

Article Addendum

Recognition without awareness in humans and its implications for animal models of episodic memory

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Key words: episodic memory, implicit memory, memory systems, animal cognition, recognition

Animal models of episodic memory—the ability to recall events from the past along with relevant spatial, temporal and other contextual detail—have been criticized on the grounds that it is difficult to determine if animals engage in the “mental time travel” that accompanies episodic recall in humans. It is possible that animals rely on mechanisms different from those operative in humans. We have added a new dimension to these concerns by showing that a test widely considered to measure episodic memory in humans could be constructed such that it measures nonconscious (implicit) memory under certain test parameters. The same parameters are common in tests frequently used to study recognition in nonhuman animals. In particular, recognition was driven by implicit memory when (1) recognition decisions could not be guided by semantic information, and (2) decisions were made with relatively high automaticity. These findings suggest that nonhuman animals may rely on implicit memory processing in many episodic-memory testing circumstances, as semantic content is minimal and automaticity is likely after the extended practice usually required. Identifying factors that promote and discourage recognition based on implicit memory is therefore necessary for creating accurate cognitive and neurobiological models of memory processing in humans and other animals.

A longstanding philosophical debate concerns knowing the extent to which conscious events like those that humans experience can also be experienced by other animals? Moreover, nonhuman animals are frequently used to examine neurobiological substrates of cognition, though the relevance of these findings to humans depends on close similarities across species in relevant neural mechanisms, cognitive

processing, and in some cases, awareness.

There are many reasons to remain skeptical of the assertion that nonhuman animals employ the same cognitive processes as humans in many circumstances.¹ A prime example concerns the challenges associated with determining if nonhumans have the capacity for episodic memory,² which refers to the ability to recall events from the past along with relevant spatial and temporal detail.^{3,4} For example, episodic recollection occurs when you remember what you consumed for dinner last night, when and where dinner occurred, the sequence of events, your specific perceptual experiences, and so on.

Episodic memory is often assessed using a recognition memory test, in which an item (such as an image or sound) is presented on more than one occasion with some delay in-between, and a respondent must decide whether a given item was presented before or whether it is new.^{4,5} One particular recognition test used frequently in memory research is the delayed matching-to-sample test.⁶⁻⁸ An object is presented for a brief period of time and, after a delay, the same object is presented along with a novel object and the respondent must select the old object that was presented initially. Conversely, in the delayed non-matching-to-sample test, the novel object is to be selected. In either case, performance in humans correlates strongly with episodic memory, in that recognition responses are made with simultaneous recollection of when the initial presentation occurred, where the object appeared initially, what thoughts occurred during the initial presentation, and other details. Moreover, humans report feeling confidence in their memory decisions and being aware of the fact that they had seen the object before. These subjective features are all hallmarks of episodic memory.⁴

It is unclear if nonhuman animals engage in this “mental time travel” or experience any confidence or awareness of retrieval during recognition tests. One can imagine that a nonhuman animal could select the old item simply because repetition enhanced visual processing fluency relative to the new item, and that the animal had learned to associate fluency with a behavior via conditioning. Correct responding for animals thus could be completely unrelated to episodic memory processing as it is understood in humans.^{3,6,9} In the past, evidence in support of this scenario had been lacking in that it had not been demonstrated whether correct responding could be accomplished based only on visual fluency rather than episodic memory.

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Submitted: 12/24/08; Accepted: 01/07/09

Previously published online as a *Communicative & Integrative Biology* E-publication: <http://www.landesbioscience.com/journals/cib/article/7822>

Addendum to: Voss JL, Baym CL, Paller KA. Accurate forced-choice recognition without awareness of memory retrieval. *Learn Mem* 2008; 15:454–9. PMID: 18519546; DOI: 10.1101/lm.971208.

In our recent report,¹⁰ we provide the first evidence that the fluency scenario is plausible by showing that recognition based only on visual fluency can occur in humans. Subjects in our experiments studied abstract kaleidoscope images that could not be easily named or associated with concepts. After a short delay, repeat images were presented alongside novel images that shared a high degree of perceptual similarity to the old images, and subjects were required to pick out the old image. Visual fluency due to repetition thus provided a valid cue to the old item. Subjects reported that this task was very difficult, but nonetheless were able to accurately segregate old items from new items. The remarkable finding is that accuracy was highest (over 80% correct) for those occasions when subjects reported guessing, which indicated no confidence in the decision and no awareness that the old image had been seen before. In contrast, accuracy was only minimally better than chance (50%) when subjects reported some confidence. This indicates that episodic memory processing was unhelpful, and suggests that subjects responded instead based on pure visual fluency.

Further evidence for this conclusion came from a manipulation of attention during the initial studying of images. Divided attention during study serves to degrade later episodic memory.¹¹ However, we found that subjects performed better after studying with divided attention than with full attention, again implicating visual fluency rather than episodic memory. In addition, these novel effects were only obtained when strategic episodic retrieval processing was limited via response signals during the recognition test, indicating that relatively automatic decisions were essential. Finally, when single old or new items were displayed one-at-a-time in random order with intervening images, rather than side-by-side, recognition accuracy was severely reduced, again indicating that accurate responding was based predominantly on a weighing of relative visual fluency. We were able to show that recognition can depend on visual fluency without episodic memory processing by examining the role of fluency in recognition for humans, who were able to verbally report on their recognition confidence, awareness and other episodic memory features.

Prior human recognition experiments never identified this pattern of effects, and there are several important parameters that set our experiments apart from these other experiments. Intriguingly, these same parameters made our study more similar to memory tests frequently used in nonhuman animals. Whereas most episodic memory experiments in humans utilize semantically rich materials, such as words and nameable objects, our experiments utilized nonverbal materials (to the extent that the kaleidoscope images did not lend themselves to being named, and any names that were elicited would be unlikely to help with later recognition). Importantly, recognition could not have been based on semantic information, as is the case when a repeated meaningful object must be discriminated from a new meaningful object. Semantic processing and episodic memory storage are closely interweaved, given that semantic elaboration robustly influences episodic memory (reviewed in refs. 12 and 13). Critically, semantic elaboration and recognition based on semantic information are unlikely in the usual testing circumstances for nonhuman animals. We also found that influences of visual fluency on recognition were observable when response signals promoted automatic responding, whereas most studies of episodic memory in humans have emphasized the benefits of deliberate memory search.¹⁴

It is highly likely that nonhuman animals develop a great deal of automaticity in response strategies during the extensive training required to learn to perform typical laboratory tasks. This extensive training might also serve to help uncover optimal performance strategies that maximize rewards, such as associating visual fluency with behavioral responses rather than engaging in strategic retrieval processing that could support episodic memory.

In summary, our findings add weight to the proposal that nonhuman animals utilize visual fluency without episodic memory when performing tasks intended to probe episodic memory. Some researchers have asserted that animal testing provides information on “episodic-like” memory^{15,16} rather than on episodic memory *per se*, and others have turned to studying natural memory behaviors in animals that embody the “what” and “where” components unique to episodic memory.¹⁷ Our findings indicate that examinations of the cognitive and neurobiological underpinnings of episodic memory in humans and other animals will miss their mark unless they simultaneously account for the many expressions of memory that can operate without the awareness of episodic retrieval.

References

1. Morgan CL. An introduction to comparative psychology. London: Walter Scott 1894.
2. Clayton NS, Bussey TJ, Dickinson A. Can animals recall the past and plan for the future? *Nat Rev Neurosci* 2003; 4:685-91.
3. Tulving E. Episodic and semantic memory. In: Tulving E, Donaldson W, (eds). *Organization of Memory*. New York: Academic Press 1972; 381-403.
4. Tulving E. Episodic memory: From mind to brain. *Annu Rev Psychol* 2002; 53:1-25.
5. Gabrieli JD. Cognitive neuroscience of human memory. *Annu Rev Psychol* 1998; 49:87-115.
6. Aggleton JP, Pearce JM. Neural systems underlying episodic memory: Insights from animal research. In: Conway MA, Aggleton JP, Baddeley AD, eds. *Episodic Memory: New Directions in Research*. New York: Oxford 2002.
7. Murray EA, Bussey TJ, Saksida LM. Visual perception and memory: A new view of medial temporal lobe function in primates and rodents. *Annu Rev Neurosci* 2007; 30:99-122.
8. Squire LR, Stark CE, Clark RE. The medial temporal lobe. *Annu Rev Neurosci* 2004; 27:279-306.
9. Hampton RR, Schwartz BL. Episodic memory in nonhumans: What, and where, is when? *Curr Opin Neurobiol* 2004; 14:192-7.
10. Voss JL, Baym CL, Paller KA. Accurate forced-choice recognition without awareness of memory retrieval. *Learn Mem* 2008; 15:454-9.
11. Mulligan NW. The role of attention during encoding in implicit and explicit memory. *J Exp Psychol Learn Mem Cogn* 1998; 24:27-47.
12. Craik FI, Lockhart RS. Levels of processing: A framework for memory research. *J Verb Learn Verb Behav* 1972; 11:671-84.
13. Craik FI, Tulving E. Depth of processing and the retention of words in episodic memory. *J Exp Psychol Gen* 1975; 104:268-94.
14. Yonelinas AP. Consciousness, control and confidence: The 3 Cs of recognition memory. *J Exp Psychol Gen* 2001; 130:361-79.
15. Griffiths D, Dickinson A, Clayton N. Episodic memory: What can animals remember about their past? *Trends Cogn Sci* 1999; 3:74-80.
16. Morris RG. Episodic-like memory in animals: Psychological criteria, neural mechanisms and the value of episodic-like tasks to investigate animal models of neurodegenerative disease. *Philos Trans R Soc Lond B Biol Sci* 2001; 356:1453-65.
17. Clayton NS, Dickinson A. Episodic-like memory during cache recovery by scrub jays. *Nature* 1998; 395:272-4.