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

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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.

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Introduction

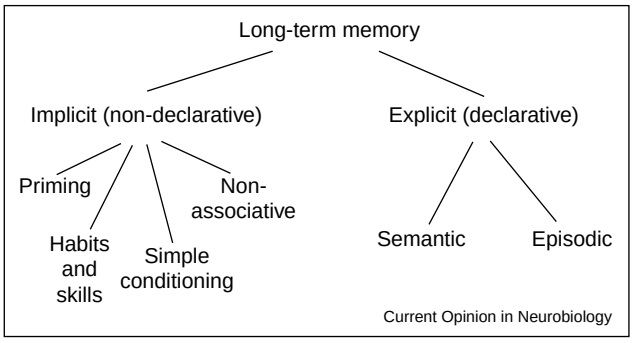
In 1972 Tulving proposed a new distinction among types of long-term memory [1]. 'Semantic memory' consists of facts about the world: water is scarce in the desert, seafood must be fresh to be safe. 'Episodic memory' subserves the ability to recall events from the personal past: running out of water on 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

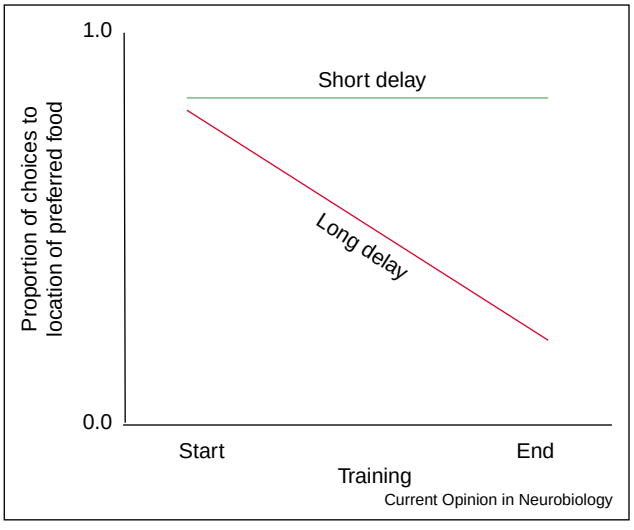
Figure 1



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.

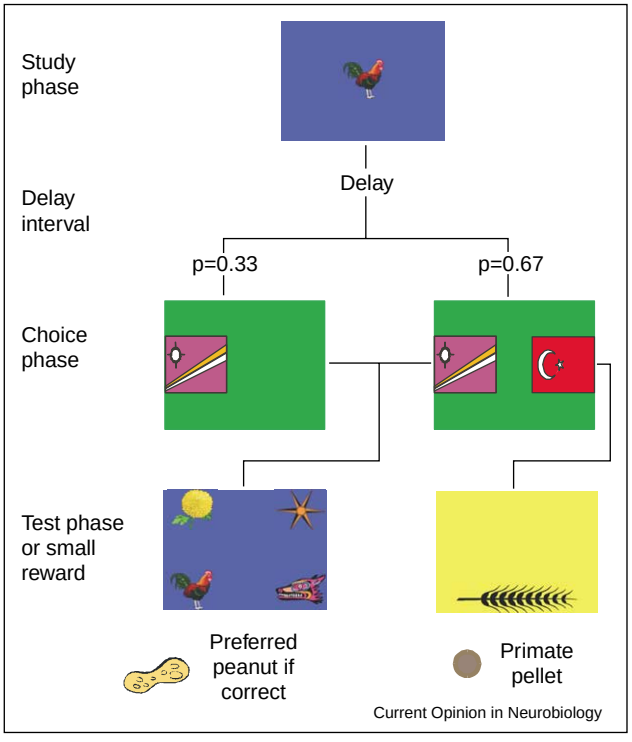
'What', 'where', and 'when' memories of one's life can take a semantic form [34,35]. For example, because we are asked so often, we all know that we were born, as well as when and where this occurred, despite lacking episodic memory for the event. By contrast, if asked a novel and unexpected autobiographical 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-impoverished 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].

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