

Mental time travel in animals?

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Are humans alone in their ability to reminisce about the past and imagine the future? Recent evidence suggests that food-storing birds (scrub jays) have access to information about what they have stored where and when. This has raised the possibility of mental time travel (MTT) in animals and sparked similar research with other species. Here we caution that such data do not provide convincing evidence for MTT. Examination of characteristics of human MTT (e.g. non-verbal declaration, generativity, developmental prerequisites) points to other avenues as to how a case for animal MTT could be made. In light of the current lack of evidence, however, we maintain that MTT is a uniquely human characteristic.

Do animals reminisce about the good old days and ponder what the future might hold for them? Humans frequently engage in such mental time travel (MTT), reliving past events and entertaining possible future scenarios [1,2] (Box 1). It has been argued that MTT is unique to humans [1,3,4], and that its emergence was a prime mover in hominid evolution [1]. Recently, a series of innovative studies on food-storing scrub jays has raised doubt about this claim. In recovering stored food, these birds appear to act in ways that depend on *what* they stored *where* and *when* in the past [5–8], and on what they might expect to happen in the future [9]. This has sparked interest in similar capacities in other species [10,11]. Although we applaud these efforts, we argue here that current evidence does not yet warrant crediting other species with MTT. By examining other characteristics of MTT we point to different ways in which evidence could be obtained if the competence were to exist in animals.

Episodic memory and the scrub jay challenge

Travelling mentally into one's past requires memory. Animals clearly have memory. But some memory researchers argue that there are distinct memory systems, raising the possibility that one of them is uniquely human. Tulving proposed that remembering an episode – what happened to me where and when – is processed in a different memory system from other types of information [4,12,13]. Episodic memory is thought to be part of the larger explicit system (i.e. comprising the memories that we can declare) [13,14] rather than the implicit system. Semantic memory – memory for facts about the world, not personal experiences – is the other explicit component. Episodic memory can be dissociated from semantic

memory in that each can be selectively impaired and each is associated with distinct cortical activity patterns [15,16]. Tulving claims that only humans have episodic memory [4,13].

Although the term is widely used, there has been some confusion about what episodic memory means, partly because Tulving modified his definition from the type of information stored (what, where and when) to an emphasis on what he terms 'autonoetic' (self-knowing) consciousness [17]. He did this because it became clear that one can *know* (semantic memory) something about what happened where and when, without *remembering* that past episode [4]. Autonoetic consciousness is the subjective (recollective) experience associated with travelling back to a point in time and re-experiencing a past event [2,17]. This requires concepts of self (the traveller) and subjective time (the dimension along which to travel) [4]. So whereas the earlier definition describes episodic memory in terms of the information encoded, the later emphasizes a specific type of recall; that is, MTT into the past.

We know that animals, from bees to monkeys, can learn from single events. But do they revisit the events that shaped their past? Innovative work by Clayton, Dickinson and their colleagues has produced perhaps the strongest case yet for episodic memory in animals [5–8,18]. Their studies on the caching and retrieval behaviour of scrub jays (Fig. 1) have shown that these animals can form integrated memories of what was cached where and when. Scrub jays appropriately adjust recovery attempts of differentially perishable food caches depending on how long ago they stored the food items. The authors concluded

Box 1. Time in the human mind

More than half of adult conversation refers to past or future events [42]. Who did what to whom and what happened next? What will happen, where and when? Many human actions are based on remote future goals. Although there is a growing literature on differences in future time orientation [43,44], the basic capacity to entertain events removed in time seems universal. Past events can be reconsidered, evaluated (e.g. regretted) and extrapolated to assess their consequences. Many aspects of human volition make sense only in the light of MTT [1], including apparent biological paradoxes such as suicide (when the future outlook is particularly bleak), celibacy and hunger strikes. Humans construct personal and community histories and plans. Strategies (for individuals or even entire countries) can be coordinated, progress reviewed and adjustments made if necessary. Temporal concepts, timekeepers and calendars have been developed to aid our orientation and plans. In short, it is safe to say that MTT is a significant human attribute, important to our dominance of the planet.

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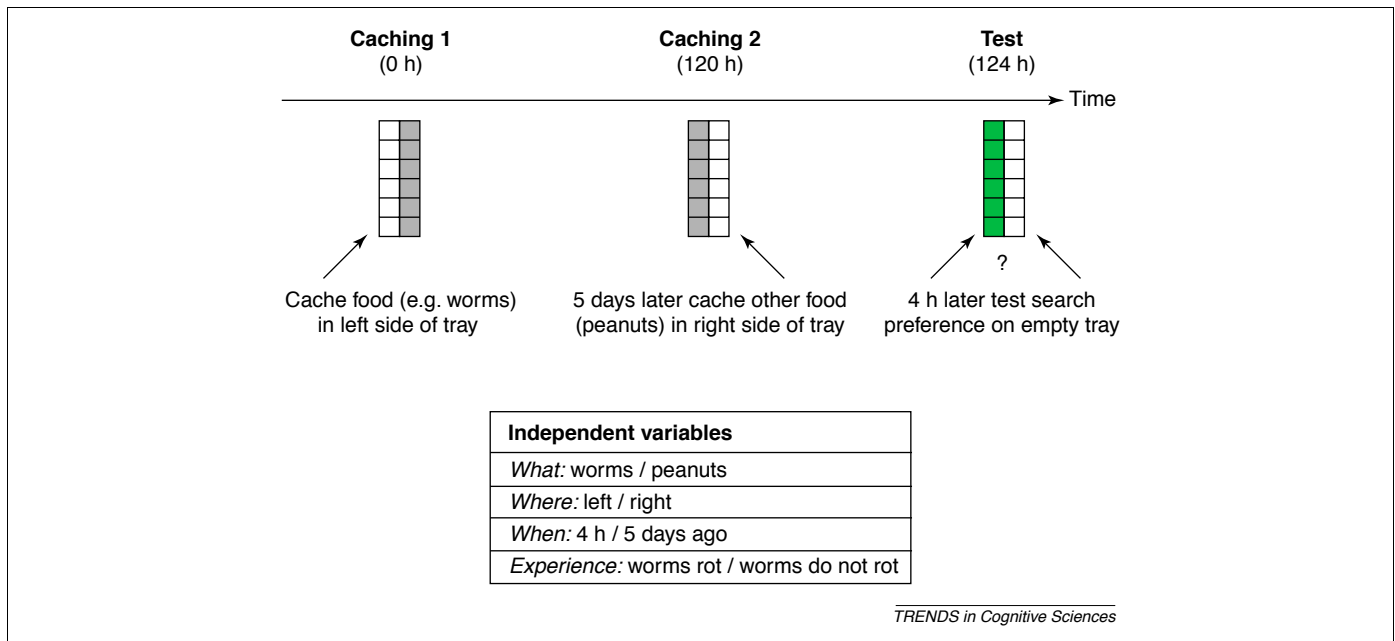


Fig. 1. Experimental design that showed memory for ‘what’, ‘where’ and ‘when’ in scrub jays [5]. Individually caged jays are given the opportunity to cache food, in sand, on one side of an ice-cube tray. In the example shown, on day 1 the birds cache worms in the left side of the tray (the other side is covered), and 5 days later they cache peanuts in the right side of the same tray (with left side covered). In the test phase, 4 hours after this, the birds are given the tray (with the food removed) and allowed to search. They show more searches on the left side than the right – revealing an apparent preference for the worms. Regardless of which food was cached first, jays generally prefer worms over nuts and search accordingly. But worms rot after a few days, whereas peanuts do not. When some of the jays were given an opportunity to learn that 124-hour-old worms are inedible, in the test phase they continued to prefer the worm side of the tray when the worms were cached second, but changed preference to the side where the peanuts were cached when the worms were cached first (and were therefore likely to be rotten). This suggests that the birds have access to information about *what* (peanuts/worms) was cached, *where* (left/right), and *when* (4 h/124 h). Various control conditions have been used to ascertain that this information is indeed what is responsible for the search behaviour at recovery [6].

that the birds show all the behavioural criteria of episodic memory [18]. But Clayton and colleagues cautiously refer to ‘episodic-like’ memory because the phenomenological experience defined by Tulving – auto-noetic consciousness – could not readily be shown to exist.

Is episodic-like memory anything like episodic memory? Clayton, Griffiths and Dickinson [18] offer the following choice:

Option 1: Insist that auto-noetic consciousness is crucial to episodic memory, which, they submit, probably makes it impossible to refute the claim of human uniqueness (because in the absence of language in animals there are no obvious behavioural manifestations).

Option 2: Characterize episodic memory in terms of the information encoded (i.e. Tulving’s earlier definition) and accept that scrub jays have it because they have been shown to encode the what, where and when information into an integrated memory.

At first sight these seem to be the only options and, as scientists, it would seem clear which option we should adopt. Hypotheses need to be falsifiable. But let us be clear what is and what is not implied if we take Option 2 and say that jays (and possibly other species) have episodic memory. It is implied that jays use what, where, when information; it is not implied that their memory retrieval is anything like remembering past episodes. In fact, the cognitive processes involved need not be *about* the past at all. As Dretske noted [19]: event A might cause cognitive change B that effects behaviour C at a later point in time, but this need not imply that B carries any information

about A itself – the mediator B might be causal rather than informational. Thus, although jays perform actions C (recovery) that make sense only in the light of A (caching what, where and when) it need not imply that B represents the past event A. B might instead be a separate system (some implicit feed-forward algorithm) that causes certain caching and recovery behaviour. In fact, even if one can show that an animal has explicit access to the information, this need not imply MTT. There is a double dissociation here [1]. One can know what happened where and when without being able to remember the event [4] (e.g. your birth) and, conversely, one can travel back in time without access to accurate when and where information. I (TS) can vividly re-experience meeting a fascinating character once in the Philippines (or was that Indonesia?) sometime in the early nineties (or was that the late eighties?). Jays might know what food is hidden where and whether it is still good to eat, without knowing how or why they know it. If we take Option 2, then, there should be no implication (although it remains a possibility) that jays recollect the past episode and reason about the present state from there. Perhaps *what–where–when* or ‘www-memory’ would be a more neutral, descriptive term than episodic memory.

Although it is interesting that jays can encode, store and use such information, we suspect that many people are fascinated by this line of work largely because it raises the possibility of human-like episodic recall (Tulving’s later definition) in animals. According to Option 1, however, this might be impossible to show, in which case the human uniqueness claim would merely be a presumption. We

argue, instead, that animals could provide evidence for MTT (even if we cannot establish ‘the feel’, i.e. autozoetic consciousness). We might call this Option 1b. We take as a working hypothesis that MTT is uniquely human because, although there could be evidence for MTT in animals, there has as yet been none forthcoming. So what could such evidence look like?

Avenues towards evidence for MTT in animals (if they had it)

Let us first see whether we can agree what phenomenon we are in fact talking about. Although there are clearly problems studying MTT in others, we can observe it in ourselves. Please recall the last conference presentation you gave. Where and when was it? What were you talking about? Who was in the audience? Can you picture yourself back there? Now let’s travel forward to your next scheduled talk or lecture. Where and when will it be? What are you going to talk about? Who will be the audience? Can you picture yourself there? Now don’t get carried away...

Language and other ways of declaring MTT

Although the phenomenological experience of MTT is private and cannot be directly assessed (even in fellow humans), we do not, of course, always keep our travels a secret. We can declare it – that is what makes it part of the explicit system. Using language, we take mutual trips down memory lane and communicate our plans and visions. Some certainly argue that language is the key difference between humans and animals, and that episodic memory can only emerge in an organism that possesses language [20]. However, there have been efforts to teach language to animals (chimpanzees, gorillas, orangutans, parrots, dolphins, seals), so evidence for MTT could come from there [21].

But could MTT not also be declared without language? It is sometimes easier to express mental travels non-linguistically, for example, through pantomime, where one re-enacts events [22]. Humans also practice their behavioural responses to foreseen, but not yet experienced, events. We can disinhibit the motor execution of mental simulations and overtly rehearse for the upcoming performance, or re-enact a fabulous goal-scoring move from last Sunday. If animals engage in MTT, they might also express it to themselves or to others in such ways. Clever experimentation may be required to establish such evidence. Some ingenious research has already made progress at creating means for animals to declare their minds: showing that monkeys can report whether or not they remember [23]. Non-verbal paradigms could be explored with children and compared with verbal tasks to validate the measure. In summary, then, we argue that the claim that MTT is uniquely human is based on the current lack of evidence from animals, not on the *a priori* impossibility of obtaining evidence.

Memory for whatever, wherever and whenever

Let us briefly go back to that last talk you gave. What was the audience’s reaction? You might have some snapshots of

what the scene looked like. But this imagery does not tend to unfold in an orderly fashion from start to finish. Instead, the chronology of our past ‘depends on a process of active, repeated reconstruction’ ([24] p. 44). Although we can describe (or re-enact) some aspects of the events, we fall short on others (what did you wear that day...?). Extensive research on episodic retrieval clearly shows that we do not simply press the rewind button and replay all the actions and perceptions from beginning to end. We actively reconstruct past events from the gist or from visual snapshots, but draw heavily on our general semantic knowledge [25]. Accuracy is not imperative. We are vulnerable to incorporating more recently acquired information [26] and tend to reconstruct in ways that help justify our current attitudes [27]. Our retrieval is often flawed, subject to interference, misinformation and updating. We argue that MTT is generative. That is, given a limited number of objects and actions, we can assemble and reassemble these elements into virtually unlimited constellations. MTT reflects our ability to imagine *whatever*, *wherever* and *whenever*, rather than our ability to faithfully record what, where and when information. Can you not go back to your last lecture and insert the idea that your Mum was sitting in the front row?

Why would humans, or any animal for that matter, have evolved a system that is at times quite unreliable? The answer is that there is no selective advantage to reconstructing the past *per se*, unless it matters for the present or future. We propose that episodic reconstruction is just an adaptive design feature of the future planning system [1]. Surprisingly, episodic future thinking has attracted far less research attention than episodic memory, but it has recently become in vogue [28]. We know that patients like K.C. or D.B., who have lost their ability to mentally travel into the past, are equally impaired in their travels into the future [16,17]. When you mentally travel forward to your upcoming talk, you can generate a variety of scenarios. Some of the elements are extrapolations from past events (is it going to be in the same lecture theatre?) and others draw on more general semantic knowledge. You can play through different possibilities just as you can play through ‘what if’ versions of past events (like inserting Mum in your last lecture). Anticipating future scenarios clearly has selective advantages because you can prepare now (e.g. practice) for anticipated contingencies. One would think that such flexible foresight would become quite obvious if animals had it (Box 2). So far there is little evidence for this (see [1,3] for reviews).

Prerequisite capacities for MTT

MTT draws on more general capacities. Open-ended generativity is achieved by use of recursive rules that allow us to combine and recombine a finite set of elements [1,29]. But we do not just jumble elements together. We can represent our representations as representations of the past, distinguish them from random hallucinations or dreams, and attempt to reconstruct the event flow as faithfully as possible. We can evaluate different scenarios as more- or less-likely future events. We think about thought. We might never know whether animals have

Box 2. Limited foresightedness

One proposal, the Bischof-Köhler hypothesis, suggests that animals' forethought is restricted because, unlike humans, they cannot anticipate future drives [1,41]. Roberts [3] recounts a revealing observation by D'Amato, which can be used to illustrate this hypothesis. His cebus monkeys were fed biscuits once a day and the monkeys would hungrily eat to satiation. Then they indulged in an apparently irrational behaviour: they would throw the remaining food out of the cage, only to find themselves hungry again some hours later. Why not guard the food to satisfy future hunger? If one is not hungry and can't imagine being hungry again, then biscuits' utility may lie in their quality as projectiles. There is no point in acting now to secure a future need one cannot conceive of. One reason for such a limit could be that travelling forward to the experiences and needs of a future self may require much the same processes as theory of mind [1]. As Hazlitt noted 200 years ago:

'The imagination by means of which alone I can anticipate future objects, or be interested in them, must carry me out of myself into the feelings of others by one and the same process by which I am thrown forward as it were into my future being, and interested in it.' ([45], p. 1).

Neither future 'self' nor present (or future) 'other' can be experienced directly and are accessible only through an act of imagination (or mental simulation [46]). A recent meta-analysis of theory of mind research has shown that young children have as much difficulty imagining another's false belief as they have recalling their own [47], suggesting a developmental synchrony between simulating one's own past and another's present. This has been supported by other studies reporting associations between theory of mind and behaviours that appear to rely on MTT [48,49]. So perhaps specific individual anticipations in animals are limited for the same reasons that their theory of mind seems limited. Humans clearly act towards satisfaction of a multitude of future needs (from shopping for the weekend's dinner to saving for retirement).

flashbacks of previous perceptions and actions, like the snapshots we can conjure up spontaneously, but that is not the question here. Could they think about these snapshots (if they had them) as past events and actively reconstruct, and reassemble them into future anticipations? Recursion in general, and meta-representation in particular, manifest in a host of other human capabilities (e.g. language, music, mathematics, theory of mind) [29,30]. Suddendorf and Corballis [1] argued that MTT is uniquely human largely on the basis that these prerequisite abilities have not yet been established in animals.

One also needs a sense of time if planning is to be effective, and a sense of self to project and relate to the present [1,4]. Of the many species tested, only the great apes seem capable of recognizing themselves in mirrors, which is a controversial non-verbal test of self [31]. Otherwise there is little to suggest animals have a self-concept that they could project along a time dimension. Animals are by no means insensitive to matters temporal, however. Various timing abilities have been demonstrated, including tracking time of day, interval timing and recall of temporal sequences [3]. Yet Roberts' review [3] concluded that the capacity of animals to act on temporal information is very limited. What competence there is, he suggested, can be attributed to basic mechanisms, such as associations with states of the circadian cycle or other relatively primitive timing mechanisms, rather than a concept of time.

Development of MTT

Developmental researchers have provided evidence that MTT is a sophisticated skill that depends on various other developments. Although agreeing on its multifaceted nature, different theories have emphasized different prerequisites for MTT into the past, including: theory of mind [1,32], self-concept [33], language and social construction [34] and temporal concepts [35]. Milestones in these prerequisites develop around ages 3 to 4 and coincide with the decline of childhood amnesia, leading most researchers to suggest this is the age at which episodic memory develops. A more limited body of evidence suggests again the ages 3 to 4 are critical to developing MTT into the future [28,36]. Even by age 5, however, children's understanding of temporal concepts such as weeks, months and years [36], and of disturbing implications of MTT, such as death [37], are still rudimentary, and appear to develop gradually over the subsequent years.

We could launch a stronger case for MTT in animals if there were parallels in their ontogeny. So what do we know about the developmental path of jays' caching behaviour? Caching in scrub jays develops in predictable stages (N.S. Clayton, 2002, pers. commun.), as it does in other birds [38]. Jays place food from a very early age. This apparent innate compulsion turns only gradually into hiding of food (and of non-useful items such as stones). Only later still do jays start cache recovery. Initially, at least, jays do not appear to cache with the future in mind.

Conclusion, with a view to the future

The current evidence suggests that scrub jays have 'www-memory' – they can encode, store and use information about *what* they cached *where* and *when*. This need not imply that they travel mentally back to the original caching event or forward to the recovery. The hypothesis that MTT is uniquely human seems only worth upholding if it can – potentially – be refuted (hence Option 1b above). We identified avenues through which a case could be made. Given at least some indication of competence at prerequisites, our closest relatives, the great apes, might be the most likely candidates.

But it is certainly worth finding out more about scrub jays' competence, and about their limits. For example, Clayton and colleagues recently provided some evidence for flexible memory use [39]. However, can jays use their skill outside of the domain of caching and recovery? Can they, for instance, learn different decay functions (e.g. use differently coloured soil with preservatives or mould to change decay time) and use them as predictors of significant non-food related events? One could present jays with choice paradigms contrasting one caching tray now versus two trays later, with differentially perishable foods to investigate delay of gratification and contrast present with future needs. The paradigm could also be used to investigate MTT prerequisites. Emery and Clayton found that jays that had pilfered others' caches would re-cache food in new sites if their own original caching had been observed by another jay [9]. One could investigate jays': (i) understanding of seeing (do they cache differentially in an area not visible to a potential pilferer); (ii) self-recognition (does their own mirror image result in similar re-caching

behaviour – if not, does a mirror image of another observer do so?); and (iii) theory of mind (do they reduce re-caching when the observer holds a false-belief, for example when the observer is not privy to a change in the hiding constellation)?

When evaluating new evidence for MTT, however, we remind scholars of Tinbergen's [40] four levels of explanation: function, causation, development and evolution. In terms of function, for example, MTT is clearly not unique in providing means for acting to enhance future survival and reproduction. All animals that have memory and a capacity to learn possess a mechanism that is future-oriented. Even the function implied by the Bischof-Köhler hypothesis [41] – to act before the adaptive problem or need is encountered – is clearly not unique to humans. Building a nest, preparing for hibernation and food caching make sense only in the light of the future needs. If we consider causation, however, we need to be alert that the same functional ends could be produced by different means. Hibernation, for example, is a species-specific universal that is displayed even if the animal has not yet experienced winter. The developmentally uniform emergence of this behavioural pattern suggests an innate, instinctual mechanism; a causal process that does not display the individual generativity evident in MTT. Scrub jays would benefit from having very accurate records of their caches, an objective that would perhaps not be served best by a generative reconstructive mechanism. Although food storing evolved independently in several species, mechanisms homologous to those involved in human MTT are more likely to be found in our primate relatives. However, humans might have evolved MTT quite recently. The earliest potential evidence could be bifacial hand axes some 1.6 million years ago, which appear to have been made and kept for repeated future use [1]. The only sure evidence of MTT, however, comes from writing.

In the earliest writings, the ancient Greeks describe the myth of Prometheus. Prometheus created humanity. He stole fire from heaven to give humans powers of the gods that distinguished them from other animals. He brought culture and technology. Prometheus literally means foresight.

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