

Episodic memory in nonhumans: what, and where, is when?

Robert R Hampton^{1*} and Bennett L Schwartz²

Episodic memory is defined as the recollection of specific events in one's past, accompanied by the experience of having been there personally. This definition presents high hurdles to the investigation of episodic memory in nonhumans. Recent studies operationalize episodic memory as memory for when and where an event occurred, for the order in which events occurred, or for an animal's own behavior. None of these approaches has yet generalized across species, and each fails to capture features of human episodic memory. Nonetheless, the study of episodic memory in nonhumans seems less daunting than it did five years ago. To demonstrate a correspondence between human episodic memory and nonhuman memory, progress is needed in three areas. Putative episodic memories in nonhumans should be shown to be; first, represented in long-term memory, rather than short-term or working memory; second, explicit, or accessible to introspection; and third, distinct from semantic memory, or general knowledge about the world.

Addresses

¹Laboratory of Neuropsychology, Building 49, Room 1B-80, National Institute of Mental Health-NIH, Bethesda, MD 20892, USA
²Department of Psychology, Florida International University, Miami, FL 33199, USA
e-mail: hamptonr@mail.nih.gov

Current Opinion in Neurobiology 2004, **14**:192–197

This review comes from a themed issue on
Cognitive neuroscience
Edited by John Gabrieli and Elisabeth A Murray

0959-4388/\$ – see front matter
© 2004 Elsevier Ltd. All rights reserved.

DOI 10.1016/j.conb.2004.03.006

Introduction

In 1972 Tulving proposed a new distinction among types of long-term memory [1]. 'Semantic memory' consists of facts about the world: water is scarce in the desert, seafood must be fresh to be safe. 'Episodic memory' subserves the ability to recall events from the personal past: running out of water on a desert hiking trip, the time you were sickened by spoiled clams at a beach party. In contrast to procedural and other types of implicit memory, semantic and episodic memories are explicit, and humans are consciously aware of them (Figure 1). A further phenomenal criterion was later added to the definition, such that episodic memory involves conscious re-experiencing of a past event [2]. In experimental settings, this re-experiencing of an event is often operationalized by asking subjects whether they 'remember' studying a recognized test

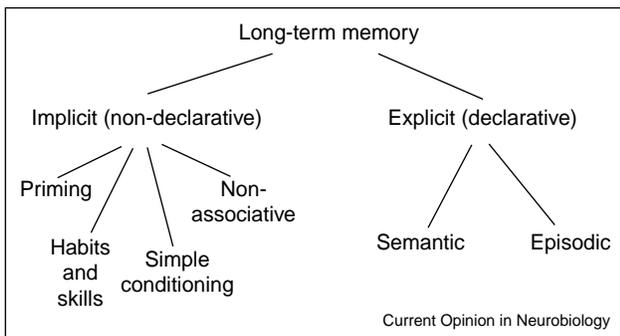
item or simply 'know' they have seen the item, without specific recollection of the study event [3]. Thus, human episodic memory is said to be characterized by conscious recollection of specific events from one's personal past. Evidence from case studies, functional imaging, and behavioral studies has demonstrated that episodic and semantic memory are distinct in humans [4–7].

Studies using nonhuman subjects permit use of investigative tools not available in studies of humans. Accordingly, efforts are ongoing to develop methods for studying the fullest possible complement of human memory systems in animals. Complementing this anthropocentric approach, comparative psychologists seek to determine which memory systems exist in various species, and how they differ across species, in an effort to understand the evolution of human and nonhuman cognition more broadly [8]. Episodic memory has proven particularly difficult to demonstrate in nonverbal species, even in principle [6,9–11,12*]. In this article we review recent experimental approaches to the study of episodic memory in nonhumans. While identifying the strengths of these studies, we also identify some criteria for episodic memory that have yet to be met. We contend that a psychologically rich demonstration of episodic memory in nonhumans is yet to be achieved.

Episodic-like memory: what, where, and when

Nonhumans retain information about sights they have seen and locations they have visited; they also mark the passage of time using interval and circadian timing mechanisms [8,13]. One approach to episodic memory in nonhumans posits that memory for what occurred, where it occurred, and when it occurred constitutes memory for an episode [14]. Food-hoarding scrub-jays (*Aphelocoma californica*) cached either wax moth larvae (which the birds' previous experience had shown to be delicious, but perishable) or peanuts (preferred less, but not perishable) in sand-filled ice-cube trays. When given the opportunity to retrieve the previously hidden food after a short delay interval the birds searched first for the still tasty larvae. By contrast, after a long interval the birds searched first in the locations where peanuts had been hidden, demonstrating that they knew what foods had been hidden in which locations, and how long ago [14]. Crucially, the delay intervals used were hours to days, outside the range in which interval timing mechanisms have been shown to operate [13], and tests were arranged to prevent use of time of day to guide food choice. Clayton and Dickinson [14] argued that this behavior demonstrated memory of a specific episode. However, in

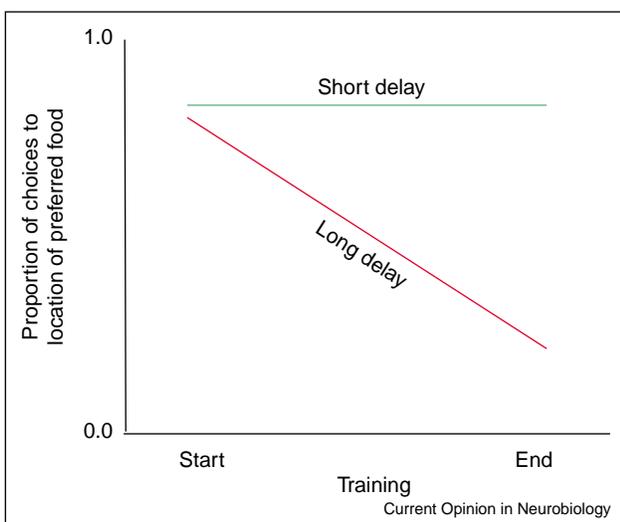
Figure 1



Taxonomy of long-term memory systems [48]. Implicit memory affects behavior without awareness. By contrast, we are consciously aware of explicit memories. Explicit memory is divided into semantic memory, representing general knowledge about the world, and episodic memory, representing personal knowledge of one's own past. Short-term, or working, memory is not depicted.

recognition of the fact that they had no direct evidence that the birds' consciously recollected the personal past, they called it 'episodic-like' memory. Since this first demonstration, Clayton and co-workers have carried out an extensive set of experiments reinforcing and extending their initial findings [14–18,19*]. The general pattern of behavior expected in a 'what-where-when' experiment is shown in Figure 2.

Figure 2



Idealized data from an experiment demonstrating memory for 'what,' 'where' and 'when'. As training progresses, subjects learn that a preferred food is available only after a short delay, whereas a less preferred food reward is available after both long and short delays. Eventually, subjects learn to search locations containing the preferred food only after a short delay, thus demonstrating that they know what foods are in which locations, and how long ago they learned this information.

Although considerable excitement resulted from the experiments with scrub-jays, the result of Clayton and Dickinson [14] has not yet been reproduced in any other species, despite efforts to do so. In experiments that closely parallel the work with scrub-jays, rats (*Rattus norvegicus*) carried preferred cheese chunks and less preferred pretzel pieces to boxes located at the ends of the arms of an eight-arm radial maze, where the food was left (Figure 3). The cheese was made unpalatable by treatment with a quinine solution (for half the rats cheese was thus degraded after short delays, for the other half after long delays). The rats showed reliable memory for the type and location of food, but they did not learn to search pretzel locations selectively after delays associated with quinine treatment of the cheese [20*]. In a related set of experiments rats also failed to learn to re-enter the first arm of the maze visited during a session to receive a large reward [21]. Monkeys also show evidence for memory of 'what' and 'where' but not 'when' in experiments in which they learn to touch specific locations in unique visual 'scenes' presented on a computer monitor [22]. Although 'scene-specific memory' has been influential in theories of hippocampal function in primates because it requires rapid context-dependent learning, it falls short as a model of episodic memory given the present criteria.

Odor order: memory for sequences of events

A different approach to studying episodic memory focuses on the order of occurrence of events. Rats encountered a 'list' of five consecutive odors. When subsequently presented with two odors from the list, normal rats, but not those with damage to the hippocampus, correctly identified which of the two test odors had occurred first in the list [23*,24*]. Earlier work had similarly shown that memory for the order of visits to locations (rather than odors) was impaired by hippocampal lesions [25,26], but interpretation of these results was complicated by the importance of the hippocampus for spatial memory generally [27]. Intact recognition memory in the rats with hippocampal damage suggests that rats do not depend on relative familiarity or relative memory trace strength to determine which odor was encountered first [23*]. However, the rats were more accurate at reporting serial order when two or three odors, rather than just one odor, had separated the target odors in the study list. In fact, the rats were unable to identify which odor came first when the test odors occurred consecutively in the study list [24*]. These results suggest that rats discriminate order on the basis of a continuous representation of order that is prone to interference between items closely spaced on the 'order continuum'. Such interference would be predicted if rats used some measure of relative memory strength to discern order, perhaps arguing against an episodic memory interpretation. That the impairment in rats with hippocampal damage was paradoxically largest when the task was easiest [24*] might offer an additional clue as to the mechanism(s) underlying order

Figure 3



Photo of the novel radial-arm maze used to parallel food caching studies conducted with birds [20]. Rats encounter relatively large pieces of cheese and pretzel on the center platform, which they carry to the boxes at the ends of the arms. In the box, the experimenter gently separates the rat from its food, leaving the food in the box and returning the rat to the central platform from which it can carry additional food to other boxes on the maze. Later, rats are allowed to search for food previously left in the various boxes. The guillotine doors surrounding the central platform permit the experimenter to control access to specific arms. This preparation permits close parallels with experiments conducted with food-hoarding birds.

memory. Potentially useful models for study of the representations underlying order memory can be found in earlier work with nonhumans [28,29]; however, these earlier studies have not generally been discussed in reference to episodic memory, presumably because performance is not based on a single study episode [30].

A matter of semantic: orienting to the past

One feature distinguishing episodic from semantic memory is that episodic memory is necessarily ‘palinscopic’ or oriented towards the past [31]. Contrast the memory of placing an apple on your desk yesterday, which is an episodic memory, with the semantic knowledge that there are apples in the grocery store. In the case of the studies of scrub-jays one could ask whether the birds remember the event of caching worms in a particular location, a memory that is oriented to the past, or simply know the current state of the world — that caches are in particular locations, and have been there for particular periods of time. In an effort to ensure that memory is oriented toward the past, a gorilla (*Gorilla gorilla gorilla*) was exposed to unique events, such as an unfamiliar human playing a guitar. Five minutes later the gorilla identified the human, using a set of photographs [32]. The gorilla similarly identified both which type of fruit was given to him and which of three familiar people had given it to him after delays of up to 24 h [33*]. Because these events are discrete, and there is no current state of the world to which they correspond at test, the authors argued that accurate performance requires memory oriented to the past. Further work will be required to test whether or not these techniques capture ‘palinscopy’ any better than standard matching-to-sample procedures.

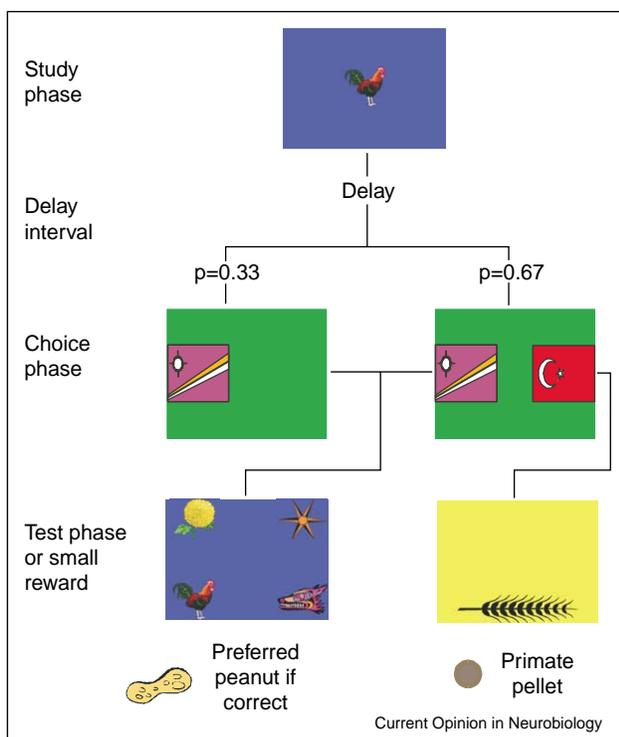
‘What’, ‘where’, and ‘when’ memories of one’s life can take a semantic form [34,35]. For example, because we are asked so often, we all know that we were born, as well as when and where this occurred, despite lacking episodic memory for the event. By contrast, if asked a novel and unexpected autobiographical question (“did you wear a blue shirt yesterday?”), episodic memory is more likely to underlie the ability to answer [35]. Two studies in which nonhuman animals were unexpectedly asked to report on their recent actions have been taken as evidence for episodic memory. Pigeons (*Columba livia*) accurately reported whether or not they had recently been pecking, even when the judgment was made under conditions in which the pigeons should not have anticipated being required to respond [35]. Similarly, dolphins (*Tursiops truncatus*) correctly responded to a ‘repeat’ command by reproducing actions that they recently performed, possibly indicating autobiographical memory for their own recent behavior [36].

Other criteria

Two important features of the memory taxonomy shown in Figure 1 have not been addressed directly by any of the studies thus far reviewed. First, because the taxonomy is one of long-term memory, any demonstration of episodic memory must be shown to be a form of long-term, rather than short-term, or working, memory. It is not clear where to place the temporal boundary between short-term and long-term memory, even within a particular species. Further complicating matters, the term working memory is used quite differently in the human cognitive [37] and animal learning [38] literatures. Second, both semantic and episodic memory are in the explicit limb of the

taxonomy of memory systems, indicating conscious experience of memory in humans. Thus, procedures used with nonhumans should discriminate between implicit and explicit memory [34]. Whereas it can be argued that it is impossible to measure memory awareness in animals [11,39], behavioral techniques have been developed that may permit a functional distinction between implicit and explicit memory nonverbal species [40–44]. Explicit memory presumably permits discrimination between remembering and forgetting, whereas implicit memory does not afford this discrimination because one is unaware of the presence of implicit memories. Rhesus monkeys and apes collect more information, or avoid memory tests entirely, when they do not know the correct response. By contrast, when they know the correct response they take the memory test directly (Figure 4; [40,42,43]).

Figure 4



Method for assessing whether nonverbal subjects know when they remember [42]. Each colored panel represents what subjects see on a computer monitor at each stage in a trial. At the start of each trial subjects study an image. A delay period follows over which subjects often forget the studied image. On two thirds of trials subjects choose between taking a memory test (right panel, left hand stimulus) and declining the test (right panel, right hand stimulus). On one third of trials subjects are forced to take the test (left panel). Better accuracy on chosen memory tests than on forced tests indicates that subjects know when they remember, and decline tests when they have forgotten, if given the option. The same general logic of providing subjects an opportunity to avoid tests, or collect more information before completing the test, has been employed in different settings [40,41,43,44].

Human episodic memory is accessible through free recall [3], but most tests of nonhuman memory are conducted in a recognition memory format. By this we mean that subjects are tested in forced-choice situations in which the originally studied material is re-presented. It is therefore possible, for example, for subjects to identify which stimulus is (relatively) familiar, and approach or avoid it as required, rather than recalling a memory of the study episode in which the stimulus became familiar. Rats demonstrated cued recall by identifying where they had encountered a distinctly flavored food after being cued with the flavor alone, and performance in these tests depended on normal hippocampal function [45]. Free recall, in contrast to cued recall, requires retrieval of the studied material in the absence of rich retrieval cues. For example, one has few cues to stimulate memory when given a blank sheet of paper and the free recall instruction, “write down as many words as you can remember from the list”. By contrast, if one is presented with a list of words and the recognition instruction, “which of these items have you seen recently?” the list offers rich cues for memory retrieval. Up to 16 h after observing food being hidden in the forest surrounding her enclosure, a language trained chimpanzee (*Pan troglodytes*) spontaneously ‘recruited’ care takers to go outside, where she then correctly located the hidden food by pointing [46]. Significantly, the chimpanzee initiated the search from indoors (where the forest was not visible), and correctly indicated the type of food hidden using a lexigram keyboard, before going outside that day (Figure 5). Retrieval of a memory for the hidden food under these cue-impo- verished conditions suggests that she freely recalled a memory of the hiding episode.

Conclusions

A psychologically rich demonstration of episodic memory in nonhumans remains elusive, but converging approaches might have it surrounded. The studies of cache recovery in scrub-jays are the most sustained effort to demonstrate episodic memory in nonhumans [14]. Yet in the five years following publication, the phenomenon has yet to be reproduced in another species. Although elements of episodic memory, such as explicitness, free recall, and orientation to the past have been demonstrated in isolation, the suite of features defining human episodic memory has not been shown in any single paradigm with nonhumans. It could be that episodic memory represents a sharp discontinuity in evolution, and that humans are unique in possessing it [6,34]. However, in order to evaluate this possibility episodic memory must be defined in purely behavioral terms [47], applicable to nonverbal species, to the fullest extent possible. The technical innovations and novel perspectives behind recent work in nonhumans go some distance towards such a redefinition of episodic memory and might compel a reconsideration of criteria for human episodic memory.

Figure 5



A chimpanzee pointing to the lexigram for 'grapes'. The chimpanzee would indicate the type of food hidden, and recruit a human to meet her outside to retrieve the food, as much as 16 h after she had watched it being hidden outdoors [46].

Acknowledgements

Preparation of this manuscript was supported by the National Institute of Mental Health Intramural Research Program. We thank T McKenzie and B Roberts for the photograph in Figure 3, and C Menzel for the photograph in Figure 5.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Tulving E: **Episodic and semantic memory**. In *Organisation of Memory*. Edited by Tulving E, Donaldson W. San Diego: Academic Press; 1972:381-403.
 2. Tulving E: *Elements of Episodic Memory*. New York: Oxford University Press; 1983.
 3. Tulving E: **Memory and consciousness**. *Can Psychol* 1985, **26**:1-12.
 4. Vargha-Khadem F, Gadian DG, Mishkin M: **Dissociations in cognitive memory: the syndrome of developmental amnesia**. *Philos Trans R Soc Lond B Biol Sci* 2001, **356**:1435-1440.
 5. Vargha-Khadem F, Gadian DG, Watkins KE, Connelly A, VanPaesschen W, Mishkin M: **Differential effects of early hippocampal pathology on episodic and semantic memory**. *Science* 1997, **277**:376-380.
 6. Tulving E: **Episodic memory: from mind to brain**. *Annu Rev Psychol* 2002, **53**:1-25.
 7. Gardiner JM, Java RI: **Recognition memory and awareness - an experimental approach**. *Eur J Cogn Psychol* 1993, **5**:337-346.
 8. Shettleworth SJ: *Cognition, Evolution, and Behavior*. New York: Oxford University Press; 1998.
 9. Suddendorf T, Corballis MC: **Mental time travel and the evolution of the human mind**. *Genet Soc Gen Psychol Monogr* 1997, **123**:133-167.
 10. Roberts WA: **Are animals stuck in time?** *Psychol Bull* 2002, **128**:473-489.
 11. Tulving E, Markowitsch HJ: **What do animal-models of memory model?** *Behav Brain Sci* 1994, **17**:498-499.
 12. Tulving E: **Episodic memory and common sense: how far apart?**
 - In *Episodic Memory: New Directions in Research*. Edited by Baddeley AD, Conway M, Aggleton J. New York: Oxford University Press; 2002:269-288.

Tulving presents his most recent account of his theory of episodic memory. Episodic memory requires the ability to see oneself as an individual extending both backwards and forwards in time (autonoesis). He claims that animals lack autonoetic consciousness, which prevents them from retrieving episodically or consciously planning for the future.
 13. Roberts WA: *Principles of Animal Cognition*. Boston: McGraw Hill; 1998.
 14. Clayton NS, Dickinson A: **Episodic-like memory during cache recovery by scrub jays**. *Nature* 1998, **395**:272-274.
 15. Clayton NS, Dickinson A: **Memory for the content of caches by scrub jays (*Aphelocoma coerulescens*)**. *J Exp Psychol Anim Behav Process* 1999, **25**:82-91.
 16. Clayton NS, Dickinson A: **Motivational control of caching behaviour in the scrub jay, *Aphelocoma coerulescens***. *Anim Behav* 1999, **57**:435-444.
 17. Clayton NS, Dickinson A: **Scrub jays (*Aphelocoma coerulescens*) remember the relative time of caching as well as the location and content of their caches**. *J Comp Psychol* 1999, **113**:403-416.
 18. Clayton NS, Yu KS, Dickinson A: **Scrub jays (*Aphelocoma coerulescens*) form integrated memories of the multiple features of caching episodes**. *J Exp Psychol Anim Behav Process* 2001, **27**:17-29.
 19. Clayton NS, Yu KS, Dickinson A: **Interacting cache memories: Evidence for flexible memory use by Western Scrub-jays (*Aphelocoma californica*)**. *J Exp Psychol Anim Behav Process* 2003, **29**:14-22.

The authors allowed scrub-jays to cache preferred crickets and less preferred peanuts. During the interval between caching and recovery, the birds were taught that crickets, which used to be edible three days after caching, now degraded over that period. Birds then avoided the cricket caches during recovery three days after caching. Thus, jays appear to retrospectively apply information acquired after a caching episode to guide retrieval.
 20. Bird LR, Roberts WA, Abroms B, Kit KA, Crupi C: **Spatial memory for food hidden by rats (*Rattus norvegicus*) on the radial maze: studies of memory for where, what, and when**. *J Comp Psychol* 2003, **117**:176-187.

The authors describe techniques for studying food 'caching' in rats on the radial maze. Rats remembered what foods had been left in which

locations, but did not learn that food was inedible after particular delays. Thus, rats showed memory for 'what' and 'where,' but not 'when'.

21. Roberts WA, Roberts S: **Two tests of the stuck-in-time hypothesis.** *J Gen Psychol* 2002, **129**:415-429.
22. Gaffan D: **Scene-specific memory for objects - a model of episodic memory impairment in monkeys with fornix transection.** *J Cogn Neurosci* 1994, **6**:305-320.
23. Fortin NJ, Agster KL, Eichenbaum HB: **Critical role of the hippocampus in memory for sequences of events.**
 - **hippocampus in memory for sequences of events.** *Nat Neurosci* 2002, **5**:458-462.

In this companion to Kesner *et al.* [24*], rats were allowed to dig in a series of sand-filled cups, each exuding a distinctive odor. Later, rats were rewarded for choosing from two cups the one with the odor that had appeared earliest in the series. Normal rats were moderately accurate (70–80% correct), but rats with hippocampal damage performed near chance. The groups did not differ in a test of recognition memory for odors, thus dissociating memory for items from memory for serial order.
24. Kesner RP, Gilbert PE, Barua LA: **The role of the hippocampus in memory for the temporal order of a sequence of odors.**
 - **memory for the temporal order of a sequence of odors.** *Behav Neurosci* 2002, **116**:286-290.

Using methods nearly identical to those described for Fortin *et al.* [23*], the authors showed that hippocampal damage impairs memory for serial order. Accuracy was higher if more than one odor intervened during study between the two odors compared at test. Hippocampal damage did not impair the ability to discriminate odors from one another.
25. Kesner RP, Novak JM: **Serial position curve in rats - role of the dorsal hippocampus.** *Science* 1982, **218**:173-175.
26. Chiba AA, Kesner RP, Reynolds AM: **Memory for spatial location as a function of temporal lag in rats - role of hippocampus and medial prefrontal cortex.** *Behav Neural Biol* 1994, **61**:123-131.
27. Nadel L: **The hippocampus and space revisited.** *Hippocampus* 1991, **1**:221-229.
28. Terrace HS, Son LK, Brannon EM: **Serial expertise of rhesus macaques.** *Psychol Sci* 2003, **14**:66-73.
29. Terrace HS, McGonigle B: **Memory and representation of serial order by children, monkeys, and pigeons.** *Curr Dir Psychol Sci* 1994, **3**:180-185.
30. Agster KL, Fortin NJ, Eichenbaum H: **The hippocampus and disambiguation of overlapping sequences.** *J Neurosci* 2002, **22**:5760-5768.
31. Tulving E, LePage M: **Where in the brain is the awareness of one's past?** In *Memory, Brain, and Belief*. Edited by Schacter D, Scarry E. Cambridge: Harvard University Press; 2000:208-230.
32. Schwartz BL, Meissner CA, Hoffman M, Evans S, Frazier LD: **Event memory and misinformation effects in a gorilla (*Gorilla gorilla gorilla*).** *Animal Cognition* 2004. Published online ahead of print, DOI: 10.1007/s10071-003-0194-7.
33. Schwartz BL, Colon MR, Sanchez IC, Rodriguez IA, Evans S:
 - **Single-trial learning of 'what' and 'who' information in a gorilla (*Gorilla gorilla gorilla*): implications for episodic memory.** *Anim Cogn* 2002, **5**:85-90.

A gorilla was given food by three familiar humans. Five minutes and 24 h after a single food presentation, the gorilla correctly selected cards associated with both the food and the human. The authors argue that the gorilla remembered episodically, because he reported both 'who' and 'what' after retention intervals consistent with long-term memory.
34. Suddendorf T, Busby J: **Mental time travel in animals?** *Trends Cogn Sci* 2003, **7**:391-396.
35. Zentall TR, Clement TS, Bhatt RS, Allen J: **Episodic-like memory in pigeons.** *Psychon Bull Rev* 2001, **8**:685-690.
36. Mercado E, Murray SO, Uyeyama RK, Pack AA, Herman LM: **Memory for recent actions in the bottlenosed dolphin (*Tursiops truncatus*): repetition of arbitrary behaviors using an abstract rule.** *Anim Learn Behav* 1998, **26**:210-218.
37. Baddeley AD: **Working memory: looking back and looking forward.** *Nat Rev Neurosci* 2003, **4**:829-839.
38. Honig WK: **Studies of working memory in the pigeon.** In *Cognitive Processes in Animal Behavior*. Edited by Hulse SH, Fowler H, Honig WK. Hillsdale, NJ: Lawrence Erlbaum; 1978:211-248.
39. Eichenbaum H, Fortin NJ: **Episodic memory and the hippocampus: it's about time.** *Curr Dir Psychol Sci* 2003, **12**:53-57.
40. Smith JD, Shields WE, Washburn DA: **Memory monitoring by animals and humans.** *J Exp Psychol Gen* 1998, **127**:227-250.
41. Inman A, Shettleworth SJ: **Detecting metamemory in nonverbal subjects: a test with pigeons.** *J Exp Psychol Anim Behav Process* 1999, **25**:389-395.
42. Hampton RR: **Rhesus monkeys know when they remember.** *Proc Natl Acad Sci U S A* 2001, **98**:5359-5362.
43. Call J, Carpenter M: **Do apes and children know what they have seen?** *Anim Cogn* 2001, **4**:207-220.
44. Smith JD, Shields WE, Washburn DA: **The comparative psychology of uncertainty monitoring and metacognition.** *Behav Brain Sci* 2003, **26**:317-374.
45. Day M, Langston R, Morris RGM: **Glutamate-receptor-mediated encoding and retrieval of paired- associate learning.** *Nature* 2003, **424**:205-209.
46. Menzel CR: **Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan troglodytes*) after extended delays.** *J Comp Psychol* 1999, **113**:426-434.
47. Clayton NS, Bussey TJ, Dickinson A: **Can animals recall the past and plan for the future?** *Nat Rev Neurosci* 2003, **4**:685-691.
48. Squire LR, Zola-Morgan S: **The medial temporal-lobe memory system.** *Science* 1991, **253**:1380-1386.