J. and Fanselow, M.S. (1992) Modality-specific retrograde amnesia of fear *Science* 256, 675–677

39 Olton, D. and Samuelson, R. (1976) Remembrance of placed passed: spatial memory in rats *J. Exp. Psychol. Anim. Behav. Process.* 2, 97–116

Coming soon to *Trends in Cognitive Sciences*

- Modularity and cognition, by M. Coltheart

- Concepts are more than categories, by K.E. Solomon, D.L. Medin and E. Lynch

- The neural correlates of consciousness, by C. Frith

- Catastrophic forgetting in connectionist networks, by R.M. French