



## Research report

## Behavioural evidence for mental time travel in nonhuman animals

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## ABSTRACT

If episodic memory is an adaptation, it must have evolved to benefit present or future survival and reproduction, rather than to provide an accurate record of the past *per se*. Recent research has documented various links between the ability to construct episodes of the past and imagine potential future episodes, and it has been argued that the former may be a design feature of the latter. Thus, claims about the existence of episodic memory in non-verbal organisms may be evaluated by examining behavioural evidence for foresight. Here we review recent data on foresight in animals and conclude that the evidence to suggest episodic memory so far is equivocal. We suggest specific experimental criteria that could provide stronger evidence. We maintain that there must be uniquely human traits for which there are no animal models and it remains possible that mental time travel depends on several such traits. Identification of what precisely is unique about the human capacity and what is not, can inform us about the nature and evolution of the human capacities.

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## 1. Introduction

Can nonhuman animals imagine the world of tomorrow? Can they regret what they did last month and envision doing it better next year? Research is beginning to address whether nonhuman animals might be able to travel mentally in time, and if so, to what extent. Although this special issue is dedicated to the study of episodic memory, we will focus here on evidence for thinking about future events. Foresight requires some memory capacities, and memory systems have been shaped, in part, by natural selection for better prediction [1]. Thus, future-directed actions may represent behavioural expressions for certain memory capacities. The current interest in studying “episodic-like” memory in nonhuman animals, in particular, has brought to the fore the need to establish behavioural indicators of episodic memory. Here we discuss the logic of this approach and review the state of the current evidence. Recent work on food-caching birds [2,3] and on great apes [4,5] suggests that they might have some capacity for flexible foresight. However, there is an ongoing debate about what precisely these studies have so far demonstrated [6–8]. We respond to this debate, review recent evidence from primate studies and suggest specific experimental criteria that could help overcome the current impasse.

## 2. Looking to the future as evidence for memory

Memory research typically involves a study phase and the main dependent variable is accuracy of retrieval. From an evolutionary perspective, however, memory capacities can only be selected on the basis of what they contribute to survival and reproduction, whether or not they accurately reflect the past [1]. This perspective might explain why our memory of past events is frequently inaccurate; subject to bias, decay and suggestion [9,10]. It may even be the case that episodic memory is merely an adaptive design feature of the ability to conceive of future events [11,10]. In other words, we may be able to recollect past events only because this mechanism allows us to imagine future events. But that proposal is difficult to assess and there are other ways in which episodic memory may increase fitness (e.g., allowing us to learn from the same event more than once [12]). Be that as it may, there is a strong case for the so-called Janus hypothesis [13,14], the idea that mentally conceiving of past events and imagining future events are closely linked in mind and brain [15,1,10,16,17].

Amnesic patients who cannot recall personally experienced events have been found to have parallel problems with future events [18–21]. There are also conditions characterised by milder disturbances in mental access to both past and future events [22,23]. Studies of impairments may of course be misleading; for instance, deficits in episodic memory may be due to a gist-based recall strategy rather than a memorial deficit *per se* [24]. However, commonalities between episodic memory and foresight are increasingly documented in other contexts. Mental time

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travels into past and future have phenomenological similarities [25,26] and share various distribution characteristics [27]. Imagining more distant events typically leads to more abstract and de-contextualized scenarios than events closer in time [26,28]. There are links in how young children acquire episodic memory and episodic future thinking [29–31], and there is a parallel decline in past and future mental time travel detail with advanced age [32]. Finally, there is growing evidence for a strong overlap in the brain areas implicated in episodic memory retrieval and imagining future events. fMRI and PET studies point to regions of the medial prefrontal cortex, and lateral and medial parts of the parietal cortex and temporal lobes (e.g. [33–36]).

The fact that these links are there does not of course mean that there are no profound differences. Obviously, episodic memory refers to events that have happened whereas the future has not yet eventuated, and in fact may often never eventuate the way it was imagined. Not surprisingly, there must be important differences in the cognitive processes involved in mental time travel into the past and future (see [37], for review). Nonetheless, if the Janus hypothesis is correct, then evidence for the latter may also be regarded as evidence for the former. This opens up an unusual way of behaviourally examining episodic memory in nonhuman animals [38,16].

### 3. Testing episodic memory

In adult humans episodic memory is generally assessed through self-reports. Much of human conversation involves recounting past episodes and planning future events. Tulving [21] argued that retrieval from episodic memory is accompanied with self-knowing, or “autonoetic”, consciousness (“this happened to me”). This introspective experience of remembering past events, according to Tulving, is the key defining characteristic of episodic recall. While such a phenomenological approach has led to useful research with human participants who, for example, can be asked to report if they remember or merely know something [39,40], it is not readily transferable to non-linguistic subjects. Thus, without language there may be little hope of ever establishing evidence for autonoetic consciousness and hence, by this definition, episodic memory in animals [41]. This may not be entirely impossible though. Suddendorf and Busby [11] pointed out some ways in which nonhuman animals could in principle have the means to report past experiences, but no convincing evidence has yet emerged. Nevertheless, it is not clear whether nonhuman animals do not have autonoetic consciousness, or whether some of them do have it and researchers have not yet been able to demonstrate this.

In light of these difficulties, many comparative researchers have returned to Tulving’s discarded initial definition of episodic memory: memory for what happened where and when [42]. Clayton and Dickinson showed that it is possible to examine memory for this kind of information in non-verbal paradigms with food-caching scrub jays [43]. They showed that these birds adjust their behaviour according to what food was stored where and when. Many studies [44–47,1,48] have since adopted this approach arguing for what, where, when memory in species ranging from mice [49] to bees [50]. In spite of this prolific spread of what we might call the *www*-memory approach there are reasons to be cautious with the comparison to human episodic memory [51,52,11]. One important issue is the question of whether the “when” information in these paradigms represents the time of a past event or whether simpler mechanisms, such as the decaying strength of a memory trace, may be sufficient to explain the behaviour [47,53,1]. Rats have been shown to record how long ago food was found, rather than when it was found, a process that need not imply mental travel into the past [53].

Furthermore, Clayton and colleagues refer to “episodic-like memory” in acknowledgment of the fact that these paradigms do not test the subjective feel (i.e., autonoetic consciousness) that is essential to meet the current definition of human episodic memory [21]. One reason human episodic memory is no longer characterised as memory for what where and when information is that there is a double dissociation here [11]. People can report what, where and when information about events (e.g., the shooting of Abraham Lincoln; one’s birth) without being able to mentally relive the events. Conversely, because episodic retrieval is based on active reconstruction and is characterised by various biases and errors, veracity of what, where and when information is not its hallmark. That is, one may recall a particular event and yet be factually wrong in its *www* specifics. Evidence for retention of accurate *www* information is not equivalent to evidence for episodic memory. For this, and some other reasons, convincing evidence for episodic memory in nonhuman animals has remained elusive [1].

If researchers find it difficult to establish clear signs of episodic memory in animals, then how could natural selection have differentiated between an individual that has semantic or procedural memory and one that has episodic memory? Unless episodic memory is a mere side product, or spandrel, there must be something enhancing fitness for it to be selected and it is difficult to conceive that this is merely the subjective feel at retrieval (i.e., autonoetic consciousness). What could be a tangible, demonstrable effect on survival or reproduction? As foreshadowed at the beginning, a memory system can be selected on the basis of what it contributes to future survival and reproduction—foresight can offer serious adaptive advantages [38,11].

### 4. Foresight in nonhuman animals

Current behaviour can not only influence current fitness, but also increase or decrease future survival and reproduction chances. Thus, there is a range of future-directed capacities evident in the animal kingdom. Mechanisms that can track significant regularities such as when and where food or reproductive partners are available are adaptive. Some species have adapted to fundamental long-term regularities such as severe seasonal changes through profound, but relatively fixed, future-directed instincts (e.g., hibernation). For instance, *E. coli* bacteria travel through the human digestive tract from a lactose-rich to a maltose-rich environment and it has recently been documented that they, when in the former, prepare for the latter by activating genes for digesting maltose [54]. This does not mean that each individual bacterium plans ahead. Natural selection has shaped this behaviour in all *E. coli*. It is an innate response to recurrent, long-term regularities of the order of significant events. But the temporal orders of significant events are not always sufficiently regular for an organism to adapt to. Some change quickly (e.g., some food sources) and an organism that can adjust its behaviour accordingly would have an advantage. Thus, mechanisms differ in the degree of flexibility they impute on individuals. Critical periods for parameter setting, imprinting, and indeed all forms of learning may be regarded as future-oriented mechanisms that allow individuals, rather than populations, to adapt to local regularities. Different memory systems may enable different future-directed potential and episodic memory is arguably the most flexible [1].

Mental time travel enables humans to re-experience and pre-experience virtually any possible event. We can imagine future situations and deduce the consequences for current choices. We can escape our current state and imagine a different state of the world and of ourselves. Much of human success depends on our foresight and this capacity may have been a key survival strategy [55]. To what extent other organisms use this strategy is beginning

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