



Episodic memory in animals: Remembering which occasion

Madeline J. Eacott*, Alexander Easton

Dept. of Psychology, Durham University, Science Site, South Road, Durham DH1 3LE, UK

ARTICLE INFO

Article history:

Received 29 May 2009

Received in revised form

22 September 2009

Accepted 5 November 2009

Available online 11 November 2009

Keywords:

Rat

Monkey

Mouse

Hippocampus

Learning

ABSTRACT

Episodic memory, the recollection of past events in one's life, has often been considered a memory specific to humans. Recent work in a variety of species has challenged this view, and has raised important questions about the nature of episodic memory itself. We present a review of the types of task proposed as episodic-like in animals and consider that these tasks require animals to demonstrate memory for specific occasions in the past. We propose that identifying episodic memory as the memory for what happened where on a specific occasion is a more encompassing definition than one that relies on information about when an event occurred. These episodic-like tasks in animals support the view that the hippocampal system is necessary for episodic memory, and that the neural substrates of episodic memory can be dissociated from those of other forms of declarative memory.

© 2009 Elsevier Ltd. All rights reserved.

Episodic memory is the conscious recollection of past events in our lives (Tulving, 1983). This type of declarative memory is particularly sensitive to the effects of ageing (e.g. Mitchell, Brown, & Murphy, 1990), disease (e.g. Graham, Emery, & Hodges, 2004) and brain injury (e.g. Aggleton & Brown, 1999). There has been much debate in the literature as to whether this is because episodic memory measures are more sensitive to a general impairment in declarative memory (Squire, Stark, & Clark, 2004) than other measures of memory, or because it relies on a separate, dissociable and presumably more vulnerable, neural system (Aggleton & Brown, 1999). Resolving this debate and understanding the neural processes underlying episodic memory is crucial to developing therapies for memory loss in a variety of conditions, and yet the understanding gained from human neuropsychology remains limited through the non-specific nature of damage within the crucial brain regions in patients. Therefore, developing animal models of episodic memory is crucial to developing our understanding of these neural mechanisms. However, as episodic memory has been intrinsically tied to conscious recall, demonstrating this in animals that do not have language to express their subjective experience is difficult, if not impossible. In recent years much progress has been made in developing animal models of episodic memory, and these models are helping us to understand the nature of the neural systems underlying episodic memory, and may also lead us to better understand the nature of episodic memory in humans

more clearly by removing the phenomenological aspects of the memory.

1. What would episodic memory in animals look like?

Episodic memory has been explicitly linked to autoeic consciousness (Tulving, 2002), the awareness that an event happened to oneself. In humans such distinctions in types of awareness can be assessed (partially) through, for example, asking participants to report whether they 'remember' something they previously experienced, or simply 'know' it to be true (Yonelinas, Kroll, Dobbins, Lazzara, & Knight, 1998). However, such distinctions are often hard to convey to participants and rely entirely on the subjective experience of the participant. Moreover, use of this definition presents further problems. First, very few studies of human episodic memory ask about the subjective experience of the participant to ensure the memory is truly episodic in nature and so set an unrealistically high threshold for identifying episodic memory in non-human species. Moreover, in humans it is possible to have the subjective phenomena of an episodic memory without having actually experienced the remembered event (Roediger & McDermott, 1995), which brings into question the value of such phenomena. Second, whilst the difficulties of probing a form of subjective experience in humans with language are acknowledged, it becomes virtually impossible to study in species that do not have language. Therefore, some authors have claimed that this definition of episodic memory ties it specifically to humans, as autoeic awareness cannot be demonstrated in other species (Clayton, Bussey, Emery, & Dickinson, 2003). This definition also ties us to the idea that the subjective experience is crucial to the memory as a whole. To some extent this is like

* Corresponding author. Tel.: +44 191 3343252; fax: +44 191 3343241.
E-mail address: m.j.eacott@durham.ac.uk (M.J. Eacott).

suggesting we cannot understand, for example, visual processing of motion in animals without being certain that they have the same form of subjective experience when they see motion. Clearly the same evolutionary advantages we gain from episodic memory could be advantageous to other species too, and we therefore have to consider whether other animals have some form of episodic memory. To do this in the first instance, some researchers have proposed we look for ‘episodic-like’ memory (Clayton & Dickinson, 1998) which will have many of the features of episodic memory, but without the need to demonstrate any conscious experience.

One approach is to consider the possible purpose of episodic memory. There are few evolutionary advantages to remembering the past unless it can influence future action. In the specific case of episodic memory where one remembers specific past episodes, this could be especially useful in imagining possible future events and planning for them on the basis of past experiences (Suddendorf & Corballis, 2007; Suddendorf & Corballis, 2008a). This view is certainly supported by recent work which indicates that patients with impairments in episodic memory for past events also have problems in imagining future events (Hassabis, Kumaran, Vann, & Maguire, 2007). However, this approach does not specifically address issues about the nature of episodic memory content, other than to establish that such future planning must be behaviourally dissociated from other types of future directed behaviours, such as instinct (Suddendorf & Corballis, 2008a).

Other approaches have considered very specifically the nature of the content of the episodic memory. In using Tulving’s initial description of episodic memory as memory which “receives and stores information about temporally dated episodes or events, and temporal–spatial relations between them.” (Tulving, 1983), Clayton and Dickinson identified that memories which carry information about what happened, where and when (what–where–when memory, Clayton & Dickinson, 1998) might fulfil the criteria for being ‘episodic-like’. Content alone cannot define an episodic memory however, as we can remember, for example, the date and place of our own birth without having an episodic memory of it. Therefore, work from this group has proposed that the what–where–when memory content should also be integrated into a single unified memory rather than three separate elements. Moreover, the integrated memory should be flexible; that is able to be accessed and used in novel situations not predicted at the point of encoding (Clayton, Bussey, & Dickinson, 2003).

2. What–where–when memory in animals

What–where–when memory as a form of ‘episodic-like’ memory was first demonstrated in Western scrub jays (*Aphelocoma californica*) who spontaneously cached food for later recovery (Clayton & Dickinson, 1998). In this study the birds were allowed to cache two types of food; worms (their preferred food) and peanuts (less preferred). The birds were then taught through experience that cached food could be recovered from the same location some time later (4 h or 124 h) but at short intervals (4 h) both peanuts and worms could be recovered fresh, whilst after long delays (124 h) only peanuts would be fresh, worms having degraded. After some training to these rules, the birds showed that given the choice of where to search to recover their caches, at short delays they would dig where worms (their preferred and still fresh food) had been cached. However, at long delays they would search where they had cached peanuts (the less preferred but unperished food) in preference to where they had cached worms (which at this delay they have learned will have degraded). This demonstrated memory for what (peanuts or worms) had been cached where (location in the caching tray) and when (recently or long ago).

Although this work in scrub jays using a natural behaviour was successful, a series of experiments attempting to demonstrate similar what–where–when memory in other species encountered problems. Bird, Roberts, Abroms, Kit, and Crupi (2003) showed that rats caching two different types of food in a radial maze could show memory for what they cached and where they cached it (by preferentially entering arms where they had cached the more preferred of the two foods), but when this preferred food was devalued at long delays (as for the scrub jays), there was no evidence that the rats modified their behaviour on the basis of a memory for when the food was cached. A similar behaviour was seen in monkeys, where once again what–where information could not be modified on the basis of food degrading at long delays (Hampton, Hampstead, & Murray, 2005). These results appeared to suggest that episodic-like memory abilities in non-human animals might be limited to scrub jays.

However, although these initial attempts at extending Clayton and Dickinson’s paradigm into other species did not show evidence for episodic-like memory, there are some caveats. One potentially important distinction is that whilst caching is an innate behaviour for scrub jays, neither rhesus monkeys nor rats usually employ this type of caching. Consequently, it is possibly that these animals have the capacity for episodic-like memory, but it is only able to be demonstrated through naturalistic behaviours that would normally exploit episodic-like memory in these species. Recent work, therefore, has moved away from caching to other types of behaviour and in rats this work has typically focussed on rats’ propensity to scavenge for food. Babb and Crystal (2006) exposed rats to a radial arm maze with three flavours of food in the arms. Some arms contained a regular chow pellet, whilst some other arms contained preferred, distinctively flavoured food pellets (raspberry or grape). The rats were then placed back into the radial maze at either a short or long delay. At short delays none of the previously baited arms contained food whilst the other arms contained rat chow, and therefore to efficiently gather the available food, the animals should visit only those arms which had not been visited previously. However, at longer delays the arms which had initially contained the preferred foods were replenished and previously unvisited arms were baited with chow, but, as in the short delays, the arms previously baited with chow remained empty. At these longer delays the rats visited the replenished arms (which were not visited at the shorter delays) and avoided entering the arms that did not replenish. This shows the rats’ memory for where (the location of the arms where food was found) and when (whether it was a short or long delay). Although this task reveals that the rats could distinguish in memory between the non-replenishing regular chow and the replenishing preferred foods, there was initially no evidence that the memory was specific for the flavour of food (i.e. differentiation between the preferred flavours). However, a second part of the experiment then devalued one of the preferred flavours (by pairing the flavour with sickness-inducing lithium chloride). Now at long delays the rats still visited the replenished non-devalued flavour arms but did not enter the replenished but devalued arms. This shows that the rats had memory for the specific flavour (what) rather than the broad category of replenishing or non-replenishing food type, as well as the arm in which it was found (where). Because the devaluation stage can only be done at the long time interval when foods are replenished it cannot be conclusively demonstrated that there was also concurrent memory of when the previous event (initial exploration of the radial maze) occurred. However, it seems likely, as the memory of when had been demonstrated in the previous phase of the task, that although the experiments tested only “where–when” and “what–where” memories, they probably represent the testing of a single and coherent “what–where–when” memory.

One problem of both the Clayton and Dickinson (1998) and Babb and Crystal (2006) paradigms is that they both require a period of

متن کامل مقاله

دریافت فوری ←

ISIArticles

مرجع مقالات تخصصی ایران

- ✓ امکان دانلود نسخه تمام متن مقالات انگلیسی
- ✓ امکان دانلود نسخه ترجمه شده مقالات
- ✓ پذیرش سفارش ترجمه تخصصی
- ✓ امکان جستجو در آرشیو جامعی از صدها موضوع و هزاران مقاله
- ✓ امکان دانلود رایگان ۲ صفحه اول هر مقاله
- ✓ امکان پرداخت اینترنتی با کلیه کارت های عضو شتاب
- ✓ دانلود فوری مقاله پس از پرداخت آنلاین
- ✓ پشتیبانی کامل خرید با بهره مندی از سیستم هوشمند رهگیری سفارشات