PERSPECTIVES

OPINION

Can animals recall the past and plan for the future?

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According to the 'mental time travel hypothesis' animals, unlike humans, cannot mentally travel backwards in time to recollect specific past events (episodic memory) or forwards to anticipate future needs (future planning). Until recently, there was little evidence in animals for either ability. Experiments on memory in food-caching birds, however, question this assumption by showing that western scrub-jays form integrated, flexible, trial-unique memories of what they hid, where and when. Moreover, these birds can adjust their caching behaviour in anticipation of future needs. We suggest that some animals have elements of both episodic-like memory and future planning.

Once upon a time, the animals were recounting the history of the forest, when the moose recalled: "I was down by the edge of the lake at the time." The snake recollects: "I was under a rock, getting ready to shed," and the hare remembers: "I was in the glen, just finishing a burrow when I got the news." The caption of Gary Larson's[1] cartoon explains: "More facts of nature: All forest animals, to this very day, remember exactly where they were and what they were doing when they heard that Bambi's mother had been shot."

Like other Larson offerings, the joke arises in part from its anthropomorphism. Although everyone remembers where they were when JFK was shot, it seems implausible that animals could possess the kind of autobiographical memory that humans take for granted. The idea that animals cannot mentally 'travel back in time' to re-experience episodes — or 'travel forwards in time' to anticipate and plan for the future — has been formally stated by theorists of animal cognition[2–6]. The mental time travel hypothesis[7] (BOX 1), in which Suddendorf and Corballis argued that mental time travel is unique to humans and that its emergence was crucial in hominid evolution, has been particularly influential. According to this hypothesis, animals cannot represent past experiences (episodic memory[8]) or anticipate future states (future planning[7]).

Developmental psychologists have also argued that mental time travel, at least in the form of episodic memory, does not develop in humans until the age of four[9–11]. It has been suggested that infants, "may be competent at learning ordered event sequences, [but] they cannot represent events as happening in unique temporal locations in their past … children's memories are not temporally organized like those of adults, because they lack a unified temporal framework that can be used to represent the systematic relations that obtain between past events in virtue of the particular times at which they happened"[12]. These authors argue that young children, like animals, are incapable of 'temporal perspective taking'.

A recurring theme is the importance of time. There is ample evidence that animals and children can time intervals lasting seconds or minutes, and many theories attribute this timing ability to internal clocks or oscillators that are started by the timed event and that operate over these short durations[13,14].

THE FAR SIDE® BY GARY LARSON

I was just getting ready to cross the interstate.

I was down by the edge of the lake at the time.

I was in the glen, just finishing a new burrow when I got the news.

I was looking for crawdads in my favorite creek

I was under a rock, getting ready to shed.

More facts of nature: All forest animals, to this very day, remember exactly where they were and what they were doing when they heard that Bambi's mother had been shot.

But this interval timing is distinct from a representation of time that can extend forward into the distant future and back into the distant past[12]. Tulving[15] refers to this sense of time as 'chronesthesia', arguing that it is "a form of consciousness that allows individuals to think about the subjective time in which they live and that makes it possible for them to 'mentally travel' in such time." Tulving[6] refers to this sense of self as 'autonoetic consciousness'. Wheeler[16] concludes that episodic memory, uniquely among memory systems, allows us to experience the world autonoetically and to travel mentally through time.

It is thought that certain brain-damaged patients are also incapable of chronesthesia. The patient K.C., who has widespread brain damage, has no problem knowing whether it is 4 p.m. or 6 p.m., but lacks an awareness of past and future time. When asked to think back to what he did yesterday, or forward to what he is going to do tomorrow, he claims that his mind goes blank, in a way that fails to differentiate the past from the future[6].

Box 1 | **The components of mental time travel**

Suddendorf and Corballis[7] explain that "The ability to travel mentally in time constitutes a discontinuity between ourselves and other animals. Mental time travel comprises the mental reconstruction of personal events from the past (episodic memory) and the mental construction of possible events in the future".

   The retrospective component: "Episodic memory receives and stores information about temporally dated phases or events, and temporal-spatial relations among those events", according to Tulving[8].

   The prospective component is described by Suddendorf and Corballis[7]: "…animals other than humans cannot anticipate future need or drive states, and are therefore bound to a present that is defined by their current motivational state. We shall refer to this as the Bischof–Köhler hypothesis…"

Another patient, H.M., who has amnesia resulting from damage to medial temporal lobe structures, also reports feelings of blankness for the periods when he has no episodic recall[17].

   The central claim of the mental time travel hypothesis is that animals, like patients such as K.C., are 'stuck in time'. In this article we take an opposing view, and review the evidence that animals are capable of both retrospective and prospective cognition.

Episodic memory

In keeping with the mental time travel hypothesis, several psychologists have argued that episodic memory is unique to humans[7,15,16,18–20]. For example, Tulving and Markowitsch[20] state that animals have a well-developed general knowledge of the world but, unlike us, cannot recall and re-experience specific past events — they are incapable of 'autonoetic consciousness'. Rather, they argue that animals learn about the general relationships between stimuli and events from specific episodes without encoding temporal information that enables animals to locate these episodes in the past.

   The definition of episodic memory in terms of consciousness makes it impossible to demonstrate episodic memory in animals, because there are no agreed non-linguistic behavioural markers of conscious experience[21]. With the possible exception of putatively language-trained apes and parrots, it is not clear how one would establish whether an animal is re-experiencing the past when retrieving a memory[22]. This dilemma can be resolved, to some degree, by distinguishing between the phenomenological and behavioural criteria for episodic memory. We propose three behavioural criteria, reflecting the content, structure and flexibility of the memory (BOX 2). Because we do not address phenomenological aspects, we refer to memory that meets these criteria as 'episodic-like' memory.

Content of episodic-like memory. Tulving[8] has suggested that episodic memory "…receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events". So, episodic memory provides information about the 'when' of events as well as 'what' and 'where' they happened. The usefulness of this 'what–where–when' criterion is that the simultaneous retrieval and integration of information about these three features of a unique experience can be demonstrated behaviourally in animals. Evidence for episodic recall in animals must therefore establish that the animals remember the 'when' of a particular event, as well as the 'what and where', so that the animal can distinguish among events that occurred at different times in the past.

   The 'when' component of episodic memory is especially crucial. Whereas two episodes might share the same 'where', or even 'what', they cannot share the same 'when'. So episodes, and episodic memories, are temporally unique and must be formed in a single exposure. If an animal receives several training trials, its behaviour does not necessarily reflect episodic memory for each of these trials, however complex and contextualized the content[23,24]. One-trial learning is not, however, sufficient for episodic memory. In certain forms of conditioning, such as flavour-aversion conditioning, the subject need not recall the events associated with eating or sickness for one-trial associative conditioning to occur[25]. Despite claims that instances of single-trial learning of a long-term memory might be analogous to episodic memory[26,27], our term 'episodic-like memory' would not be applied to single-trial learning unless it also satisfied our other criteria. Furthermore, the temporal content cannot be encoded simply in terms of familiarity. The distinction between familiarity-based recognition and episodic recall is important because the two processes are psychologically distinct[28–30], and are thought to engage different areas of the human brain[31–34].

   The content criterion of episodic memory also distinguishes episodic memory from semantic memory (general factual knowledge about the world). The difference between episodic and semantic memory in humans is often referred to in terms of remembering and knowing: episodic memory is concerned with remembering specific personal experiences, whereas semantic memory is concerned with what one knows about the world. Although it is generally accepted that animals can remember semantic-like information, the crucial question for the mental time travel hypothesis is whether they are also capable of episodic recall. Whereas semantic memories can be divorced from the spatial and temporal context in which they were acquired, episodic memories are concerned with specific events in one's personal past that involve information about the 'when' as well as the 'what' and 'where'.

Structure of episodic-like memory. By the content criterion, we do not mean merely that an animal or human must be able to indicate its knowledge of some 'what', some 'where' and some 'when', with no connection between the three. The what, where and when must represent the same event by being bound together in an integrated representation, so that retrieving any one feature of an episode automatically retrieves the other features[22,35]. This type of representation differs from other possible representations of what, where and when, such as a linear 'where–what–when' representation in which some elements are not directly connected. In this example, because the 'where' and 'when' elements are not directly connected, an animal using this representation to guide its behaviour would be unable to discriminate two episodes sharing the same 'what'. This idea will become clearer later when we discuss the integrated representations of food-caching scrub-jays.

Box 2 | **Behavioural criteria for episodic-like memory in animals**

Content: recollecting what happened, where and when on the basis of a specific past experience.
Structure: forming an integrated 'what–where–when' representation.
Flexibility: episodic memory is set within a declarative framework and so involves the flexible deployment of information.

Box 3 | **The flexibility of declarative memory**

Cohen[39] explains that "a declarative code permits the ability to compare and contrast information from different processes or processing systems; and it enables the ability to make inferences from generalizations across facts derived from multiple processing sources. Such a common declarative code thereby provides the basis for access to facts acquired during the course of experiences and for conscious recollection of the learning experiences themselves".

Flexibility of episodic-like memory. Episodic memory is a form of declarative memory, which can be contrasted with non-declarative memory[36,37]. Non-declarative memory is inaccessible to conscious recall, and is thought to include motor skill learning, priming and simple forms of conditioning. The memory representations that are formed during such learning are thought to be relatively situation-specific and inflexible. By contrast, declarative memory can support flexible deployment of information (BOX 3) in novel situations[38]. Because human episodic memory is set within a declarative framework, and therefore supports the flexible deployment of the encoded information[39], the same should be true of animals' episodic-like memory. So our third criterion for episodic-like memory is its flexible deployment in new situations.

Episodic-like memory in animals
Most studies of animal memory have not tested episodic recall in a way that meets these criteria. For example, monkeys can be trained to choose between two complex objects on the basis of whether they are the same as (delayed matching-to-sample) or different from (delayed non-matching-to-sample or oddity) an object that they were shown at the start of the trial. Although the monkey might recall episodically the events at the start of the trial[40], a simpler explanation is that the monkey learns to choose (or avoid) the most familiar object[21,25]. By requiring the monkeys to recognize a stimulus but not to recollect where and when it was previously seen, these tasks can be solved by familiarity rather than episodic recall. The same argument can be applied to spatial memory tasks such as delayed matching-to-place in the water maze, in which the animal has to keep track of the locations of a hidden platform that moves from day to day[41].

Fortin and colleagues[42] have examined temporal memory using a sequence task that they argue draws on more than just simple familiarity. On each trial, rats were presented with five sand-filled cups, in each of which they found food. Each cup of sand contained a different odour, with the five odours in a series selected randomly from a pool of twenty odours on each trial. After a short delay, the rats were presented with two of the

sand-filled cups. Control rats, but not those with hippocampal lesions, learned to select the cup with the odour that had occurred earlier in the sequence. Even if we accept that this discrimination depends on memory (rather than on the discrimination of traces of the odour left on the whiskers and fur), there are several reasons to be cautious in accepting it as evidence for episodic-like memory.

First, the sequence task required no more than discrimination based on relative familiarity. Fortin and colleagues[42] addressed this issue by testing the rats' ability to recognize recently presented odours. The rats were given a series of five odours as before, but now the choice test was between one of the five odours that the animal had encountered in the preceding sequence and a second odour that had not appeared in that sequence. Hippocampal lesions produced a deficit in the sequence task but not in the recognition version, leading to the conclusion that the sequence task was not mediated by familiarity. The assumption made is that the odour recognition in this task must involve a familiarity judgment, rather than some other mechanism. Even if we accept this assumption, the temporal memory demonstrated in the sequence task could be solved by interval timing, with the presentation of each odour starting an internal interval timer, and the discrimination being based on the states of the timers at choice. There is good evidence that rats are capable of independent, asynchronous timing over relatively short intervals[13]. Furthermore, whatever the temporal encoding that is deployed in this task, it does not meet the content criterion for episodic-like memory as there is no evidence that the rats remembered the location of the different odours.

Other studies have demonstrated what–where episodic-like memory in the absence of evidence for temporal encoding. Schwartz and Evans[22] reviewed eight studies that indicated that primates can remember where a specific event occurred. For example, Menzel[43] allowed a chimpanzee, Panzee, to observe an experimenter hiding different food items in various locations outside her enclosure. What–where memory was inferred from the observation that when the experimenter returned, often hours later, Panzee

spontaneously indicated her memory for the hiding event by selecting a food item from a lexigram and pointing to the location of that item. Schwartz and colleagues[27] have also reported what–who memory in a gorilla, King, that encoded not only the type of food but also who gave it this food. Without the 'when' component, however, such studies do not meet the content criterion.

Similarly, Day and colleagues[44] have developed a paired-associate task for tapping the what–where content of memories for trial-unique events in rats. Paired-associate tasks are used to test episodic recall in humans[45,46] by presenting the subject with a list of word-pairs followed by a test of cued recall in which the subject is shown one member of the stimulus pair and asked to remember the other. In the rat version, the animal is exposed to two successive paired associates followed by a cued recall test for one of the pairs. In this case, the rat associates the spatial location of a cup of food with a specific flavoured food by finding flavour 1 in location 1 and flavour 2 in location 2. In the cued-recall test, the rat is presented with one of the two flavours. It must search in the location where it previously found this flavour to gain more food. The animals performed significantly above chance on these cued-recall tests, showing some form of recall of the 'what and where' of these pairings. As the flavour–location pairs were trial-unique, the paired-associate task might involve episodic recall of the previous encounter with the flavour in a particular location. However, the tasks did not require the rats to register when the episode occurred. The rats simply have learned where different foods were located, a representation that was updated with each new encounter with a new food–location pairing. Therefore, according to this account, the task requires a semantic-like 'what–where' representation but not episodic-like memory[47].

Episodic-like memory in birds
None of the studies described so far have required the animal to remember the spatio-temporal context of a particular event. A different strategy for testing whether animals are capable of episodic-like memory is to adopt an ethological perspective and to consider cases in nature in which an animal might need to retrieve and integrate information about what happened, where and when during a specific experience. One candidate is food-caching: the animal hides food for future consumption and later relies on memory to recover its caches. We will describe our experiments in this area in the context of our three criteria for episodic-like memory (BOX 2).
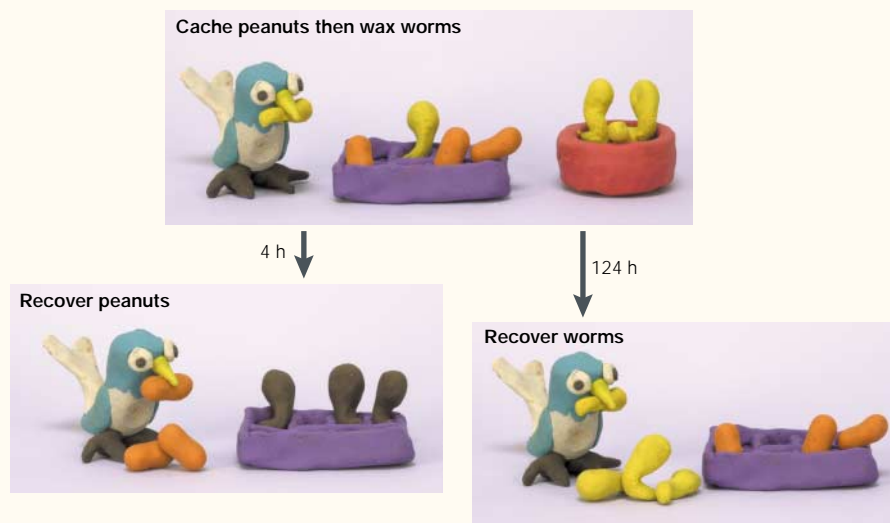
Figure 1 | **A cartoon of the procedure used to test episodic-like memory in western scrub-jays.** Birds in the 'degrade' group cache perishable wax worms and non-perishable peanuts (orange), which they are allowed to recover at a later date. If a short time has elapsed between caching and recovery then their preferred food items, the worms, are still fresh (yellow) and the birds should prefer to recover the worms. But if a long time has elapsed between caching and recovery then the worms will have decayed (brown) and the birds should prefer to recover the peanuts.

Content. In a series of experiments, food-caching western scrub-jays cached perishable worms and non-perishable nuts in distinct sites in sand-filled caching trays, and were allowed to recover their caches at a later date[48,49] (FIG. 1). The birds cached in different trays on different days so they had to keep track of which foods they cached where on a given day (FIG. 2). The 'degrade' group were trained that their preferred food, wax worms, decays over time, whereas the nuts do not perish. The birds searched preferentially for the wax worms if they were given the opportunity to search for them a short time after caching, but switched to searching for nuts after longer intervals during which the worms had decayed. They continued to show this searching pattern on memory tests in which the foods were removed before recovery, and the trays were filled with fresh sand so that the birds could not rely on cues from the food. By contrast, the 'replenish' group did not have the opportunity to learn that wax worms perish, so they continued to search for worms regardless of the delay between caching and recovery. This result indicates that the birds remembered both when and where they cached the different foods. But an alternative explanation is that the degrade group used familiarity judgements about the caching tray to determine whether to search for worms or for nuts. If the tray was relatively familiar because it had been seen a short time ago then they should search for worms; if the tray seemed unfamiliar because caching had occurred several days ago then they should search for nuts.

To rule out discrimination by relative familiarity, the birds were tested using a new procedure in which they cached the two foods on opposite sides of the same tray on different days, as opposed to caching one food and then the other immediately afterwards. By restricting access to the left or right side of the tray, the birds could be made to cache worms in one side of the tray and then to cache nuts in the other side of the same tray the next morning (or vice versa). The birds were then allowed access to both sides of the tray in the afternoon, when all the caches had been removed. To solve this task the birds cannot rely on discrimination by relative familiarity because the tray is always relatively familiar, and the only difference between the two conditions is whether the worms were cached first or last. So the bird must remember when worms and nuts were cached, as well as the location of these caches. Whereas the replenish group selectively searched for worm caches irrespective of whether worms were cached first or last, the degrade group searched for worms if they had been cached recently, but searched for nuts otherwise. The jays could also keep track of different perishable foods that decay at different rates, and could make temporal generalizations about when perishable items should degrade, as well as remembering the relative time since caching when the same food is cached in distinct sites at different times[50]. In principle, the temporal control of cache recovery could be mediated by interval timing rather than a chronesthetic-like representation[51].

However, interval timing in animals has only been demonstrated across seconds or minutes, and we think it improbable that interval clocks started by each caching episode could operate across hours and even days.

This behaviour meets the 'what–where–when' content criterion for episodic-like memory. To avoid searching sites that would have contained the perished and therefore unpalatable food, the birds must remember what they cached, where and when. Because the visuo-spatial cues identifying each cache site were trial unique, the birds must have recalled the what, where and when information that was unique to each caching episode. These results go at least some way towards meeting Tulving's[8] original definition of episodic memory in terms of 'temporally-dated experiences' and 'temporal–spatial relations'.

Structure. We have argued that the jays encode information about what happened during a specific past event, and when and where the event occurred in an integrated representation[50]. By this we mean that the components of the event are bound together in memory so that interrogating an episodic memory for any one feature of the episode will automatically retrieve the other features. In the absence of such binding, an animal would be unable to discriminate between different episodes that shared common features. Consider a memory structure of a caching episode in which the site of a cache location retrieves a representation of the food cached at that location, which then retrieves the information about the times at which this food has been cached. Because this linear 'where–what–when' memory does not include any direct integration or binding of the 'where' and 'when' information, the bird would be unable to discriminate episodes in which it cached the same food in different locations at different times. Both locations would retrieve a representation of the common food, which then would retrieve temporal information about both caching episodes, rendering them indiscriminable. The bird would not know when it cached the food in this location. The issue of the integration or binding of episodic-like memories in animals has received little attention, although our jays could discriminate between episodes in which they cached the same food in different locations at different times[50].

Flexibility. Our final criterion for episodic-like memory, flexible deployment, also remains largely uninvestigated. Flexibility is a defining characteristic of declarative memory because

Figure 2 | **A western scrub-jay caching wax worms.** Birds hide the food items in trial-unique, visuo-spatially distinct caching trays filled with sand in which they can bury caches.

the information is encoded in a representational form that does not specify how this information is to be used in controlling behaviour. So an episodic memory should be able to interact with general knowledge (semantic-like memory) even if this information were gained after the episode had been encoded. Consider the case of the jay caching perishable food. If the jay establishes some wax-worm caches, and then subsequently discovers that worms generally degrade more quickly than originally thought, the bird should be able to update its knowledge about the rate of perishability and change its search behaviour accordingly, even though the episodic information about the worm caches was encoded before the acquisition of the new semantic-like knowledge about their decay rates. We found that the jays could do this — if they cached perishable and non-perishable items in different locations in one tray, and then subsequently discovered that worms from another tray had degraded more quickly than they expected, then when given the original tray back the birds switched their search preference in favour of the nuts. The birds continued to search for the perishable food if it had been cached recently. To our knowledge, this is the only demonstration of declarative flexibility in which animals can update their information after the time of encoding[52].

We therefore conclude that the jays acquire and update generic knowledge about the rates at which the different food types perish and integrate this information with their bound memory for a specific caching episode to flexibly control their search preferences at recovery.

So the behaviour meets our three criteria for episodic-like memory.

We know of no mammalian examples that meet these three criteria. However, one could conceive of a mammalian model based on a foraging requirement for perishable foods that ripen as well as degrade, perhaps using fruit-eating mammals, such as some bats and primates[53]. As with the caching model, this example is both ethologically relevant and amenable to rigorous laboratory control. With carefully designed experiments, one could test whether these animals can encode the 'what, where and when' of a foraging trip before the fruits have ripened and therefore know when to revisit a particular tree at a time when the fruit will be ripe.

Future planning

The Bischof–Köhler hypothesis. Mental time travel is useful not only for episodic memory — travelling back in time — but also for travelling forwards in time, to anticipate future needs (future planning). Like episodic memory, future planning has been thought to be unique to humans, in part because of the reliance on language for assessing such abilities. Implicit in the Bischof–Köhler hypothesis (BOX 1) is the idea that non-human animals might be unable to dissociate a previous or

future mental state from their current one, and might therefore be unable to take actions to ensure that a future need will be satisfied. A sated animal might be unable to understand that it will be hungry again later and so "a full-bellied lion is no threat to nearby zebras, but a full-bellied human may be"[54].

Prospective behaviour and planning. Future planning applies only to behaviour that is oriented to the future and involves learning. It is important to distinguish mental time travel into the future from simple prospective behaviour, because species-specific behaviours that seem to involve the anticipation of future states might not involve planning. For example, some populations of black-capped warblers in Germany migrate southwest towards Africa in the winter, whereas others migrate west to Britain. When birds from these different populations were housed in captivity and allowed to breed, the offspring showed the same migratory orientation as their genetic parents, irrespective of the environment in which they had been raised[55]. So although this migratory behaviour might seem to have some of the features of prospective behaviour, it does not involve future planning. However, other cases of migratory behaviour, such as elephants migrating to water sources in anticipation of a drought, might involve future planning[56]. It would need to be demonstrated that this migration occurs in anticipation of the onset of thirst for this behaviour to qualify as future planning.

Criteria for future planning. Mental time travel into the future can be characterized in the same terms as mental time travel into the past. As with mental reconstructions of previous events, mental preconstructions of future scenarios are declarative, and draw on both episodic future thinking and semantic knowledge[57]. So, as with episodic memory, we can characterize the crucial features of future planning in terms of content, structure and flexibility (BOX 4). Note that in the context of future planning the 'when' is important because the subject must dissociate a future mental state from the current one to take action to ensure that a future need will be satisfied, independent of the present need.

Box 4 | **Behavioural criteria for future planning in animals**

Content: anticipating what will happen, where and when on the basis of previous experience.
Structure: forming an integrated 'what–where–when' representation.
Flexibility: in much the same way as episodic memory, future planning interacts with semantic knowledge and must therefore rely on flexible deployment of information.

Observed during caching

Observer

Storer

In private during caching

Storer

↓ 3 h

↓ 3 h

In private during recovery

Storer   Old tray   New tray

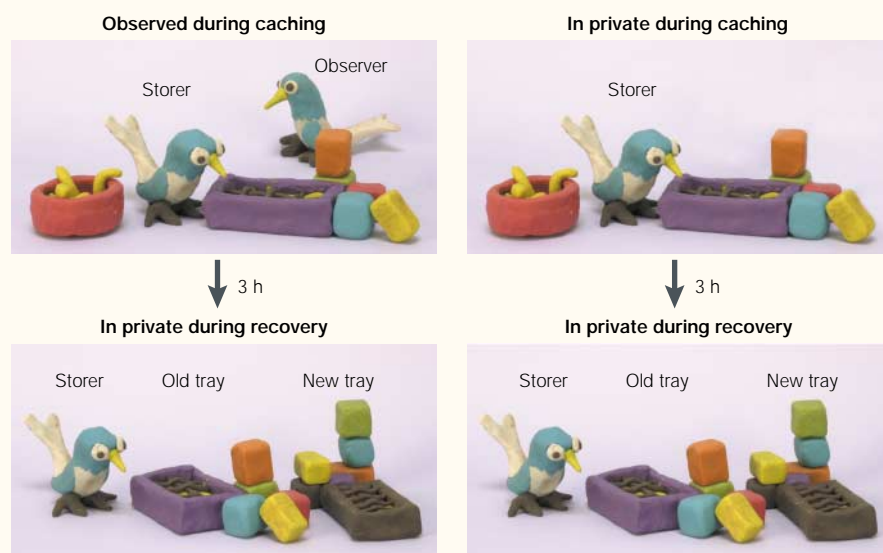**In private during recovery**

Storer   Old tray   New tray

Figure 3 | **A cartoon of the procedure used to test whether the western scrub-jays could adjust their caching strategies to minimize potential stealing by other birds.** On some trials the birds cache while observed by a conspecific, whereas on other trials they cache in private. The birds are always allowed to recover their caches in private.

Future planning in animals. There is good evidence that animals can show local expectation of future events such as goal-directed actions (for example, a rat pressing a lever to get food in the immediate future). However, there are two reasons why this is not evidence of future planning as envisaged by the Bischof–Köhler hypothesis. First, prospective cognition requires anticipation of future events over a timescale of at least hours, if not longer. Showing that an animal can learn to anticipate a reinforcer that will occur a few seconds or minutes after a response will not suffice because the learning can be promoted by the contiguity between the reinforcement and the memory of the correct response. Second, instrumental responding for a food reward by a hungry animal is controlled by its current motivational state. Future planning involves actions that are relevant to the individual's future motivational state.

Some primates can manufacture and use tools. Chimpanzees, for example, have been described carrying stones over long distances to be used for cracking nuts found in an area that lacked stones[58]. Although this example might indicate that chimpanzees can anticipate a future event[59], their ability to do so might be limited. The preparation of a tool to crack nuts might be largely bound up in the act of consuming the nuts in the near future. These signs of anticipatory thought concern items that are relevant to the individual's current motivational state: in this example, the chimpanzee's anticipatory use of tools is bound by the context of the animal's current hunger state. This

behaviour need not involve future planning, for there is no reason to believe that it requires an explicit reference to a future need state. In short, future planning is the ability to anticipate future needs and desires, independent of current needs and desires, and over longer timescales than the short timescales sufficient for instrumental responding such as lever-pressing for food reward.

As with episodic memory, an alternative approach is to consider behaviours that might require the ability to travel forwards in time. At first sight, food caching would seem to manifest prospective cognition because food-caching animals hide food for future consumption and over long retention intervals. Of course food-caching would not be an example of future planning if the individuals instinctively cached all food items irrespective of the consequences. Caching must be sensitive not only to the motivational state at the time of recovery but also to knowledge about the state of the caches themselves. A recent experiment on the caching behaviour of western scrub-jays indicates that this might be useful for testing future planning in animals. If caching is controlled by prospective cognition, we should expect the birds to anticipate the conditions at future recovery opportunities on the basis of past recoveries, and to use these anticipated conditions to control present caching.

Caching is competitive and costly, because another individual might steal the caches. Emery and Clayton[60] tested whether jays could adjust their caching strategies to minimize

potential stealing by other birds. The birds were allowed to cache either in private (when the other bird's view was obscured) or while a conspecific was watching, and then to recover their caches in private (FIG. 3). Scrub jays that had experience of stealing another bird's caches subsequently re-cached food in new cache sites during recovery trials, but only when they had been observed caching. Conspecifics without this experience did not do so, even though they had observed other jays caching. These results indicate that the re-caching in new sites that are unknown to the observer depends on the previous experience of having stolen food cached by other scrub jays. As re-caching does not depend on the presence of the potential thief, the scrub jays must relate information about their previous experience as a thief to the possibility of future stealing by another bird, and modify their caching strategy accordingly. The next important step is to establish whether jays are sensitive to a future motivational state as opposed to the current one.

Conclusions and future directions
We have argued that, contrary to the Bischof–Köhler hypothesis, some animals can travel mentally backwards into the past, and forwards into the future. But many outstanding questions remain. For example, we have considered episodic memory and future planning as manifestations of a single ability, mental time travel. Future work will be required to establish whether episodic memory and future planning are inextricably linked, or whether it is possible to have episodic memory without future planning, and vice versa. Studies of the effects of brain damage might clarify this issue and help to identify aspects of cognition that are unique to episodic memory and future planning. Such studies will also shed light on the brain regions that are involved in mental time travel. For example, patients with damage to the prefrontal cortex show deficits in episodic memory and future planning[16]. So does the prefrontal cortex contain the machinery of mental time travel? Similarly, is the hippocampus vital for both episodic memory and future planning, or just for episodic memory? Are these brain structures necessary and/or sufficient for episodic memory and future planning? And if some of the best examples of episodic-like memory and future planning are to be found in birds, what are the neurobiological implications, given that birds do not have a structure homologous to the mammalian cortex? One question is whether these abilities are found generally among vertebrates or are restricted to a few species, perhaps those with high social

intelligence. And further studies will be required to establish the extent to which the retrospective and prospective cognition studies in jays and other animals really model the episodic memory and future planning experienced by humans.

To begin to answer such questions, mammalian models will be required. The jay studies we have described have rekindled interest in the possibility that non-human mammals might be capable of episodic memory and future planning. To achieve a mammalian model, it might be necessary to identify appropriate natural behaviours that can be transferred to the laboratory, such as foraging for fruit. The behaviour can then be assessed as to whether it meets our three criteria — content, structure and flexibility. Contact can then be made between the findings from these animal models and the human literature. We have discussed how this has been problematic when using criteria that are dependent on language and consciousness. Perhaps the best way to make such contact, then, will be to subject human episodic memory and future planning to these same behavioural criteria.

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