The episodic nature of episodic-like memories

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Studying episodic memory in nonhuman animals has proved difficult because definitions in humans require conscious recollection. Here, we assessed humans’ experience of episodic-like recognition memory tasks that have been used with animals. It was found that tasks using contextual information to discriminate events could only be accurately performed using recollection, not familiarity. However, tasks using temporal information to discriminate events could be accurately performed using either recollection or familiarity. The results strengthen the position that some episodic-like recognition memory tasks are a valid model of episodic memory. However, tasks that rely on temporal information may be susceptible to non-episodic strategies.

Episodic memory is the memory of specific events in one’s life. In humans, episodic memory is associated with conscious recollection of the event (Tulving 1983) and a sense of “mental time travel” (Suddendorf and Busby 2003; Suddendorf and Corballis 2008). Consequently, it has been argued that episodic memory is unique to humans (e.g., Suddendorf and Busby 2003; Suddendorf and Corballis 2007) and so cannot be investigated in nonhuman animals. However, this view has been challenged recently by approaches that have explored similar types of memory in animals (Clayton and Dickinson 1998; Eacott and Norman 2004; Eacott et al. 2005; Babb and Crystal 2006; Kart-Teke et al. 2006; Good et al. 2007; Ferkin et al. 2008). These approaches have focused on a content-based description of the memory, building on Tulving’s (1983) definition of human episodic memory as that which “receives and stores information about temporally dated episodes or events, and temporal–spatial relations between them,” referred to as what–where–when (here termed wwwhen) (Clayton and Dickinson 1998; Clayton et al. 2001) or what–where–which occasion memory (here termed wwwwich) (Eacott and Norman 2004; Easton and Eacott 2008; Eacott and Easton 2010). These definitions also require that the content (wwwhen or wwwwich) is integrated into a single representation that can be used flexibly (Clayton et al. 2003b). Such content-based descriptions of episodic memory do not deny the conscious experience of remembering in humans, but instead allow investigation of the neural mechanisms involved without considering the subjective experience (Eacott and Easton 2007; Easton and Eacott 2008). Thus, content-based approaches to episodic memory allow the dissociation of content from subjective experience.

Nonetheless, failing to demonstrate conscious recollection of an event distinguishes studies in animals from episodic tasks typically used with human participants and, therefore, this type of memory in animals has been termed “episodic-like” (Clayton and Dickinson 1998). Despite attempts to show that memory in rats has many of the characteristics of episodic memory in humans (Eichenbaum et al. 2005), this evidence is indirect. However, recently there have been attempts to explore in humans wwwhen content-based episodic tasks (Hayne and Imuta 2011; Holland and Smulders 2011) modeled on the episodic-like memory tasks used with animals (Clayton and Dickinson 1998). In these studies, adults (Holland and Smulders 2011) and children as young as 3 yr (Hayne and Imuta 2011) showed recall of what, where, and when of an event, partially fulfilling the content-based description of episodic-like memory, although in the latter case flexibility and integration of the content (Clayton et al. 2003a) were not specifically addressed. If the experience of human participants in such content-based episodic-like memory tasks is similar to that in more conventional episodic tasks typically used with humans, then the validity of episodic-like memory tasks in animals is strengthened and has implications for the view that episodic memory is uniquely human.

In humans, the experience of episodic memory has been extensively studied within recognition memory studies using the remember/know paradigm. Using this approach, participants can be asked about their subjective experience when they recognize an object and report whether they remember having seen it or just know. Remembering is associated with the conscious recollection of the encoding event and, therefore, reflects an episodic memory (e.g., Yonelinas 2001). In contrast, simply knowing something has been seen before, but being unable to recollect the encoding event gives a sense of familiarity that is not episodic in nature (e.g., Yonelinas 2001). Participants in Holland and Smulder’s (2011) wwwwhen episodic memory task were asked whether, overall, their experience in the task was one of remembering or knowing; the vast majority reported an experience of remembering. However, Holland and Smulder’s (2011) task was not a recognition task and so not directly comparable to tasks in which remember/know is used to dissociate recollection and familiarity processes. Moreover, it was not possible in their task to relate participants’ subjective experiences with their performance in the task that may be, we shall argue, crucial.

Therefore, we examined the experience of human participants in recognition memory tasks that have been used to assess episodic-like memory in animals (e.g., Eacott and Norman 2004; Kart-Teke et al. 2006; Good et al. 2007). As recognition tasks, these are amenable to the remember/know paradigm in humans and are directly comparable to tasks used with animals.

Using human participants, we tested the subjective experience associated with two forms of episodic-like memory tasks, wwwhen (Clayton and Dickinson 1998) and wwwwich (Eacott and Norman 2004), based on tasks that have previously been used with nonhuman animals (Eacott and Norman 2004; Good et al. 2007). This was contrasted with the experience associated with recognition memory for objects. Both accuracy of the memory and the associated subjective experience were assessed. Based on the claim that wwwhen and wwwwich episodic-like memory tasks specifically require recollection that in humans is associated with a subjective experience of remembering, we made the
following predictions. If the episodic-like memory questions (wwwhen or wwwwhich) are truly episodic in nature, then they will be able to be accurately answered only by the process of recollection. Therefore, only those responses associated with the experience of remembering (marking the process of recollection) will be reliably accurate, while those associated with the experience of knowing (marking the process of familiarity in the absence of recollection) will not. In contrast, as simple object recognition (what questions) can use the processes of either recollection or familiarity, answers associated with the experience of both remembering and knowing responses will be reliably correct. These predictions stand regardless of the relative proportions of remember and know responses given on any task. In order to test the hypotheses over two different levels of difficulty, one group of participants (Group Distracter) had a short filled interval between acquisition and test, while the other group (Group Immediate) did not. The study also allowed us to examine the proposal from Holland and Smulders (2011) that the experience of memory in an episodic-like task will overwhelmingly be one of remembering, not knowing.

Two groups of participants were tested, a mixture of male and female undergraduate students at Durham University. Group Immediate consisted of 29 students aged 21–23 yr. Group Distracter initially consisted of 39 students aged 18–20 yr, but data from two participants were excluded for failure to provide experiential ratings for all responses, resulting in a final group size of 37. Participants were tested in groups within time-tabled teaching slots (Group Immediate and Group Distracter, separately).

The study phase consisted of a PowerPoint slide projected onto a large screen. For Group Immediate, two introductory slides were initially presented. The first (the instruction slide) outlined the task, while the second (the training slide) explained the remember/know judgment (based on Rajaram 1993). The slides were read to the participants and the opportunity to seek clarification given before the study proper began. This consisted of two event slides (see Fig. 1). The event slides each consisted of the same nine items (abstract objects from Graphicxtras.com) in one of nine spatial locations against a distinctive background. The background changed between event slides 1 and 2 and the locations of particular objects also changed between slides, but the objects and the locations themselves were common to both slides.

Each event slide was presented for 30 sec, separated by 1 min, during which a blank slide was presented. For Group Immediate, the test phase began immediately following the end of the presentation of the second event slide. Participants were instructed to turn over their individual paper answer sheets and answer the questions.

For Group Distracter, the procedure was identical to that of Group Immediate with the exception that the instruction slide was followed by the two event slides, with the training slide being presented after the event slides before the test phase (see Fig. 1). Thus, Group Distracter had a filled break between the second event slide and the test phase that lasted ~1 min.

The test phase was identical for both groups. It consisted of nine questions in three blocks. Each block of questions consisted of one of each question type. For each question, there were two answer options and participants were instructed to circle one as their answer. Participants were instructed to guess if they did not know the answer. For what questions (“Which of these symbols have you seen before?”), the options were a previously seen symbol and a similar novel symbol (order counterbalanced across participants). For wwwhen questions (“On which slide did you see this symbol in this particular location?”), the options were first slide and second slide, while for wwwwhich questions (“On which slide did you see this symbol in this particular location?”), the options were patches of the backgrounds from Events 1 and 2 and the words “chequered” or “zebra” as appropriate (see Fig. 1). The order of questions within each block and between blocks was counterbalanced across the group, and the correct answer was also counterbalanced for each question. For each question, participants also had to indicate the experience associated with their decision (remember, know, or guess) and indicate on a scale of 1–5 how confident they were with their answers (except guesses, where zero confidence was assumed). Examples of the questions are shown in Figure 1.

Thus, in summary, participants sequentially viewed two screens, each consisting of a number of not-easily-named symbols displayed in different locations on a distinctive background (see Fig. 1). The same symbols were present on each screen but their location changed between screens. Memory for the identity of the symbols (what questions) or their location within the specific screen was tested, the latter prompted either by cueing the participant to the first or second screen (wwwhen questions) or to the distinctive background (wwwwhich questions).

Each participant answered nine questions (three of each question type: what, wwwhen, wwwwhich). Each response was reported as one of three types of subjective experience (remember, know, or guess). Guess responses were 2%, 17%, and 22% of the total responses for what, wwwhen, and wwwwhich, respectively, for Group Immediate, and 8%, 18%, and 35%, respectively, for Group Distracter. Excluding guesses, 69% and 47% of wwwhen and wwwwhich questions, respectively, were associated with a remember experience (Group Immediate), and 71% and 60%, respectively, for Group Distracter. This compares with 85% (Group Immediate) and 78% (Group Distracter) for what questions.
Therefore, overall it was not the case that memories produced with either the wwwhen or wwhich episodic questions were overwhelmingly associated with a remember, rather than a know, experience.

Each answer could be either correct or incorrect. However, as each participant gave three responses for each question type, some participants contributed more than one response of a given experiential type for a question type. Therefore, in order to ensure independence of data for analysis, only the first response of each type of experience (remember, know, or guess) for each question type was statistically analyzed. Where appropriate, the performance of each was compared against chance using binomial probabilities. These values for remember and know judgments are set out in Figure 2.

Using this data set, guesses made up 5%, 20%, and 27% of responses for what, wwwhen, and wwhich, respectively, for Group Immediate, and 12%, 24%, and 37%, respectively, for Group Distracter. Excluding guesses, the proportion of remember responses for wwwhen and wwhich were 60% and 45%, respectively, for Group Immediate, and 64% and 54%, respectively, for Group Distracter. This compares with 78% (Group Immediate) and 71% (Group Distracter) for what questions. Therefore, again it is not the case that the answers to episodic questions are overwhelmingly associated with remember experiences.

However, answers associated with an experiential response (i.e., remember, know, or guess) could be correct or incorrect. The proportion of answers associated with a remember response that were correct was significantly greater than chance for each question type for both groups (Group Immediate: what, P < 0.0001; wwwhen, P < 0.0001; wwhich, P < 0.01; Group Distracter: what, P < 0.0001; wwwhen, P < 0.0001; wwhich, P < 0.01). The proportion of answers associated with a know response that were correct was significantly greater than chance for each question type for both groups (Group Immediate: P = 0.48) nor Group Distracter (P = 0.19) showed above chance levels of accuracy for answers associated with a know response. As the pattern of data is matched across groups, the data were combined to increase the power, and the pattern of results remained constant: what (P < 0.0001) and wwwhen (P < 0.0001) know responses remained above chance levels of accuracy, while the accuracy of know responses for wwhich questions did not differ from chance levels (P = 0.11). Guesses to what questions were relatively rare, and so in order to increase power the two groups were combined for this analysis. Nonetheless, the power remained low, so despite a slight suggestion that such guesses were accurate (7/8 correct), this did not reach statistical significance (P = 0.07). However, for neither wwwhen nor wwhich was there any suggestion that guessed answers were above chance levels of accuracy (Group Immediate: wwwhen: P = 0.50, wwhich, P = 0.39; Group Distracter: wwwhen: P = 0.30, wwhich, P = 0.44). Therefore, the only type of responses that were not above chance levels of accuracy were know responses to the wwhich questions and all responses rated as guesses by the participants.

The confidence ratings of the answers given were also considered in order to investigate the possibility that know responses were less accurate in the wwhich task merely because they represented low-confidence answers. Only those responses from the above analysis that were rated as being high confidence (i.e., rated 4 or 5 on a 5-point scale) were further analyzed. Overall, while 88% of remember responses were rated as high confidence, only 48% of know responses were similarly highly rated. For this reason, the data from the two groups were combined to maintain power with this reduced data set (see Fig. 3). Here, it was found that the proportion of high-confidence answers associated with a remember response that were correct was again significantly greater than chance for each question type (what, P < 0.0001; wwwhen, P < 0.0001; wwhich, P < 0.0001). As before, the proportion of answers associated with a know response that was correct was significantly greater than chance for both what and wwwhen questions (P < 0.05 and P < 0.01, respectively). However, as above, for the wwhich questions, the answers associated with a know experience were not above chance levels of accuracy (P = 0.61). Therefore, the pattern of results found is entirely consistent whether considering all confidence levels or only those responses that are rated as being high confidence.

The results confirm that, as is reported in the literature (e.g., Yonelinas 2001; Fortin et al. 2004; Vann et al. 2009), object recognition (what questions) can be accurately performed by either recollection or familiarity-based processes, as answers associated with both remember and know responses were highly accurate. However, as episodic memories rely on recollection of the event being remembered, we hypothesized that if wwwhen and wwhich memories are truly episodic in nature, they would only be reliably correct when associated with an experience of remembering. As know responses indicate the processes of familiarity in the absence of recollection, answers to the hypothesized episodic questions (wwhich and wwwhen) that are associated with the experience of knowing were hypothesized not to be significantly accurate. In line with this hypothesis we found that one type of episodic-like memory question (wwhich) was only accurately answered using recollection. However, contrary to our hypothesis, the other episodic-like question (wwwhen) could be correctly answered either using recollection or familiarity.
answered using either recollection or familiarity-based mechanisms. In addition, contrary to previous reports in the literature (Holland and Smulders 2011), answers to questions based on episodic-like tasks previously used with animals were not overwhelmingly associated with the experience of remembering rather than knowing.

Before considering the implications of these findings, we will consider whether there is a confound that might explain the data. It is possible that know responses may simply reflect lower confidence responses and, therefore, would be inherently more likely to be incorrect (e.g., Wixted and Squire 2011). If this were the case, the difference between wwwhen and wwwwich in the accuracy of know responses might be due merely to more low-confidence responses in the latter. However, this possibility was discounted when only high-confidence answers were examined. Although know responses in general tended to have lower confidence than remember responses, this is in line with previous findings (e.g., Wixted and Squire 2011), i.e., remember responses are predominantly high confidence, while know responses can be associated with confidence levels across the confidence range. Nonetheless, when only high-confidence answers were examined, the pattern of results was unchanged, and even high-confidence know responses to wwwwich questions were not above chance levels of accuracy. Thus, confidence itself cannot explain the difference between the accuracy of remember and know responses between wwwwich and wwwhen.

Although the results from the what questions confirm much previous work (e.g., Yonelinas 2001), the results from the wwwwich question are the first demonstration that an episodic-like recognition memory task resembles episodic memory in requiring recollection for accurate performance. However, the result for wwwwhen questions is surprising and contrary to our initial predictions. Here, a task, which it has been claimed is dependent on episodic-like memory, has been found to not always require recollection for accurate performance, suggesting that it may not, in fact, be truly episodic.

There are two potential explanations for this unexpected result. First, wwwhen questions may simply not tap episodic memory. This would be surprising given that it has been argued that wwwwhen tasks are simply a subtype of wwwwich occasion tasks (Easton and Eacott 2008; Eacott and Easton 2010), and the results from the wwwwich questions confirm that they require episodic memory in order to be accurately answered. An alternative explanation is that the requirement for episodic memory in the wwwwhen task can be overcome by the use of an alternative, nonepisodic strategy based on familiarity of subcomponents of the event. This suggestion is supported by the fact that many know responses were produced even to the wwwwich episodic-like questions, albeit at chance levels of accuracy. Therefore, there is some sense of familiarity about the event being asked about, but that for wwwwich it is uncorrelated with the correct answer. As events are hypothesized to be remembered through episodic memory (using recollection, not familiarity), it may seem paradoxical that there can be such a sense of familiarity (whether accurate or not). However, we propose that a participant may respond that they know the answer because they have a sense of familiarity about some component(s) of the memory (e.g., having seen the object being asked about before, or the combination of object and location) without having recollection of the event as a whole. Thus, a participant who cannot recall the whole event and thus has no experience of remembering may nonetheless have an experience of familiarity based on subcomponents of the event (e.g., the object or object–location configuration). The strength of this sense of familiarity will depend on how long ago the familiar components were previously seen. For example, if the object–location configuration were previously seen in the first slide, it might be associated with a weaker memory trace than if it were seen in the more recent second slide. Therefore, the strength of the memory trace might allow the participants to make judgments about whether the familiar event (e.g., the familiar object–location pairing) was seen in the first or second slide. Such a sense of familiarity for the what–where subcomponent of the event, combined with trace strength information (how long ago) may be sufficient to allow correct answers to the wwwhen questions. This explanation would suggest that memory trace strength acts as a temporal cue for object–location memory, giving the appearance of wwwhen memory, but more accurately being a memory of what–where–how long ago, which is not a form of episodic memory (Roberts et al. 2008). However, if true, this explanation raises the question of why the wwwwich questions are not also subject to the same trace strength mechanisms. Providing that the temporal order of the contexts is encoded, the strength of the memory trace provides information about which context the object–location configurations was seen in, as well as whether it was the first or second event. Although we did not specifically ask our participants whether they could remember the order in which the two contexts were presented, it is likely that they could. Although this suggests that the same information is available in both, the results suggest that only the wwwhen question is answerable using familiarity-based trace strength mechanisms. It is plausible that the very nature of the wwwhen question cued participants to consider temporal order and, thus, spontaneously use trace strength. Although this strategy was potentially available for the wwwwich questions, the wording of the question may have instead cued a different search strategy based on memory for the content of the memory rather than its temporal occurrence. Although, at present, this remains only a possibility, it is an intriguing one: The different results for the wwwhen and wwwwich questions were gained from participants who were answering both types of questions, and the trace strength strategy appears to have been used for only one type of question (wwwhen), despite the fact that it was potentially available for both. This supports the view that in nonhuman animals wwwwhen tasks may be vulnerable to solution by nonepisodic mechanisms (Roberts et al. 2008), whereas wwwwich tasks may be less susceptible to such confounds (Easton and Eacott 2008; Eacott and Easton 2010).

It should be noted that the above discussion suggests that determining the temporal order of two events does not necessarily rely on episodic memory. However, there is evidence from rats (e.g., Fortin et al. 2002), monkeys (e.g., Charles et al. 2004), and human neuropsychological patients (e.g., Mayes et al. 2001) that temporal order judgments are hippocampally dependent, and that impairment in temporal order judgments in amnesic patients may be a result of the lack of access to recollection mechanisms. We acknowledge that there is good evidence that making temporal order judgments relies on episodic memory where those judgments cannot rely on trace strength. In these cases, making a temporal order judgment necessitates memory for the two occasions on which the events occurred. However, in those cases where differences in the trace strength of two events provide a readily available and reliable cue (such as the current task and, therefore, the similar tasks used in rodents) this can be used, and, so, such order judgments do not necessarily require episodic memory (Roberts et al. 2008).

We would note that the current data do not distract from the position that episodic memory can be considered in terms of content-based descriptions rather than phenomenological experience (Eacott and Easton 2007, 2010; Easton and Eacott 2008). Although we have used the phenomenological experience of the participants to validate the episodic-like memory tasks as models of episodic memory, we maintain that the phenomenological
experience is not in itself necessary. Rather, we claim that if episodic-like memory tasks in animals rely on the same system as episodic memory in humans, then when tested in humans they should give rise to the same phenomenological response (i.e., recollection) as episodic tasks, but not because the conscious recollection is a critical component of the episodic memory. Indeed, it remains a possibility that episodic memories do not require conscious recollection any more than it requires a memory for all content (i.e., an episodic memory in which you cannot remember every detail, such as the smell present on that occasion, is no less an episodic memory than one where that information is accessible). However, in animal studies of episodic-like memory, the burden of proof requires that we demonstrate memory that cannot be explained using nonepisodic alternatives, as debriefing of nonhuman participants to determine the experience of the memory is not possible. With the current data, we have provided further evidence (in addition to data from animals that meet the criteria of episodic-like memory set out by Clayton and colleagues (e.g., Clayton et al. 2003a), which for some of these episodic-like memory tasks (namely

"which" occasion) a nonepisodic solution to the task is less likely, as it requires recollection. It is possible that other tasks that do not meet these criteria remain valid models of episodic memory, but their validity cannot be as assured as that of the task we present here.

In conclusion, the results of the current study provide support for equivalence of content-based episodic-like recognition memory tasks ("which" occasion) used with animals and more conventional tasks used with human participants. This strengthens the conclusions drawn from use of this task with nonhuman populations (e.g., Eacott and Norman 2004; Langston and Wood 2010; Easton et al. 2011; KE Davis, A Easton, MJ Eacott, J Gigg, in prep.). Moreover, as a recognition memory task, it can be simply adapted to provide a comparable test of episodic memory for use with humans, including other nonverbal populations such as human infants (cf. Hayne and Imuta 2011).

References


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