



Review

Prospective cognition in animals

C.R. Raby, N.S. Clayton*

Department of Experimental Psychology, University of Cambridge, Cambridge CB2 3EB, UK

ARTICLE INFO

Article history:

Received 10 June 2008

Received in revised form 1 December 2008

Accepted 7 December 2008

Keywords:

Episodic future thinking

Foresight

Prospection

Semantic future thinking

ABSTRACT

The debate about whether or not animals have foresight has focused on whether animals can be shown to have episodic future thinking, that is the ability to travel mentally in time and see themselves in the future. This focus has distracted from consideration of other forms of foresight that animals demonstrate. We propose a framework for examining future-oriented behaviours and then discuss the evidence for future thinking in animals. In the final section we examine some perspectives of future thinking and suggest that there are future-oriented capabilities of animals that do not involve mental time travel but may yet involve future thinking which deserve further investigation.

© 2008 Elsevier B.V. All rights reserved.

Contents

1. A framework for examining future-oriented behaviour	315
1.1. A taxonomy of future-oriented behaviour	315
1.1.1. Fixed action patterns	315
1.1.2. Learnt associations	315
1.1.3. Prospective thinking	315
1.2. Semantic and episodic cognitive systems	316
1.2.1. Psychological evidence	316
1.2.2. Neural imaging evidence	316
1.2.3. Developmental evidence	316
1.3. Categorising future-oriented behaviours	316
2. The evidence for prospective thinking in animals	317
2.1. Prospective memory	317
2.2. Self-control	317
2.3. Anticipation	318
2.4. Goal-directed behaviour	318
2.5. Future planning?	318
3. Perspectives on future thinking	319
3.1. What is future thinking?	319
3.1.1. Extrapolating from the Bischof-Köhler hypothesis	319
3.2. Semantic prospection	319
3.3. Evolution of the episodic cognitive system	320
3.4. Function of the episodic and semantic cognitive systems	321
4. Conclusion	322
Acknowledgements	322
References	323

Sara Shettleworth has suggested a moratorium on studies of “mental time travel” in animals until its psychological and

behavioural components have been better specified (Shettleworth, 2007b, p. 333). Mental time travel describes the ability to project yourself into your personal past and remember or re-experience specific events or to project yourself into your personal future and imagine or pre-experience possible events. The hot debate for a decade or more has been whether or not this ability is

* Corresponding author. Fax: +44 01223 333564.

E-mail address: nsc22@cam.ac.uk (N.S. Clayton).

uniquely human (e.g. Clayton et al., 2003a, b, 2008; Roberts, 2002, 2007; Suddendorf and Busby, 2003; Suddendorf and Corballis, 1997, 2007a; Tulving, 2005; Zentall, 2005). Shettleworth observes firstly that we can never know what another species' mental experiences are like and secondly that the search for a yes or no answer to whether any cognitive process is uniquely human distracts from understanding what components of a given cognitive process species do share and why (Shettleworth, 2007b).

Here we argue that with respect to the future-oriented abilities of animals the 'do-they-don't-they have it?' debate has certainly diverted attention from an appreciation of what animals are capable of with respect to future thinking and future planning, and in particular that the potential of semantic prospection, that is to say the ability to think about the future without projecting yourself into the future, has been largely overlooked. In this paper, we shall propose a taxonomy of future-oriented behaviours, review animal behaviour against these definitions and suggest that the focus on mental time travel has indeed been detrimental to the consideration of future prospection in animals.

1. A framework for examining future-oriented behaviour

1.1. A taxonomy of future-oriented behaviour

There are a number of different kinds of future-oriented behaviour that we organise according to the following taxonomy. We distinguish between those behaviours that, while having future consequences, do not necessarily require a sense of the future from those for which some sense of the future seems to be a prerequisite. For the latter, we identify three categories, only one of which need necessarily involve mental time travel, namely actions deriving from episodic future thinking. We define each of these categories in turn.

1.1.1. Fixed action patterns

Future-oriented behaviour does not necessarily require future thinking. So called fixed action patterns can be triggered, for example, by a seasonal cue. Nest building and provisioning, hibernation and migration are classic future-oriented behaviours in which there is no evidence of planning or even of future-awareness, but rather these behaviours are controlled by changes in photoperiod, temperature and hormones. Fabre (1916) lyrically relates his experiments with the digger wasp, *Bembex*, whose maternal behaviour of constantly supplying her larva with flies appears to be solely driven by her nest entrance. If this is destroyed she neither recognises nor responds to her larva but treads on it and pushes it out of the way in her frantic search for her nest entrance. Evidence that such behaviours are heritable comes from the studies of migratory restlessness in the black-capped warbler; when a south-west migrating population was interbred with a south-east migrating population the resulting offspring migrated due south (Berthold et al., 1992). Fixed action patterns, then, are relatively inflexible behaviours, often extremely elaborate, that have consequences in the future but for which no sense of the future by the organism demonstrating the behaviour is necessary Fig. 1.

1.1.2. Learnt associations

Other future-oriented responses may arise as a consequence of a stimulus reliably predicting a reward resulting in a conditioned response which is not cognitively mediated. The classic examples include dogs salivating at the sound of a bell that predicts the arrival of food and of rats learning to associate pressing a lever with the delivery of food (Pearce, 1997).

Adams and Dickinson (1981) demonstrated that associatively learnt behaviour can be goal-directed. They showed that rats can have the outcome not just of food but of the specific food on offer in mind when they press the lever-press. Rats would stop pressing the lever if the reward was devalued suggesting that they have the specific food reward in mind and lose interest in obtaining it once its value is reduced. The assumption is that this does not demonstrate future thinking, the sight of the lever simply stimulates a representation of the reward.

Animals can also rapidly learn time-place associations and use this information in order to decide when and where to forage for food. In a series of elegant experiments by Biebach and colleagues, garden warblers were given a choice of rooms to visit from a central compartment with food being available at different times of day in each room. They found that the birds rapidly learned within just seven trials which room to visit when, based on the time of day (Biebach et al., 1989). Clock-shifting experiments demonstrated that this time-place learning was controlled by the animal's endogenous circadian rhythm. For a full account of how such mechanisms might work see Shettleworth (1998).

1.1.3. Prospective thinking

In our analysis of prospective thinking, we shall make a distinction between prospective memory, semantic future thinking and episodic future thinking which are discussed in turn below.

1.1.3.1. Prospective memory. Prospective memory is included here because as measured in humans it requires some form of future thinking. However there is a difference between the way in which it is measured in humans and in animals. Prospective memory or prospective coding in animals is commonly used to refer to an animal's use of short-term or working memory in tasks that involve delays between the stimulus and the opportunity to respond (Thorpe et al., 2004), for example rats can learn to visit all the arms in a radial maze without duplication (Cook et al., 1985). To do this they may either use a representation of the arms they have already visited (retrospective memory) or a representation of the arms still to be visited (prospective memory). Thorpe et al. (2004) summarise retrospective memory as referring to what an animal has seen up until it is faced with a choice and prospective memory as referring to a choice that an animal anticipates making. Prospective memory measures an animal's ability to retain to-be-made responses across a short delay. However, Thorpe and colleagues make the point that this is different from the term as used when applied to humans, when it is understood as a form of long-term memory referring to remembering to carry out an action at an appropriate future moment (Baddeley, 1997). The important difference is that in

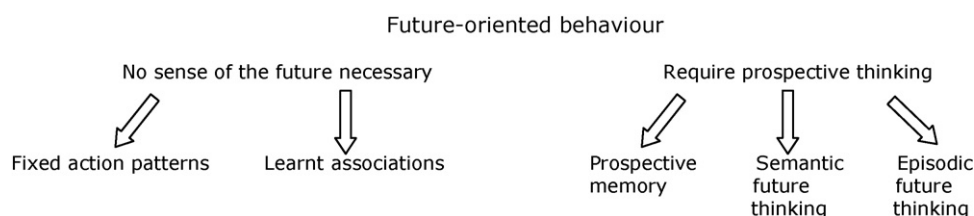


Fig. 1. Types of future-oriented behaviour.

animal experiments the task context at test explicitly prompts the action, whereas this is not so in human prospective memory tasks.

1.1.3.2. Semantic future thinking. Semantic future thinking is the ability to form scenarios or projections set in the future which do not involve envisaging yourself personally experiencing the future event. These may be general knowledge scenarios which will reoccur, for example what is likely to happen when you arrive at an airport to get on a plane; specific future events, for example knowing that there is going to be a general election this year; or personal events such as knowing that you are due to visit the dentist. They are often script-based and derive from both semantic and episodic memories. Semantic memory can include temporal information about when events took place but without a sense of having personally lived them. Semantic future thinking is set in a semantic future. The concept of future has a semantic meaning but, unlike episodic future thinking, it does not involve mental time travel and individuals do not envisage themselves in the future.

1.1.3.3. Episodic future thinking. The essential difference between episodic future thinking and semantic future thinking is that episodic future thinking is a personal projection into the future in which the mental time travellers are themselves part of the imagined future scenario. In humans it may take the form of a precise plan (I am going shopping tomorrow), a likely but undecided future event (seeing yourself in possible future holiday destinations) or the extremely implausible (winning the lottery and planning what you would do with the money). Humans of course typically combine both episodic and semantic future thinking; envisaging a trip to the airport may combine semantic knowledge of what is likely to happen with episodic future thinking about details of the particular trip you are taking.

1.2. Semantic and episodic cognitive systems

If the only difference between semantic and episodic prospection is that episodic prospection involves mental time travel or 'pre-experiencing' aspects of what might happen what evidence is there for the distinction of semantic and episodic cognitive processes? Here we summarise three main lines of argument: psychological, neural imaging and developmental.

1.2.1. Psychological evidence

A number of neuropsychological case studies confirm that patients with impaired episodic memory also have impaired episodic future thinking but may retain semantic memory and semantic future thinking. Tulving and colleagues (Rosenbaum et al., 2005; Tulving, 1985, 1989) report the case of K.C. who, as a result of brain injury following a motorcycle accident lost all memory of any personal experiences although he could remember personal facts about himself such as names of schools that he attended as well as general knowledge. He was also unable to imagine anything he might personally do at any future time. Klein et al. (2002) and Atance and O'Neill (2001) refer to four further cases in which the patients have apparently lost the ability to plan for or even be aware of any personal future events while retaining variable levels of semantic knowledge about the future. There is also evidence for people with impaired semantic memory retaining the ability to recall recent episodic memories (Graham et al., 2000; Hodges and Graham, 2001).

Further psychological evidence that semantic and episodic cognition are mediated by different memory systems comes from memory recall experiments demonstrating that there is a difference between remembering and knowing in normal, healthy adults (Rajaram, 1993; Tulving, 1985), and that older people show a deterioration in 'remember' responses relative to young people but not in 'know' responses (Mäntylä, 1993).

1.2.2. Neural imaging evidence

Neural imaging studies confirm that the retrieval of semantic and episodic memories activate different areas of the brain although there is some debate as to exactly which areas. Tulving (2002) cites fMRI studies which show that semantic retrieval is localized largely in the left temporal and left frontal regions of the brain while retrieving episodic memories activates the right prefrontal cortex. Aggleton and Brown cite evidence that episodic encoding and retrieval rely on the hippocampus, fornix, mammillary bodies and the anterior thalamic nuclei while semantic knowledge involves the perirhinal cortex of the temporal lobe and the medial dorsal nucleus of the thalamus (Aggleton and Brown, 1999). Graham reports that patients with semantic dementia show atrophy of the inferior and lateral regions of the left temporal lobe (Graham et al., 2000). Wiggs, however (Wiggs et al., 1999) found that episodic memories activated the medial parietal cortex, retrosplenial cortex, thalamus and cerebellum but did not activate as much right frontal cortex as retrieving semantic information.

Conway (2005) concludes that episodic memory is a posterior temporo-occipital system and that what he calls autobiographical memory, which refers to known not remembered personal facts and so equates to personal semantic memory, is, a prefrontal anterior-temporal system. Okuda et al. found that both future and past episodic tasks activated a number of frontal and medial temporal lobe areas which were not activated by a semantic control task and that areas in the anteromedial frontal pole showed greater activation during future tasks than past tasks (Okuda et al., 2003). The story is far from simple, not least because the two types of memory are often activated at the same time and both types of memory are frequently used in the generation of future thinking but there is general agreement that episodic and semantic thinking can be distinguished in terms of brain activity.

1.2.3. Developmental evidence

There is some evidence for the later development of the episodic cognitive system in children. Children below the age of 2 seem to have no concept of past and future; they gradually develop this skill between 3 and 5 years old (e.g. Suddendorf and Corballis, 1997). Hudson et al. (1995) found that between the ages of 3 and 5 children's ability to describe a script-based future event (semantic) did not improve while their ability to plan for a specific future event improved significantly. Busby and Suddendorf (2005) report that 3-year olds can produce answers to questions about events displaced in time as readily as 4-year olds but their responses were much less likely to be based on reality than 4-year olds. Others (Atance and Meltzoff, 2005; Atance and O'Neill, 2005a, b) also found 3 to be the critical age at which children begin to describe possible episodic future events, for example using modal verbs such as 'I am going to', and I 'might'. Atance and O'Neill also conclude that these differences are not a result of differences in the children's general language abilities as they get older (Atance and O'Neill, 2005b).

These three lines of evidence suggest that there are identifiably different episodic and semantic cognitive systems that develop at different times. However, the neurophysiological evidence also suggests that the two systems are very closely linked although how and to what extent remains to be established as and when we can specify precisely what each part of the brain network contributes to each system.

1.3. Categorising future-oriented behaviours

What sort of evidence then would allow us to conclude that a behaviour comes from one part of this framework of future-oriented behaviours or another?

It would be hard to improve on Suddendorf and Busby's summary of behaviours common to fixed action patterns: "Behavioural

programmes [that] tend to be fixed to a particular domain, universal to members of the species and displayed even when the individual has never before experienced the event that will make the behaviour meaningful in the future” (Suddendorf and Busby, 2005, p. 112). These behaviours are inflexible responses to cues in the environment that are insensitive to consequences. They are either on or off. Associative learning is a response to a cue that reliably predicts a certain outcome, for example a light predicts the availability of food and the rat learns to press a lever to obtain that food. It differs from fixed action patterns in that there is a certain degree of flexibility. The strength of the response increases with the number of pairings of the cue and the outcome and the behaviour gradually extinguishes if the cue no longer reliably predicts the outcome. Where fixed action patterns are either on or off, associative learning is more akin to a dimmer switch that allows the strength of the response to vary but not the type of response.

One of the most frequent criticisms of demonstrations of future-oriented behaviour in animals is that they can be explained by associative learning. However, these criticisms often ignore the experimental evidence that temporal contiguity between events has been shown to be an important factor in whether associative learning occurs, for example the rate at which rats lever-press for a food reward decreases with the delay between the press and the delivery of food (Dickinson et al., 1992). Although the degree of temporal contiguity varies across different response systems it is typically measured in seconds and there is always a decline in learning over longer delays between the stimulus and the reinforcer. The longest observed delays have been found for flavour aversion conditioning that can occur with a delay between tasting the flavour and the induction of illness of a few hours (see (Riley and Baril, 1976) for a bibliography). There are two measures then that would suggest a behaviour is not a fixed action pattern or associative learning: one is if the behaviour shows flexibility beyond a simple increase or decrease of strength of response and the other is if the delay between the anticipatory act and the supposed reinforcer is implausibly long.

The question of what behaviours reliably indicate future thinking in non-speaking animals is the crux of the problem. Fixed action patterns and associative learning can only be triggered through perception of a stimulus whereas future thinking can be triggered top-down from the frontal lobes (Suddendorf and Corballis, 2007a). Hence while fixed action patterns and learnt associations are only manifest in observable behaviour, prospective thinking may or may not result in behaviour that is objectively observable. Even when a future-oriented behaviour is observed what is the evidence that this behaviour is cognitively mediated by future thinking? Turning the debate on its head, if one could eliminate the possibility that the behaviour is either a fixed action pattern or associative learning, what other options are there than that the behaviour is mediated by some level of prospective cognition? This however gets no closer to concluding what kind of prospective cognition may be at work.

Defining behaviours that constitute prospective memory is reasonably straightforward as it is a term that has been coined to apply to observed behaviours by animals in experimental situations. As discussed above an animal that can be shown to anticipate making certain responses to a stimulus is said to be showing prospective memory. The behaviour is cued by a stimulus but shows levels of flexibility that demonstrate that is more than associative learning. Rats, for example, anticipating that they have a number of arms of a radial maze still to visit must update this information every time that they visit an additional arm. Behaviour that is termed prospective memory however still begs the question of what cognitive processes are mediating the behaviour and whether anticipation necessitates future thinking, however immediate.

The most problematic question, and the one that is the main subject of the rest of this paper, is what behaviours demonstrate semantic or episodic future thinking and whether it is possible to distinguish between semantic and episodic future thinking. The holy grail of establishing that animals can think about the future is to demonstrate that an animal is capable of making provision for a need that it does not currently have but that it will have in the future. The reason that this is the holy grail is precisely because it is the only behaviour that it is agreed would unambiguously demonstrate future thinking. We argue, however, that there are many other behaviours of animals that suggest future thinking and that cannot be dismissed on the grounds that they do not reach the holy grail. We discuss the experimental evidence for future thinking in animals in the next section.

2. The evidence for prospective thinking in animals

2.1. Prospective memory

Zentall (2005) cites evidence for short-term prospective memory in rats who appear to switch strategy half way through visiting each arm of a radial maze from remembering where they have been to anticipating where they need to go next (Cook et al., 1985) and similarly for pigeons in a comparable task in which they had to select all response keys once only (Zentall et al., 1990). He suggests that this is evidence that animals can represent future events and is analogous to a mental shopping list in humans. However, Thorpe et al. (2004) observe that the task context in these and similar experiments explicitly prompt remembering and so cannot be regarded as true prospective memory and really only measure the animal's capacity to retain to-be-performed tasks which are explicitly prompted. They favour animal timing tasks, such as hummingbirds remembering to revisit blooms at the rate at which they regenerate nectar as evidence of prospective memory, particularly as males will interrupt courtship to visit replenished blooms (Gill, 1988). However, such behaviour can be mediated by interval timing mechanisms common in many animals, (e.g. Gibbon et al., 1984; Shettleworth, 1998) and the question remains whether this type of time–place association is cognitively mediated.

2.2. Self-control

Another approach to trying to establish whether animals have any sense of the future has been to test animals on self-control experiments in which, typically, they have to ignore an immediate small reward in order to obtain a larger reward a short time later. Rats and pigeons seem to be unable to learn self-control, opting for an immediate small reward rather than the delayed larger reward (reviewed in Roberts, 2002). Two macaque monkeys did show self-control but over a short timescale (Tobin et al., 1996). Marmosets and tamarins both value a smaller reward now over a large reward in the future but marmosets will wait significantly longer than tamarins for a large reward. The researchers suggest this may be due to their differing feeding ecologies; marmosets consume significantly more tree sap than the insectivorous tamarins which require more patience to obtain (Stevens et al., 2005).

Monkeys and apes also appear to have a form of so called temporal myopia, failing to choose a larger reward over a smaller once the smaller reaches a certain size and throwing their food out of the cage when they are satiated (Silberberg et al., 1998) which Roberts (2002) interprets as the animals being unaware that they will be hungry again in the future. However, Zentall (2005) points out that this fails to take into account an ethological view, namely that saving food in the wild might not be adaptive if you are a member of a mobile social group and equally that self-control may not have been

adaptive for most species as environments tend to be unstable and a delayed reward may be an uncertain reward.

Naqshbandi and Roberts (2006) agree that in the wild choosing an immediate gain when foraging may be the most adaptive strategy and may not reflect an inability to anticipate the future. In support of their argument they cite experiments by Flora and Workman (1995) which show that rats can exercise self-control over a few seconds if they receive a small reward immediately upon making a self-control choice with a greater reward following later. In this context a study by Stephens and Anderson (2001) showed that Blue-jays choose an immediate reward when presented with a conventional self-control experiment but when presented with a more naturalistic choice in which a decision to leave a feeding patch leads to a small amount of food in a short time while the decision to stay leads to a larger amount in a longer time the jays tended to stay.

2.3. Anticipation

Rats can learn to anticipate a reward up to 30 min into the future although this was a predictive relationship triggered by a retrieval cue and performance declined inversely with the length of the delay (Flaherty and Checke, 1982). They can also learn to take an action (choosing an arm of a T-maze) that generates a reward in a different place (in the startbox of the T-maze) 60 min into the future (Lett, 1975). It is argued that this is an example of long-delay associative learning cued by putting the rat into the T-maze but this raises the question of whether the lack of temporal contiguity is compatible with an associative learning explanation.

Experiments on Western scrub-jays have shown that these birds can learn to stop caching wax worms, a preferred food, if it is always degraded or pilfered at recovery relative to a less preferred food that is not, and that this is not accounted for by their losing their taste for the wax worms (Clayton et al., 2005; de Kort et al., 2007). Furthermore, only the birds that have pilfered others' food in the past, and not the birds who have never been thieves themselves, will re-cache food in private, and they do so if – and only if – they have been observed caching by another jay (Emery and Clayton, 2001). These experiments suggest that the jays can anticipate that their caches might be stolen or inedible in the future and adjusting their behaviour appropriately, based on their experience of having been thieves in the past or of finding their caches degraded or pilfered in the present. If so, this behaviour may be an example of cued prospective cognition prompted by the caching trays. A possible alternative explanation of the decrease in caching foods which the birds have experienced as degraded and pilfered on recovery is that they associate the particular caching tray with finding bad or absent food and so avoid caching that type of food there without any sense of the future. However, it is harder to find an equivalent explanation for the re-caching by thieves when observed, and the absence of this behaviour in those that have not been thieves, even though both groups had been victims of cache pilferage.

2.4. Goal-directed behaviour

A number of researchers have demonstrated future-oriented behaviours in apes. Apes have been observed sharpening sticks to use as tools for termite fishing prior to searching for termites and carrying stones over long distances to use for cracking nuts (Boesch and Boesch, 1984; Goodall, 1986; Lawick-Goodall, 1971). Suddendorf and Corballis describe experiments conducted by Döhl with the chimpanzee Julia who learnt to look as many as five steps ahead in a sequential problem-solving task involving selecting the right key to open a box which led to opening further boxes with keys until reaching the box that contained the reward or the box that contained nothing (Suddendorf and Corballis, 1997). Menzel (2005) describes a number of experiments with Panzee the chimpanzee

in which food or other desirable objects were hidden at some distance in woods outside her cage. In order to recover these items Panzee had to recruit human help and let them know via the use of lexigrams, laser pointers and video both what the object was and where it was located. Noser and Byrne recently published a study on chacma baboons (Noser and Byrne, 2007) showing that these baboons visit out-of-sight scarce fruit sources early in the morning by-passing other more abundant food sources on the way which they utilized in a more leisurely manner later in the day on their return journey.

2.5. Future planning?

All the ape behaviours described above are future-oriented but they are arguably all motivated by the animals' existing motivational state of hunger. The Bischof-Köhler hypothesis (Suddendorf and Corballis, 1997) states that animals are unable to dissociate another mental state from their present one and so are incapable of anticipating future needs or drive states and are hence unable to travel mentally in time. We later question whether even if true this precludes any kind of future thinking but in any event there have been a number of experiments that aim to show that animals are capable of acting for a future motivational state which would unambiguously demonstrate a capacity for forethought.

Naqshbandi and Roberts (2006) gave both squirrel monkeys and rats who were not thirsty a desirable food that however also induced thirst and then deprived them of water for a period of time. The animals were given a choice of quantities. If they chose the larger quantity the water was removed for a longer period of time than if the animal chose the smaller quantity of food. Squirrel monkeys gradually reversed their preference for choosing the larger quantity of food which the authors suggest indicates that they were anticipating their future thirst at a time that they were not thirsty. Suddendorf and Corballis (2008) take the view that the squirrel monkeys behaviour can be explained by associative learning although it is open to question whether that is likely over the 30 min and 3 h delays respectively between presentation of the smaller and larger quantities of food and the return of the water bottles.

Raby et al. (2007) gave western scrub-jays food to cache when they were not hungry in the evening and they cached significantly more food in a place in which they might experience hunger the following morning relative to a place in which they never experienced hunger in the morning. They also preferentially store a food in a place in which they are not given that food for breakfast relative to a food that they are given in that place for breakfast when given these foods the evening before. On the grounds that this behaviour is both a novel action (i.e. no associative learning can have occurred) and that it is appropriate to a motivational state other than the one the animal is in at that moment. Shettleworth describes these experiments as the first that unambiguously meet the requirements for future planning (Shettleworth, 2007a).

While acknowledging that "it remains possible that the birds cache food in anticipation of a future appetite" (Suddendorf and Corballis, 2008, p.2e) Suddendorf and Corballis suggest that as a result of counterbalancing half of the scrub-jays should have expected to receive breakfast the following morning. However as the birds had only received three experiences of each condition it is unlikely that they had learnt a specific alternation pattern in that time. Suddendorf and Corballis also suggest that the jays may simply be caching according to a general heuristic to balance food sources, a point also made by Premack (2007), but even if the birds are operating within such a heuristic this does not exclude the possibility that the cognitive processes that allow them to implement this heuristic involve some form of foresight (see Clayton et al., 2008, for detailed discussion).

A study by Mulcahy and Call on tool carrying in apes is claimed by the authors to “represent a genuine case of future planning” (Mulcahy and Call, 2006, p.1039). This conclusion is based on apes carrying a tool that could be subsequently used to obtain a reward away from the place that the rewards were available and returning with it an hour later or, in the case of two apes, the next day and using it to obtain the reward. However, with the exception of one orang-utan, overall the apes carried a tool that was suitable to use to obtain the reward back into the test room less than half the time, about the same number of times that they took unsuitable tools. In addition the way that the experiments were conducted cannot exclude the possibility of associative learning or that their behaviour was cued by their current motivational state (Shettleworth, 2007a; Suddendorf, 2006).

However a recent study by Osvath and Osvath seems to overcome the objections to Mulcahy and Call’s study. Their subjects, two chimpanzees and an orang-utan, consistently selected the correct tool to obtain a food reward that would be available in a different room and at a future time. They then kept the tool and took it to the room in which the reward was available at that later time. In a second experiment given the choice between a variety of tool-like objects and a grape (to which they are very partial) they still selected the tool that could be used to obtain the future favoured food reward significantly more often than the grape and they never selected the non-functional tools. In a further experiment when they could choose one object from two trays which were offered in succession, they chose the functional tool from a choice of four tools on the first tray but ignored the identical functional tool on the second tray and picked a grape instead. Finally the subjects were given a choice of four tools, one of which could be used to obtain the reward but on each of twelve trials the functional object was different and had not been seen by the apes before. The novel functional tool was selected by the apes significantly more often than the other objects. It would seem that these apes are able to select a tool for future use in circumstances that rule out cueing by a stimulus and associative learning, that they overcome the drive to eat a grape now in favour of obtaining fruit soup in the future and that they can select a tool on the basis of functionality rather than on previous experience (Osvath and Osvath, 2008).

3. Perspectives on future thinking

3.1. What is future thinking?

A number of cognitive neuroscientists, notably Tulving, and Suddendorf and Corballis, have argued eloquently for mental time travel as a uniquely human ability (Suddendorf and Corballis, 1997, 2007a; Tulving, 2002, 2005). Their arguments are based on a variety of pre-requisites for mental time travel that in their view animals do not have, as well as the late ontogenetic development of the episodic cognitive system in children. We entirely agree that mental time travel is an extraordinary skill and whether or not other animals have this skill humans can certainly travel mentally further, faster and more flexibly than any other living creature. We think, however, that the focus on attempting to prove whether or not non-human animals can travel mentally in time has limited appreciation and investigation of the future-oriented abilities that animals do exhibit. We question a common extrapolation of the Bischof-Köhler hypothesis, ask what future thinking is possible using the semantic cognitive system, with which it is usually agreed that animals are endowed, and finally, question the extent to which the episodic cognitive system is really understood.

3.1.1. Extrapolating from the Bischof-Köhler hypothesis

The Bischof-Köhler hypothesis and the evidence that animals can act for a future motivational state have been discussed. The

corollary of the Bischof-Köhler hypothesis is often taken to be that if an animal is being driven by a current motivational state then it cannot be said to be exercising future thinking. However, this does not necessarily follow: as human beings we are perfectly capable of exercising future thinking, whether episodic or semantic, when driven by a current motivational state (e.g. I am hungry and I am going to go into town and get a bowl of soup from the German café) so why is there any reason to suppose that in so far as an animal is capable of future thinking it cannot exercise this ability while driven by a current drive state?

Goal-directed action falls into the category of behaviours that are driven by a current motivational state. The theory is that the motivational state stimulates a mental representation of the goal and subsequent behaviour is directed to achieving that goal. A simple thought experiment makes it quite clear that for human beings the question of whether there is any future thinking involved depends both on the temporal contiguity of the stimulus and achievement of the goal and on the complexity of achieving the goal. Thirst may prompt you to go to the tap with little future thinking between the stimulus and the goal. Cold weather might prompt you to book a holiday in the sun with a considerable amount of planning, forward thinking and mental time travel involved.

Noser and Byrne’s chacma baboons (Noser and Byrne, 2007), discussed in our review of evidence for prospective thinking in animals, are demonstrating goal-directed behaviour but this is goal-directed behaviour of a very different level of complexity to rats pressing levers for food. It involves some level of temporal sequencing as well as the ability to hold in mind an out-of-sight resource which is valued sufficiently high to motivate the baboons to by-pass other more readily available food sources. At minimum the baboons must have a representation of the fruit trees in mind and some sense that they are on the way to that goal. If a human being proposed postponing tea to walk first to the blackberry bushes at the other end of the farm we would certainly regard this as an ability to think about the immediate future. While a clear demonstration that an animal can plan for a future motivational state is undoubtedly the strongest evidence for foresight, the fact that action is taken to meet a current motivational state does not exclude the possibility that future thinking is involved.

3.2. Semantic prospection

It is generally agreed that many animals have a semantic cognitive system. Explaining what is meant by semantic memory as far as humans are concerned presents few problems. It is generalised knowledge or retained facts acquired through different senses which model the organism’s world and which can be accessed flexibly and used in a variety of ways. The knowledge may be personal including autobiographical facts, personal characteristics and awareness of body position in space. It may be knowledge of a specific event (e.g. place of birth) or of general characteristics of the world (rain is wet).

If we accept the evidence that past and future capabilities are linked in the episodic and in the semantic cognitive systems then presumably organisms capable of semantic memory are also capable of semantic prospection. But what exactly does this mean? Patients with brain damage which affects their episodic cognitive system are unable to envisage anything that they may personally do in the future. They are however capable to varying degrees of semantic prospection. K.C. has a concept of the future as an aspect of physical time (Tulving, 2005), other patients can describe what might happen if they were to go to a restaurant or can discuss future events likely to take place in the public domain such as medical breakthroughs (Atance and O’Neill, 2001).

The only distinguishing difference between the episodic and the semantic cognitive systems that has been described is the auto-

noetic sense of having personally experienced the event in question or of the possibility of personally experiencing an imagined future event. Presumably all other kinds of future thinking can be achieved with the semantic cognitive system. Knowing that a general election will take place this year, that there will be a major earthquake in San Francisco in the future and that the earth will eventually be burned up by the sun can be easily seen to be semantic prospection. Knowing about events that will happen to other people in the future is also comprehensible in semantic terms, e.g. that your neighbour is going on holiday, that your sister is going to a restaurant that you both know for dinner tomorrow or that your child is going to go to university next year. Harder to separate from episodic future thinking is semantic thinking about one's own personal future. Knowing that you are going to a meeting with Professor X next week is semantic knowledge but, and particularly if you have met Professor X before at the same location, the semantic knowledge is liable to be intermingled with episodic sensations about the likely atmosphere and 'feel' of the meeting.

What then is semantic future thinking in animals? In humans semantic prospection requires knowledge that there is a future.

What is going on in an ape's mind when it is preparing a stick to use for termite fishing? At minimum it must be seeing the stick as a potential termite probe (Whiten and Byrne, 1991). In order to account for the ape's carrying out the behaviour of finding a stick, sharpening the end and taking it to the termite nest in the correct sequence it must have some ability to order events in time in its mind which raises the question of whether that necessitates some sense of at least the immediate future. Even if it is not envisaging itself going to use the stick to fish for termites it may be using semantic prospection to see the act of termite fishing set in the near future.

Suddendorf and Corballis will go as far as conceding that Panzee's knowledge of where the items she desires are hidden in the wood and recruiting human help to recover them indicates that she is deploying semantic memory for future-directed action (Suddendorf and Corballis, 2007a). Her behaviour surely constitutes a plan for the recovery of the item, and again begs the question of whether this requires any sense of the future and whether she is employing semantic future thinking in developing this plan.

We have argued in the section on prospective thinking in animals, with reference to the Raby and colleagues study on whether scrub-jays can make provision for the future (Raby et al., 2007), that there is no reason to believe that scrub-jays might have learnt an alternation pattern in a short time which would enable them to precisely discriminate whether or not they would be due breakfast in the morning. Another possibility is that the jays are simply using semantic prospection to determine where to cache food and that if this lacks the temporal particularities of episodic future thinking they would cache the food where it will be needed in a generalised future. It certainly seems very difficult to explain the behaviour of Osvath and Osvath's apes (Osvath and Osvath, 2008) without concluding that they have some understanding of what is to come whether or not they specifically envisage themselves in the future drinking fruit soup with a hose.

The problem of course is that, as has so often been observed, a fundamental problem in studying prospective cognition in animals is the lack of language. In the absence of language or any agreed non-linguistic markers, animals' mental states must be inferred from their behaviour. A number of studies on memory have shown that there is no necessary correlation between behaviour and conscious experience even in humans; behaviour can be driven by knowing without remembering or by consciously re-experiencing (Tulving, 2002). Tulving (1999) observes that, with the single exception of episodic memory, all forms of learning and memory are oriented towards what is to come. Some sense of the future, then, would seem to be much more important for animals than sense

of the past. Using past experience does not necessitate knowing that you have learnt it in the past. Does future planning necessitate future thinking? Is it possible to form a plan of what to do in the future, immediate or otherwise, without any understanding or sense of the future or does the very act of planning assume at least a semantic understanding that there is a future, however short-term?

An additional problem arises because almost all episodic future thinking could be achieved using semantic prospection by extracting the auto-noetic and phenomenological elements, in effect by seeing oneself from the outside rather than from the inside as if one were considering the future plans of a third person. This raises the question of why the episodic and semantic cognitive systems are distinct in humans. Did they evolve separately and at different times and do they serve different functions?

3.3. *Evolution of the episodic cognitive system*

Tulving (2002) and Suddendorf and Corballis (1997) believe that the available evidence supports the hypothesis that the episodic cognitive system was built on earlier systems including the semantic cognitive system and that, before the emergence of the episodic cognitive system, humans, in common with other animals, could learn from their experiences but were not consciously or 'auto-noetically' aware that they were doing so.

There are three main arguments for supposing the later phylogenetic emergence of the episodic cognitive system. The first is the claim that there is no evidence that non-human animals think about subjective time but many, especially birds and mammals, do appear to possess semantic memory systems demonstrated by their ability to learn and flexibly express information (Tulving, 2005). The second is that while episodic memories always have a semantic component, semantic memories do not always have an episodic component (Wheeler et al., 1997). The third is the later ontogenetic development and earlier deterioration in old age of episodic thinking relative to semantic, (e.g. Tulving, 2005; Wheeler et al., 1997). The hypothesis is that semantic memory allows organisms to acquire and make use of their personal experiences without being conscious that they are doing so (knowing) and that episodic memory, which is dependent on a sense of oneself in subjective time, is built on top of the older semantic system and gives people auto-noetic access to their personal past (remembering) (Tulving, 2005).

Conway (2005) takes a different view. He argues that episodic memory is a phylogenetically older system that allows most species to operate effectively in their day to day environment. What he calls autobiographical memory, which seems to refer to known not remembered personal facts and so equates to personal semantic memory, is, in his view, a neuroanatomically more recent prefrontal anterior-temporal system which sits on the top of episodic memory. His theory is that autobiographical memory is knowledge based and conceptually organised and provides an organising context for episodic memory, providing an access route that locates memories in meaningful ways. He further predicts that organisms which do not have this more recent system will not be able to engage in long-term planning.

Some interesting theories have been put forward about the evolutionary pressures that might have led to the emergence of mental time travel. Savage-Rumbaugh (1994) suggested that deforestation during the Miocene led to the evolution of bipedal hominids whose infants could no longer be transported by clinging on. Increased support and monitoring of their young was then needed which may have led to the expansion of the ability to keep several things in mind which in turn could have led to the carrying of items such as tools and weapons not needed for immediate use. According to this theory this was the beginning of being able to predict and influence the environment, rather than just react to it, leading to the

unique ability humans have today of being able to shape almost any environment on earth to their own ends.

Osvath and Gärdenfors (2005) argue for the co-evolution of anticipatory cognition and the Oldowan cultural niche, the first tool assemblages in prehistory. They propose that deforestation led to expanding savannahs with a commensurate reduction in floral food resources but an increase in herbivores. This led to an extension of the Oldowan culture in time and space. The considerable distances between the source of the raw material for tools and the killing sites, for example, demonstrates a delay between the acquisition of a tool and its use. Adaptations for long ranging, among which was anticipatory cognition, increased fitness. Bipedalism freed the hands and arms for activities other than locomotion, in particular for precision throwing and efficient transportation of tools and weapons—probably, as Osvath and Gärdenfors note essential for the survival of “a small and clawless slow biped with reduced canines” (Osvath and Gärdenfors, 2005, p. 5). The development of anticipatory cognition and symbolic communication allowed co-operation and the division of labour: for example different individuals carrying different items useful to the whole group such as weapons, tools and water; males specialising in hunting while females gathered plants and cared for the young. Osvath and Gärdenfors suggest that the complex cognitive traits which are necessary precursors for future thinking were present in the common ancestor of apes and hominids (and are still present today in apes) and that selective pressures rapidly brought about this form of cognition in the hominid line.

Both the Savage-Rumbaugh and Osvath and Gärdenfors theories start from the premise that mental time travel is uniquely human, and look for explanations in human evolution that account for this as a difference between humans and other animals. Osvath and Gärdenfors believe that the precursors of these skills may have been present in apes but of course they may also have been present in other species. There is evidence, for example, for the convergent evolution of intelligence in apes and corvids, from experimental evidence that they have similar high-level cognitive skills not present in other descendants of the common ancestors in either line (Emery and Clayton, 2004).

From an ethological perspective non-human animals must also have been subjected to evolutionary pressures, climatic or otherwise. Clayton et al. (2001) discuss cases in which an animal would benefit from integrated what–where–when memories, for example brood parasitic birds who need to keep track of the location of potential host nests, the status of the clutch and the time of laying to successfully add their eggs at the appropriate time. While, as we have discussed, exhibiting such behaviour is not evidence for specific mental processes that accompany the behaviour, identifying a type of behaviour in an animal that is of ethological benefit to that animal for which humans use certain cognitive skills is at least an interesting area of research. Apart from food-caching, future-oriented behaviours that might fall into this category include keeping track of ripening fruit or replenishing nectar levels of flowers or when females come into oestrus.

3.4. Function of the episodic and semantic cognitive systems

Another line of enquiry is to consider the possible different function of episodic and semantic cognitive systems. Autobiographical memory, as the term is generally used, comprises both semantic and episodic memories. There are aspects of one's personal past that one knows as fact without re-experiencing. Indeed, one only has to bring to mind an episodic memory to realise what a small percentage of one's past can be stored in this manner. Consider a recent meal out with friends; flashes of the occasion come to mind but it would be impossible to recall every detail of the evening and conversation in chronological order. One retains an

overall impression of the feeling of parts of one's past – being at school for example – and individual scenes can be replayed, but the bulk of one's knowledge about oneself is stored semantically. This of course is essential, trying to store the particularities of every event experienced would result in what Hegdé calls a ‘combinatorial explosion’ (Hegd , 2007, p. 324). This raises the interesting question of whether the episodic and semantic cognitive systems are adapted to different functions.

Suddendorf and Corballis (1997) conjecture that episodic memory is not in itself adaptive but a coincidental by-product of the adaptive development of future thinking. To be useful, future thinking must be a generative process combining different aspects of experience, knowledge and imagination to effectively envisage various possible future scenarios and take appropriate actions. There is evidence that people do something similar with episodic memories, updating them whenever they are retrieved and then re-storing the updated version which would explain their well-known unreliability in corresponding to reality—for example the common experience of people remembering the contents of conversations they have taken part in or events they have witnessed differently (Kinsbourne, 2005; Schacter and Addis, 2007; Suddendorf and Corballis, 1997, 2007a).

Bluck (2003), however, does see an adaptive function for episodic memory which would also explain its flexibility and propensity to change over time. She reviews three functions of autobiographical memory: *self*—knowledge of oneself in the past and as projected into the future are essential for self-continuity and self-development; *social*—allowing us to understand and empathize with others as well as facilitating social interaction by providing material for conversation and the sharing of memories; and *directive*—using old information to solve problems in the present and to predict future events.

We suggest that while episodic memory seems to make a much richer contribution to the possible social function of autobiographical memory than semantic, it may not be essential for the directive function even though it is brought into service in this function, at least in humans. Both Nelson (1992) and Dessalles (2007) also think that the main function of episodic memory is social—to tell stories and to share specific information. Perhaps the development of the two cognitive systems was driven by different evolutionary pressures, semantic memory evolving from the adaptiveness of learning from experience and episodic as a social tool promoting a sense of self and understanding of others alongside theory of mind? In this scenario the two then integrate adaptively to form enhanced autobiographical memory and more vivid, personalised and generative future thinking.

This theory ties in with the view that mental time travel is impossible without a conscious sense of self (Suddendorf and Corballis, 1997; Tulving, 2002) and indeed Suddendorf and Corballis also suggest that the likely precursors of mental time travel, including the ability to attribute mental states to others, may have evolved as a result of the pressures of an increasingly complex social structure. The relationship between large relative brain size and sociocognitive skills has also been noted (Barrett et al., 2003). Perhaps it is no coincidence that scrub-jays, who also have very large brains relative to their size (Pravosudov and de Kort, 2006), appear to be one of the few animals other than apes that are capable of some elements of theory of mind that cannot be explained by behavioural cueing (Dally et al., 2006; Emery and Clayton, 2001).

One of the questions about episodic memory is how the whole is put together. There certainly seem to be elements that are not an integrated part of the stored memory. One of the essential elements for mental time travel defined by Tulving, and by Suddendorf and Corballis, is a conscious sense of subjective time (Suddendorf and Corballis, 1997; Tulving, 2002). However episodic memory is not temporally organised, the temporal order of events is not encoded

into episodic memory traces and that the perception of a chronological past depends on a process of active and repeated construction which may include having to add a sense of 'pastness' (Friedman, 1993, 2005). In addition Yonelinas suggests that the detection of familiarity and the utilization of retrieval mechanisms may be additive and separate processes (Yonelinas, 2001).

Perhaps the key to the development of mental time travel lies not in episodic memory traces themselves but in tools that have evolved (in the human mind, at least) to translate those traces into conscious, phenomenological, chronologically placed (however vaguely) images of the self. Could the preconditions for mental time travel proposed by Suddendorf and Corballis (1997) – a sense of subjective time; an autothetic sense of self that can be dissociated from self-concept in the present; the capacity for meta-representation; the ability to attribute an event to an earlier/future self (which parallels the ability to attribute mental states to other people); and an understanding of the relation between perception and the formation of knowledge – have enabled processes that modulated memory traces which already existed into a quite different form in the human mind? In this context evidence that the activity in the right prefrontal cortex during episodic memory retrieval signifies a retrieval attempt rather than successful retrieval is interesting (Wheeler et al., 1997).

As we have commented the only distinguishing difference between episodic and semantic memory is the sensation of remembering rather than knowing about the event. Episodic memories are not even necessarily veridical, they only seem so to the person experiencing the 'feeling' of an event having happened. Is it possible that all memory is effectively stored semantically and that the episodic cognitive system's role is to add the phenomenological autothetic elements and the sense of time past and time future as these memories are reconstructed or future scenarios are envisaged?

Further support for something of the sort comes from the phenomenon of childhood amnesia; while even pre-verbal young children can remember autobiographical events at the time of their occurrence they do not retain these memories, most adults cannot remember events from their childhood before about the age of 3–4 (Conway, 2005; Nelson, 1992; Perner and Ruffman, 1995; Suddendorf and Corballis, 1997). Children below the age of 4 largely lack Suddendorf and Corballis' preconditions for mental time travel. They have a very limited ability to order events in time and their sense of self does not develop a temporal dimension before about 3–4. Their ability to meta-represent, as demonstrated by pretend play, develops between 2 and 4. In particular they do not have a fully developed theory of mind before 4 and have a problem representing their own and others' former mental states. Below the age of 4 they also do not understand the source of their knowledge, they report the content of learning without being able to recall the learning event itself. Also, they do not seem to understand the sense of 'pastness' implied by the word 'remember'.

The development of these attributes around the age of 4 coincides with the end of childhood amnesia which Suddendorf and Corballis conjecture is because the development of the ability to use meta-representation and theory of mind to attribute past mental states to themselves and others is the essential element that allows the child's personal past experiences to be reconstructed (Suddendorf and Corballis, 1997). Wheeler et al. (1997) regard autothetic, which is dependent on a developed prefrontal cortex, as the essential element in the ability to form episodic memories and suggest that the failure to recollect events from early life is due to the late development of autothetic. Without autothetic events can be encoded in semantic memory but not in episodic memory so this is not a question of amnesia, there are just no episodic memories stored by young children (or most animals) to recall in later life.

Suddendorf and Corballis have rejected the idea that the episodic cognitive system effectively adds the phenomenological elements

to memory on the grounds that the loss of episodic memory in amnesic patients is not merely the loss of phenomenological sensation but has fundamental consequences for the sufferer (Suddendorf and Corballis, 2007b). We agree that it does but until the precise contribution of each part of the brain to episodic and semantic cognitive processes can be determined and this related back to the specific brain damage in individual patients there is still much that is uncertain about exactly how the two systems integrate and what each contributes to any given act of mental time travel.

4. Conclusion

The evolution of all of Suddendorf and Corballis' attributes necessary for mental time travel is likely to have been gradual. Each of these elements can be argued to have been separately adaptive, and not all of them are necessarily driven by the same evolutionary pressures. The possible absence of the whole package in non-human animals does not exclude the potential for some elements being present to some degree; for example some sense of past and future without either the extent of the human sense of subjective time or the same phenomenological experience of it. Again, the fact children below the age of 3 have some notion of the past even if it is a simple one limited to the idea of 'before now' or thinking of events as having been completed (McCormack, 2001) and some temporal reconstructive capacity with the ability to reproduce details of past events especially when cued (Nelson, 2005), supports this idea. It is conceivable that other species of animals could also have autobiographical knowledge, including episodic memory traces that they could access and use at least in the short-term without having the fully developed episodic or semantic cognitive systems of an adult human.

The absence of an episodic cognitive system does not preclude the ability to take actions for the future, only the ability to pre-experience them or project oneself into the future. While the evidence to date raises the possibility that apes and western scrub-jays at least can perceive a future beyond the hour or so established to date as the likely future thinking capacity of the rat, it may still be a very short-term future compared to human beings. Perhaps the capacity of the semantic cognitive system is sufficient to meet these needs. The studies on humans with brain lesions who apparently cannot mentally conceive of or talk about their own personal future (Atance and O'Neill, 2001; Klein et al., 2002; Rosenbaum et al., 2005; Tulving, 1985, 1989) say nothing about whether these patients are capable of taking any *actions* for their personal future, and whether or not they are self-aware about the reasons for such actions. It would be interesting to know whether they can.

We agree with Bar (2007) that foresight is not necessarily an all-or-none phenomenon and that the suggestion that foresight is a continuum that is present in animals to the extent that it is needed for survival in their own environments is at least as plausible as the suggestion that they do not have it at all. Suddendorf and Corballis lump together all forms of foresight other than mental time travel rather dismissively as "future-directed capacities" (Suddendorf and Corballis, 2007b, p. 343). We agree with Sara Shettleworth's observation that searching for proof as to whether or not episodic future thinking is uniquely human is not the most productive focus and we believe that the full range of these 'future-directed capacities' of animals merit further investigation.

Acknowledgements

Our thanks to Dr. Cristina Atance, Professor Tony Dickinson and Dr. Amanda Seed for their comments on this manuscript and to the BBSRC and University of Cambridge for financial support.

References

- Adams, C.D., Dickinson, A., 1981. Actions and habits: variations in associative representations during instrumental learning. In: Spear, N.E., Miller, R.R. (Eds.), *Information Processing in Animals: Memory Mechanisms*. Lawrence Erlbaum Associates Inc., Hillsdale, NJ, pp. 143–165.
- Aggleton, J.P., Brown, M.W., 1999. Episodic memory, amnesia and the hippocampal-anterior thalamic axis. *Behavioral and Brain Sciences* 22 (3), 425–489.
- Atance, C.M., Meltzoff, A.N., 2005. My future self: young children's ability to anticipate and explain future states. *Cognitive Development* 20 (2005), 341–361.
- Atance, C.M., O'Neill, D.K., 2001. Episodic future thinking. *Trends in Cognitive Sciences* 5 (12), 533–539.
- Atance, C.M., O'Neill, D.K., 2005a. The emergence of episodic future thinking in humans. *Learning and Motivation* 36 (2), 126–144.
- Atance, C.M., O'Neill, D.K., 2005b. Preschoolers' talk about future situations. *First Language* 25 (1), 5–18.
- Baddeley, A., 1997. *Human Memory: Theory and Practice*. Psychology Press, Hove, UK.
- Bar, M., 2007. The continuum of "looking forward" and paradoxical requirements from memory. *Behavioral and Brain Sciences* 30 (3), 315–316.
- Barrett, L., Henzi, P., Dunbar, R., 2003. Primate cognition: from 'what now?' to 'what if?'. *Trends in Cognitive Sciences* 7 (11), 494–497.
- Berthold, P., Heilbig, A.J., Mohr, G., Querner, U., 1992. Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360, 668–670.
- Biebach, H., Gordjin, M., Krebs, J.R., 1989. Time-and-place foraging by garden warblers, *Sylvia borin*. *Animal Behaviour* 37, 353–360.
- Bluck, S., 2003. Autobiographical memory: exploring its functions in everyday life. *Memory* 11 (2), 113–123.
- Boesch, C., Boesch, H., 1984. The nut-cracking behavior and its nutritional importance in wild chimpanzees in the Tai National-Park, Ivory-Coast. *International Journal of Primatology* 5 (4), 323–323.
- Busby, J., Suddendorf, T., 2005. Recalling yesterday and predicting tomorrow. *Cognitive Development* 20 (3), 362–372.
- Clayton, N.S., Bussey, T.J., Dickinson, A., 2003a. Can animals recall the past and plan for the future? *Nature Reviews Neuroscience* 4 (8), 685–691.
- Clayton, N.S., Bussey, T.J., Emery, N.J., Dickinson, A., 2003b. Prometheus to Proust: the case for behavioural criteria for 'mental time travel'. *Trends in Cognitive Sciences* 7 (10), 436–437.
- Clayton, N.S., et al., 2008. Response to Suddendorf & Corballis (2008) in defence of animal foresight. *Animal Behaviour* 76, E9–E11.
- Clayton, N.S., Dally, J., Gilbert, J., Dickinson, A., 2005. Food caching by western scrub-jays (*Aphelocoma californica*) is sensitive to the conditions at recovery. *Journal of Experimental Psychology: Animal Behavior Processes* 31 (2), 115–124.
- Clayton, N.S., Griffiths, D.P., Emery, N.J., Dickinson, A., 2001. Elements of episodic-like memory in animals. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 356 (1413), 1483–1491.
- Conway, M.A., 2005. Memory and the self. *Journal of Memory and Language* 53, 594–628.
- Cook, R.C., Brown, M.F., Riley, D.A., 1985. Flexible memory processing by rats: use of prospective and retrospective information in the radial maze. *Journal of Experimental Psychology: Animal Behavior Processes* 11 (3), 453–469.
- Dally, J.M., Emery, N.J., Clayton, N.S., 2006. Food-caching Western Scrub-Jays keep track of who was watching when. *Science* 312, 1662–1665.
- de Kort, S.R., Correia, S.P.C., Alexis, D.M., Dickinson, A., Clayton, N.S., 2007. The control of food caching by Western scrub-jays: where and when to cache. *Journal of Experimental Psychology: Animal Behaviour Processes* 33 (4), 361–370.
- Dessalles, J., 2007. Storing events to retell them. *Behavioral and Brain Sciences* 30 (3), 321–322.
- Dickinson, A., Watt, A., Griffin, W.J.H., 1992. Free-operant acquisition with delayed reinforcement. *Quarterly Journal of Experimental Psychology* 45B, 241–258.
- Emery, N.J., Clayton, N.S., 2001. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* 411, 443–446.
- Emery, N.J., Clayton, N.S., 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* 306 (5703), 1903–1907.
- Fabre, J.H., 1916. *The Hunting Wasps*, pp. 305–322.
- Flaherty, C.F., Checke, S., 1982. Anticipation of incentive gain. *Animal Learning and Behaviour* 10 (2), 177–182.
- Flora, S.R., Workman, M.D., 1995. Distributed reinforcement during delay to large reinforcement may increase "self-control" in rats. *Psychological Reports* 76, 1355–1361.
- Friedman, W.J., 1993. Memory for the time of past events. *Psychological Bulletin* 113, 44–66.
- Friedman, W.J., 2005. Developmental and cognitive perspectives on humans' sense of the times of past and future events. *Learning and Motivation* 36 (2), 145–158.
- Gibbon, J., Church, R.M., Meck, W.H., 1984. Scalar timing in memory. *Annals of the New York Academy of Sciences* 423 (may), 52–77.
- Gill, F.B., 1988. Trap line foraging by hermit hummingbirds: competition for an undervalued renewable resource. *Ecology* 69 (6), 1933–1942.
- Goodall, J., 1986. *The chimpanzees of Gombe: patterns of behavior*. Harvard University Press, Cambridge, MA.
- Graham, K.S., Simons, J.S., Pratt, K.H., Patterson, K., Hodges, J.R., 2000. Insights from semantic dementia on the relationship between episodic and semantic memory. *Neuropsychologia* 38 (3), 313–324.
- Hegd e, J., 2007. Mental time travel sickness and a Bayesian remedy. *Behavioral and Brain Sciences* 30 (3), 323–324.
- Hodges, J.R., Graham, K.S., 2001. Episodic memory: insights from semantic dementia. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 356 (1413), 1423–1434.
- Hudson, J.A., Shapiro, L.R., Sosa, B.B., 1995. Planning in the real world: preschool children's scripts and plans for familiar events. *Child Development* 66 (4), 984–998.
- Kinsbourne, M., 2005. A continuum of self-consciousness that emerges in phylogeny and ontogeny. In: Terrace, H., Metcalfe, J. (Eds.), *The Missing Link in Cognition: Origins of Self-Reflective Consciousness*. OUP, Oxford, pp. 142–156.
- Klein, S.B., Loftus, J., Kihlstrom, J.F., 2002. Memory and temporal experience: the effects of episodic memory loss on an amnesic patient's ability to remember the past and imagine the future. *Social Cognition* 20 (5), 353–379.
- Lawick-Goodall, J., 1971. *In the Shadow of Man*. Dell, New York.
- Letz, B.T., 1975. Long delay learning in the T-maze. *Learning and Motivation* 6, 80–90.
- M antyl a, T., 1993. Knowing but not remembering: adult age differences in recollective experience. *Memory and Cognition* 21 (3), 379–388.
- McCormack, T., 2001. Attributing episodic memory to animals and children. In: Hoerl, C., McCormack, T. (Eds.), *Time and Memory: Issues in Philosophy and Psychology*. Clarendon Press, Oxford.
- Menzel, C.R., 2005. Progress in the study of chimpanzee recall and episodic memory. In: Terrace, H., Metcalfe, J. (Eds.), *The Missing Link in Cognition*. OUP, Oxford, pp. 189–224.
- Mulcahy, N.J., Call, J., 2006. Apes save tools for future use. *Science* 312, 1038–1040.
- Naqshbandi, M., Roberts, W.A., 2006. Anticipation of future events in squirrel monkeys (*Saimiri sciureus*) and rats (*Rattus norvegicus*): tests of the Bischof-Kohler hypothesis. *Journal of Comparative Psychology* 120 (4), 345–357.
- Nelson, K., 1992. Emergence of autobiographical memory at age 4. *Human Development* 35, 172–177.
- Nelson, K., 2005. Emerging levels of consciousness in early human development. In: Terrace, H., Metcalfe, J. (Eds.), *The Missing Link in Cognition: Origins of Self-Reflective Consciousness*. OUP, Oxford, pp. 116–141.
- Noser, R., Byrne, R.W., 2007. Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, *Papio ursinus*. *Animal Behaviour* 73, 257–266.
- Okuda, J., et al., 2003. Thinking of the future and past: the roles of the frontal pole and the medial temporal lobes. *Neuroimage* 19 (4), 1369–1380.
- Osvath, M., G ardenfors, P., 2005. Oldowan culture and the evolution of anticipatory cognition. *Lund University Cognitive Studies* 122, 1–16.
- Osvath, M., Osvath, H., 2008. Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Animal Cognition* 11 (4), 661–674.
- Pearce, J.M., 1997. *Animal Learning and Cognition*. Psychology Press, Hove, 333 pp.
- Perner, J., Ruffman, T., 1995. Episodic memory and autogenetic consciousness: developmental evidence and a theory of childhood amnesia. *Journal of Experimental Child Psychology* 59, 516–548.
- Pravosudov, V.V., de Kort, S.R., 2006. Is the western scrub-jay (*Aphelocoma californica*) really an underdog among food-caching corvids when it comes to hippocampal volume and food caching propensity? *Brain Behavior and Evolution* 67 (1), 1–9.
- Premack, D., 2007. Human and animal cognition: continuity and discontinuity. *Proceedings of the National Academy of Sciences of the United States of America* 104 (35), 13861–13867.
- Raby, C.R., Alexis, D.M., Dickinson, A., Clayton, N.S., 2007. Planning for the future by western scrub-jays. *Nature* 445, 919–921.
- Rajaram, S., 1993. Remembering and knowing: two means of access to the personal past. *Memory and Cognition* 21 (1), 89–102.
- Riley, A., Baril, L.L., 1976. Conditioned taste aversion: a bibliography. *Animal Learning and Behaviour* 4, 1s–13s.
- Roberts, W.A., 2002. Are animals stuck in time? *Psychological Bulletin* 128, 473–489.
- Roberts, W.A., 2007. Mental time travel: animals anticipate the future. *Current Biology* 17 (11), R418–R420.
- Rosenbaum, R.S., et al., 2005. The case of KC: contributions of a memory-impaired person to memory theory. *Neuropsychologia* 43 (7), 989–1021.
- Savage-Rumbaugh, E.S., 1994. Hominid evolution: looking to modern apes for clues. In: Quiatt, D., Itani, J. (Eds.), *Hominid Culture in Primate Perspective*. University Press of Colorado, Niwot, pp. 7–49.
- Schacter, D.L., Addis, D.R., 2007. The ghosts of past and future. *Nature* 445, 27.
- Shettleworth, S.J., 1998. *Timing & Counting, Cognition, Evolution & Behaviour*. OUP, Oxford, pp. 333–378.
- Shettleworth, S.J., 2007a. Planning for breakfast. *Nature* 445, 825–826.
- Shettleworth, S.J., 2007b. Studying mental states is not a research program for comparative cognition. *Behavioral and Brain Sciences* 30, 332–333.
- Silberberg, A., Widholm, J.J., Bresler, D., 1998. Natural choice in nonhuman primates. *Journal of Experimental Psychology: Animal Behavior Processes* 24 (2), 215–228.
- Stephens, D.W., Anderson, D., 2001. The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. *Behavioral Ecology* 12 (3), 330–339.
- Stevens, J.R., Hallinan, E.V., Hauser, M.D., 2005. The ecology and evolution of patience in two New World monkeys. *Biology Letters* 1 (2), 223–226.
- Suddendorf, T., 2006. Foresight and evolution of the human mind. *Science* 312, 1006–1007.
- Suddendorf, T., Busby, J., 2003. Mental time travel in animals? *Trends in Cognitive Sciences* 7 (9), 391–396.
- Suddendorf, T., Busby, J., 2005. Making decisions with the future in mind: developmental and comparative identification of mental time travel. *Learning and Motivation* 36 (2), 110–125.
- Suddendorf, T., Corballis, M.C., 1997. Mental time travel and the evolution of the human mind. *Genetic Social and General Psychology Monographs* 123 (2), 133–167.

- Suddendorf, T., Corballis, M.C., 2007a. The evolution of foresight: what is mental time travel and is it unique to humans? *Behavioral and Brain Sciences* 30, 299–313.
- Suddendorf, T., Corballis, M.C., 2007b. Mental time travel across the disciplines: the future looks bright. *Behavioral and Brain Sciences* 30 (3), 335–351.
- Suddendorf, T., Corballis, M.C., 2008. New evidence for animal foresight? *Animal Behaviour* 75 (5), e1–e3.
- Thorpe, C.M., Jacova, C., Wilkie, D.M., 2004. Some pitfalls in measuring memory in animals. *Neuroscience and Biobehavioural Reviews* 28, 711–718.
- Tobin, H., Logue, A.W., Chelonis, J.J., Ackerman, K.T., May, J.G., 1996. Self-control in the monkey *Macaca fascicularis*. *Animal Learning and Behaviour* 24 (2), 168–174.
- Tulving, E., 1985. Memory and consciousness. *Canadian Psychology* 26 (1), 1–12.
- Tulving, E., 1989. Remembering and knowing the past. *American Scientist* 77 (4), 361–367.
- Tulving, E., 1999. On the uniqueness of episodic memory. In: Nilsson, L., Markowitsch, H.J. (Eds.), *Cognitive Neuroscience of Memory*. Hogrefe & Huber, Seattle, WA, pp. 11–42.
- Tulving, E., 2002. Episodic memory: from mind to brain. *Annual Review of Psychology* 53, 1–25.
- Tulving, E., 2005. Episodic memory and autoevidence: uniquely human? In: Terrace, H., Metcalfe, J. (Eds.), *The Missing Link in Cognition: Evolution of Self-Knowing Consciousness*. Oxford University Press, New York, pp. 3–56.
- Wheeler, M.A., Stuss, D.T., Tulving, E., 1997. Toward a theory of episodic memory: the frontal lobes and autoevidence consciousness. *Psychological Bulletin* 121 (3), 331–354.
- Whiten, A., Byrne, R.W., 1991. The emergence of meta-representation in human ontogeny and primate phylogeny. In: Whiten, A. (Ed.), *Natural Theories of Mind: Evolution, Development, and Simulation of Everyday Mindreading*. Blackwell, Oxford, pp. 267–281.
- Wiggs, C.L., Weisberg, J., Martin, A., 1999. Neural correlates of semantic and episodic memory retrieval. *Neuropsychologia* 37 (1), 103–118.
- Yonelinas, A.P., 2001. Components of episodic memory: the contribution of recollection and familiarity. *Philosophical Transactions of the Royal Society B: Biological Sciences* 356, 1362–1374.
- Zentall, T.R., 2005. Animals may not be stuck in time. *Learning and Motivation* 36 (2), 208–225.
- Zentall, T.R., Steirn, J.N., Jackson-Smith, P., 1990. Memory strategies in pigeons' performance of a radial-arm-maze analog task. *Journal of Experimental Psychology: Animal Behavior Processes* 16 (4), 358–371.