Mental Time Travel: Can Animals Recall the Past and Plan for the Future?

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Introduction

In an influential paper that was published in 1997, Suddendorf and Corballis argued that we humans are unique among the animal kingdom in being able to mentally dissociate ourselves from the present. To do so, we travel backwards and forwards in the mind's eye to remember and reexperience specific events that happened in the past (*episodic memory*) and to anticipate and preexperience future scenarios (*future planning*). Although physical time travel remains a fictional conception, mental time travel is something we do for a living, and the fact that we spend so much of our time thinking about the past and the future led to Mark Twain's witty remark that "my life has been filled with many tragedies, most of which never occurred."

Mental time travel then has two components: a retrospective one in the form of episodic memory and a prospective one in the form of future planning. In formulating their *mental time travel hypothesis*, Suddendorf and Corballis were the first to suggest that episodic memory and future planning are intimately linked and can be viewed as two sides of the same coin so to speak. In fact, their proposal consisted of two claims. In addition to integrating the retrospective and prospective components of mental time travel, they also argued that such abilities were unique to humans and reflected a striking cognitive dichotomy between ourselves and other animals. The latter idea was not new, however, but rather an extension of what others have argued makes episodic memory special.

Indeed in his seminal studies of human memory, Tulving coined the term episodic memory in 1972 to refer to the recollection of specific personal happenings, a form of memory that he claimed was uniquely human and fundamentally distinct from semantic memory, the ability to acquire general factual knowledge about the world, which he argued we share with most, if not all, animals. Ever since he made this remember–know distinction, most cognitive psychologists and neuroscientists have assumed that episodic memory is special because of the experiential nature of these memories, namely that our episodic reminiscences are accompanied by a subjective awareness of currently reexperiencing an event that happened in the past, as opposed to just knowing that it happened. Of course we also have many instances of knowledge acquisition in which we do not remember the episode in which we acquired that information. For example, although most of us know when and where we were born, we do not remember the birth itself nor the episode in which we were told when our birthday is, and therefore such memories are classified as semantic as opposed to episodic.

Episodic and semantic memory, then, are thought to be marked by two separate states of awareness; episodic remembering requires an awareness of reliving the past events in the mind's eye and of mentally traveling back in one's own mind's eye to do so, whereas semantic knowing only involves an awareness of the acquired information without any need to travel mentally back in time to personally reexperience the past event. It is for this reason that in later writings, Tulving has argued that one of the cardinal features of episodic memory is that it operates in 'subjective time,' and he refers to the awareness of such subjective time as *chronesthesia*.

Language-based reports of episodic recall suggest that the retrieved experiences are not only explicitly located in the past but are also accompanied by the conscious experience of one's recollections, feeling that one is the author of the memory, or of traveling back not in any mind's eye but in *my* mind's eye, what Tulving called *autonoetic consciousness*. In other words, Tulving and others argue that episodic memory differs from semantic memory not only in being oriented to the past, but specifically in the past of the owner of that memory. So while some semantic knowledge, such as the birth date example described earlier, does involve a datable occurrence, these memories are fundamentally distinct from episodic memories because they do not require any mental time travel. As William James so aptly wrote "Memory requires more than the mere dating of a fact in the past. It must be dated in *my* past."

From a biological perspective, the characterization of episodic memory in terms of these two phenomenological properties of consciousness, namely autonoesis and chronesthesia, presents major problems for two reasons. The first is that positing a subjective state of awareness is difficult to integrate with evolutionary processes of natural and sexual selection, which operates on behavioral attributes such as reproductive success and survival rather than on mental states. The second is that this definition makes it impossible to test in nonverbal animals, in the absence any agreed behavioral markers of non-Linguistic consciousness. Adopting an ethological approach to comparative cognition necessitates two requirements. The first is that the memory needs to be characterized in

terms of behaviorally defined properties as opposed to purely phenomenological ones, such as the types of information encoded. Indeed, we shall argue that the ability to remember what happened, where and how long ago is a critical behavioral criterion for episodic memory. The second requirement is the identification of an ethological context in which these memories would confer a selective advantage. Note that by doing so, we transform this debate about the human uniqueness of mental time travel into an empirical evaluation in non-Linguistic animals as opposed to restricting it to the realms of philosophical personal ponderings. But before doing so, let us return to the two claims made by the mental time travel hypothesis: (1) future planning and episodic memory are subserved by a common process, mental time travel, and (2) this process is uniquely human. We shall evaluate each of these claims in turn, and argue that there is good evidence to support the first claim, but that considerably more controversy surrounds the second component of Suddendorf and Corballis' thesis.

Evidence to support the first claim comes from a number of sources. First, studies of brain activity while engaged in either memory retrieval or future-oriented tasks identify a specific core network of regions in the brain of healthy human adults that support both episodic recollection and future planning. Moreover, there are patients such as DB and KC, who show specific impairments in episodic but not semantic memory, and these patients have similar deficits in episodic but not semantic forethought. Finally, studies of cognitive development in young children suggest that episodic memory and future planning both emerge at about the same age, and are not properly developed until children reach the age of about four.

Is Mental Time Travel Unique to Humans?

Regarding the second claim about the uniqueness of episodic memory and future planning, if we are to adopt an ethological approach of the form we outlined earlier, then the question becomes one of asking where in the natural world these two processes might intersect, in which species, and under what conditions. One classic candidate is the food-caching behavior of corvids, members of the crow family that include jays, magpies, and ravens as well as the crows. These large-brained, long-lived, and highly social birds hide food caches for future consumption, and rely on memory to recover their caches of hidden food at a later date, typically weeks if not months into the future. So clearly food-caching is a behavior that is oriented toward future needs. Indeed, the act of hiding food is without obvious immediate benefit and yields its return only when the bird comes to recover the caches it made. Given that these birds are dependent on finding a significant number of these caches for survival in the wild, it seems likely that the selection pressure for an excellent memory for the caches would have been particularly strong, especially as they cache year round.

These birds also cache reliably in the laboratory, providing both ethological validity and experimental control. At issue, however, is whether or not these birds episodically remember the past and plan for the future. For these reasons, we shall now turn our attention to assessing the evidence as to whether or not these food-caching corvids can remember the past and plan for the future.

Episodic Memory

As we stated earlier, language-based reports of episodic recall in humans suggest that the retrieved experiences are not only explicitly located in the past but are also accompanied by the conscious experience of one's recollections. From a comparative perspective, the problem with this definition, however, is that in the absence of agreed non-Linguistic markers of consciousness, it is not clear how one could ever test whether animals are capable of episodic recollection. For how would one assess whether or not an animal can experience an awareness of the passing of time and of reexperiencing one's own memories while retrieving information about a specific past event.

Behavioral criteria for episodic memory

This dilemma can be resolved to some degree, however, by using Tulving's original definition of episodic memory, in which he identified episodic recall as the retrieval of information about 'where' a unique event occurred, 'what' happened during the episode, and 'when' it took place. The advantage of using this definition is that the simultaneous retrieval and integration of information about these three features of a single, unique experience may be demonstrated behaviorally in animals. Clayton and Dickinson termed this ability '*episodic-like memory*' rather than episodic memory because we have no way of knowing whether or not this form of remembering is accompanied by the autonoetic and chronesthetic consciousness that accompanies human episodic recollections. Indeed, we have argued that the ability to remember the 'what-where-and-when' of unique past episodes is the hallmark of episodic memory that can be tested in animals.

Empirical tests of episodic-like memory

We focus our analysis on one particular species of food-caching corvid, the western scrub-jay, capitalizing on one feature of their ecology, namely, the fact that these birds cache perishable foods, such as worms, as well as nondegradable nuts, and as they do not eat rotten items, recovering perishable food is only valuable as long as the food is still fresh. In a classic experiment published

in 1998, we tested whether the jays could remember the 'what, where, and when' of specific caching events.

Although the birds had no cue predicting whether or not the worms had perished other than the passage of time that had elapsed between the time of caching and the time at which the birds could recover the caches they had hidden previously, the birds rapidly learned that highly preferred worms were fresh and still delicious when recovered 4 h after caching, whereas after 124 h, the worms had decayed and tasted unpleasant. Consequently, the birds avoided the wax worm caches after the longer retention interval and instead recovered exclusively peanuts, which never perish. Following experience with caching and recovering worms and peanuts after the short and long intervals, probe tests, in which the food was removed prior to recovery, showed that they relied on memory to do so rather than cues emanating directly form the food. Subsequent tests revealed that the jays could remember which perishable foods they have hidden where and how long ago, and irrespective of whether the foods decayed or ripened.

Since the initial studies, a number of other laboratories have also turned their attention to the question of whether or not animals have episodic-like memory. Using paradigms analogous to those employed with the jays, there is now good evidence that rats, mice, and magpies can remember the what-where-and-when and what-where-and-which of past events.

Forethought

If forethought, at least in the form of episodic future thinking, falls under the general umbrella of mental time travel and is the reason for why episodic memory evolved in the first place as we suggested in the introduction, then we should expect to find a concomitant development of episodic memory and episodic future thinking. So if one accepts the evidence that the scrub-jays can episodically recall the past, at least in terms of the behavioral criteria, then these birds should also be capable of planning for the future. The topic is of course a controversial one, and indeed there is much debate about whether non-human animals are capable of forethought (see, e.g., the arguments of Suddendorf and Corballis, and the responses from my laboratory). For how does one test whether the jays' caching decisions are controlled by future planning?

Behavioral criteria for future planning

The first distinction that one must draw is between prospectively oriented behavior and future planning. Several anticipatory activities, including migration, hibernation, nest building, and food-caching, are clearly conducted for a future benefit as opposed to a current one, but they would not constitute a case of future planning unless one could demonstrate the flexibility underlying cognitive control, and thereby rule out simpler accounts in terms of behavior triggered by seasonal cues or previous reinforcement of the anticipatory act.

So the first issue to address is whether the caching behavior of the jays is sensitive to its consequences. To do so, once again we capitalized on the fact that the jays love to eat and cache fresh worms but that they do not eat them once they have degraded. We used a variant of the Clayton and Dickinson (1998) caching paradigm in which the jays were given fresh worms and nuts to cache before recovering them 2 days later. In contrast to the original experiments on episodic-like memory, in which the state of the worm caches varied with the retention interval, in the future-planning experiment, the worms were always degraded at recovery in order to investigate their choice of what to cache, as opposed to where to search at recovery. The objective of this experiment was to assess whether or not the birds could learn that even though the worms were fresh at the time of caching there was no point in caching them because they would always be degraded and therefore unpalatable at the time of recovery. The jays rapidly learned to stop caching the worms, even though they continued to eat the fresh worms at the time of caching, thereby demonstrating that caching is indeed selective to its consequences in the sense that the jays could learn what not to cache.

The Bischof–Köhler hypothesis

Suddendorf and Corballis have also argued that a critical feature of future planning is that the subject can take action in the present for a future motivational need, independent of the current motivation. Indeed, they argued that mental time travel provided a profound challenge to the motivational system in requiring the subject to suppress thoughts about one's current motivational state in order to allow one to imagine future needs, and to dissociate them from current desires.

To illustrate this distinction between current and future motivational states, consider the following example. A current desire for a croissant at breakfast may lead to an early morning trip to the local baker. Of course it will take some time to reach the market, and therefore the croissant will not be eaten now but in a few minutes time. But although the croissant will be eaten at a future time as opposed to the present, this behavior would not fulfill the Bischof–Köhler criterion because the action is governed by one's current motivational state. By contrast, going to the baker's shop in order to ensure that there are croissants for tomorrow's Sunday brunch would be an example of the future planning envisaged by the Bischof–Köhler hypothesis because this action would be performed for a future motivational need, independent of one's current needs.

This hypothesis was inspired by a comparative perspective, from reviewing the evidence for human and

non-human primate cognition, and indeed it has led to a number of tests of whether animals can dissociate current from future motivational needs. In one study to address this issue, Naqshbandi and Roberts gave squirrel monkeys the opportunity to choose between eating four dates and eating just one date. Eating dates makes monkeys thirsty, but rather than asking the monkeys to chose between water and the dates, the experimenters manipulated the delay between the choice (one vs. four dates) and receiving water such that the monkeys received water after a shorter delay if they had chosen the one date rather than the four dates. The monkeys gradually reversed their natural preference for four dates, suggesting that they were anticipating their future thirst. However, because the monkeys received repeated trials in which they learnt the consequences of their choices, one can give a simple associative explanation in terms of reinforcement of the anticipatory act by avoidance of the induction of thirst.

More convincing evidence for a dissociation of current and future motivational states comes from a study by Correia, Dickinson, and Clayton on the food-caching scrub-jays. Like many other animals, when sated of one type of food, these birds prefer to eat and cache another type of food. Correia and colleagues capitalized on this specific satiety effect to test whether the birds would choose to cache the food they want now or the food they think they will want when they come to recover their caches in the future. In the critical group, the birds were sated on one of two foods that were both then made available for caching. Then, immediately prior to the recovery of these caches, they were sated on the other food. Consequently, the food that was valuable at recovery was the one that was less valuable at the time of caching. At the beginning of the experiment, the birds cached the food they desired at the time, but then rapidly switched to storing preferentially the food that was valuable at the time of recovery rather than the one they wanted to eat at the time of caching, suggesting that the jays can plan future actions on the basis of what they anticipate they will desire in the future as opposed to what they need now. So this study supports the notion that jays can dissociate future from current motivational needs, and therefore provides direct evidence to challenge the Bischof–Köhler hypothesis (for further discussion see our recent review in *Animal Behaviour*).

For the skeptic, however, this kind of task need not require prospective mental time travel because the scrub-jay does not need to imagine a future situation. Suppose that the act of recovering a particular food recalls the episode of caching that food. If the bird is hungry for that particular food, then recovering it will be rewarding and therefore this could directly reinforce the act of caching the food through the memory of doing so. The point is that such memory-mediated reinforcement does not require the bird to envisage future motivational states.

Tulving's spoon test

Tulving has argued that it is possible to test whether animals are capable of such episodic future thinking, and devised what he calls the 'spoon test,' which he argues is a 'future-based test of autonoetic consciousness that does not rely on and need not be expressed through language.' The test is based on an Estonian children's story tale, in which a young girl dreams about going to a birthday party. In the dream, all of her friends are eating a delicious chocolate mousse, which is her favorite pudding, but alas she cannot because she does not have a spoon with her, and no one is allowed to eat the pudding unless they have their own spoon. As soon as she gets home she finds a spoon in the kitchen, carry it up to her bedroom and hides – or caches – it under her pillow, in preparation for future birthday parties and even dreams of future birthday parties for that matter.

The point then is to use past experience to take action now for an imagined future event. To pass the spoon test, an animal must act analogously to the little girl carrying her own spoon to a new party, a spoon that has been obtained in another place and at another time. Is there any evidence that animals and young children can pass this spoon test? Although some animals, notably primates and corvids (namely the scrub-jays we discussed earlier), have been shown to take actions now based on their future consequences, most of these studies have not shown that an action can be selected with reference to future motivational states independent of current needs as discussed in the previous section.

Mulcahy and Call were the first to devise a spoon test for animals. In their study a variety of species of non-human apes were first taught to use a tool to obtain a food reward that would otherwise have been out of reach, before being given the opportunity to select a tool from the experimental room, which they could carry into the sleeping room for use the following morning. Although most of the subjects did choose the correct tool on some trials, the individual patterns of success for each subject was not consistent across subsequent trials, as one would expect if they had a true understanding of the task. Furthermore, the apes received a number of training trials, so reinforcement of the anticipatory act cannot be ruled out. A more convincing case of planning was provided by Osvath and Osvath. In a recent series of experiments, these authors demonstrated that when selecting a tool for use in the future, chimpanzees and orangutans can override immediate drives in favor of future needs.

One of the most striking examples of the spoon test in animals comes from recent studies of the food-caching scrub-jays. In the laboratory, work by Raby and colleagues showed that our jays can spontaneously plan for tomorrow's breakfast without reference to their current motivational state. The birds were given the opportunity to learn that they received either no food or a particular type of

food, for breakfast in one compartment, while receiving a different type of food for breakfast in an alternative compartment. Having been confined to each compartment at breakfast time for an equal number of times, the birds were unexpectedly given the opportunity to cache food in both compartments one evening, at a time when there was plenty of food for them to eat and therefore no reason for them to be hungry. Given that the birds did not know which compartment they would find themselves in at breakfast tomorrow and on the assumption that they prefer a variety of foods for breakfast, we predicted that if they could plan for the future, then they should cache a particular food in the compartment in which they had not previously had it for breakfast.

This the birds did, suggesting that they could anticipate their future desires at breakfast time tomorrow when they would be hungry. Importantly, because the birds had not been given the opportunity to cache during training, we can in this experiment rule out an explanation in terms of mediated reinforcement of the anticipatory act. These findings led Shettleworth to argue that "two requirements for genuine future planning are that the behavior involved should be a novel action or combination of actions and that it should be appropriate to a motivational state other than the one the animal is in at that moment . . . Raby et al. describe the first observations that unambiguously fulfill both requirements."

Although it seems clear that the scrub-jays and chimpanzees do pass the spoon test, at issue, however, is whether or not these tasks truly tap episodic future thinking. Indeed, we have argued that in the absence of language, there is no way of knowing whether the jays' ability to plan for future breakfasts reflects episodic future thinking, in which the jay projects itself into tomorrow morning's situation, or semantic future thinking, in which the jays acts prospectively but without personal mental time travel into the future. In the latter case, all that the subject has to do is to work out what has to be done to ensure that the implement is to hand, be it a spoon, some other tool, or a food-cache. In no sense does this task require the subject to imagine or project one's self into possible future episodes or scenarios. As Raby et al. have argued, however, what these studies do demonstrate is the capacity of animals to plan for a future motivational state that stretches over a timescale of at least tomorrow, thereby challenging the assumption that this ability to anticipate and act for future needs evolved only in the hominid lineage.

Concluding Remarks

The mental time travel hypothesis of Suddendorf and Corballis makes two claims. We have argued that the first claim that episodic memory and future planning are intimately linked and subserved by the same common process of mental time travel has good support. However, we challenge the second claim about human uniqueness. Indeed, we have argued that at least some animals, notably a few primates and corvids, are capable of recollecting the past and planning for the future. In the case of the scrub-jays, the functional account of caching appears to be reflected in the psychological processes underlying this behavior; by fulfilling the behavioral criteria we have outlined, they therefore show at least some elements of episodic memory and forethought. It also serves as a superb illustration of the integration of the retrospective and prospective components of mental time travel for there is no benefit to the animal of hiding food at the time of caching. The benefit occurs when recovering the caches at a future time, and to do so effectively, the jays must rely on their episodic-like memories of past caching events to know where to search for their hidden stashes of food.

See also: Intertemporal Choice; Time: What Animals Know.

Further Reading

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Relevant Websites

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http://www.neuroscience.cam.ac.uk/directory/profile.php?nsclayton – Professor Nicky Clayton: Cambridge Neuroscience.

http://www.youtube.com/watch?v=y_MnwNyX0Ds – Bird Tango.

http://www.sciencemag.org/cgi/content/full/315/5815/1074.