Do animals live in the present?
Current evidence and implications for welfare

Michael Mendl *, Elizabeth S. Paul

Centre for Behavioural Biology, Department of Clinical Veterinary Science,
University of Bristol, Langford House, Langford, BS40 5DU, UK

Available online 11 March 2008

Abstract

The importance of understanding the mental experiences of animals in order to assess their welfare was recognised by the 1965 UK Brambell Committee Report. The report further suggested that the extent to which animals live life in the present moment has a major impact on their capacity for suffering. Limited ability to recall previous events and imagine future ones would protect animals from the worry, ‘rumination’ and associated emotional disorders that contribute so much to human suffering. We investigate these suggestions in the light of new evidence on the capacity of animals to travel mentally through time, and with reference to the subjective experiences of human amnesic patients who are indeed ‘stuck in time’, living their lives in the present. The key human abilities for mental time travel are episodic memory and episodic future thinking, characterised by an ability to place events in time (what, where, when (www)), and to consciously recall or imagine these events. Tests of www memory, recollection vs. familiarity memory, single-trial learning, episodic vs. semantic encoding, and forward planning have been used to investigate whether such cognitive systems also exist in animals. The evidence indicates that some studied species show behaviour consistent with the capacity for mental time travel, while others do not. The extent to which animals consciously experience mental time travel remains unknown. In terms of the implications for welfare, research on human amnesics with damage to brain structures involved in episodic memory suggests that animals lacking mental time travel would miss the beneficial consequences of using previous experience to plan and organise future behaviour, but also the detrimental consequences of being able to ruminate on the recalled past and worry about the imagined future. Emotional responses, including future-directed anxiety would be temporally bound by the presence of relevant stimuli or cues and, therefore, potentially short-lived. However past experiences could, through the actions of non-episodic memory systems attributable to other brain structures, still impact on emotional state via (implicit) learning of associations between cues and emotional events. Cumulative effects of past experience on stress response mechanisms and baseline stress or mood states would also be expected to occur. Mental time travel may thus...
bring both welfare benefits and problems. Absence of this ability by no means releases animals from many effects of the environment, including the past, on their emotional state.

© 2008 Elsevier B.V. All rights reserved.

Keywords: Mental time travel; Episodic memory; Episodic future thinking; Welfare

1. Introduction

Do animals live in the present? This seemingly esoteric question was raised by the ethologist Bill Thorpe, a key member of the Brambell Committee who, in an appendix to the Brambell Report (1965), wrote “Human suffering is often very largely a matter of prolonged anxiety and imaginative anticipation of further pain—both of which are incomparably less well developed in most animals as far as we can see. There is no doubt that many types of animals live in the present to an extent which is hard for a human being to conceive. But, even so, many animals not only remember the past but fear the future, at least to some degree; and the extent to which they do so is of vital moment to our task.” Thorpe and the Brambell Committee seemed to be implying that a poorly developed ability to travel mentally through time would render non-human animals (hereafter animals) less susceptible to the quality and scale of suffering that humans can experience as a result of our capacity to recall previous events and worry about future ones. Conversely, if animals were shown to have sophisticated mental time travel abilities, this should dramatically alter how we view their capacity for suffering and poor welfare. Similar suggestions have since been made by others (Duncan and Petherick, 1991; Suddendorf and Busby, 2003a; UK Companion Animal Welfare Council (CAWC), 2003; Mendl and Paul, 2004; Abeyesinghe et al., 2005) including Lea (2001) who, assuming that the facility of language allows mental time travel, wrote “If I hurt a non-linguistic animal, perhaps I only hurt it for as long as the pain lasts: if I hurt a linguistic animal, I cause it to fear for as long as it can see the pain coming, I hurt it for as long as the pain lasts, and I cause it to smart with recollected pain for as long as the memory lasts. So every hurt is multiplied, as it were, by three—in fact, if we wanted to be quantitative, perhaps by much more.”

Lea’s statement illustrates that the question of whether animals live in the present may not be such a trivial one after all. We agree with the Brambell Committee’s view that to fully understand the potential for suffering in other species, answers to this question must be sought. To this end, Suddendorf and Corballis (1997) have recently stimulated interest by arguing that the human ability to travel mentally through time is indeed unique. Other animal species lack this capacity and hence are ‘stuck in time’, living their lives in the present. This has generated argument and new data from animal studies (e.g. Roberts, 2002; Clayton et al., 2003a; Hampton and Schwartz, 2004), and it is now timely, over 40 years on from the Brambell Report, to re-consider the issue from an animal welfare perspective. Our aim in this paper is to review recent research in order to investigate the Brambell Committee’s suggestion that animals mainly live their lives in the present. We also analyse how and why we might expect mental time travel to affect animal suffering and welfare. We start by describing the cognitive systems and processes that are likely to be involved in mental time travel. We then draw from research on human amnesic patients to consider the subjective experience of mental time travel and what it might be like to lack this ability and to live in the present. We then review recent evidence for the existence of mental time travel in animals, and conclude by considering the implications for animal welfare.
2. Mental time travel: the importance of episodic memory and episodic future thinking

What did you eat for breakfast today, and what are you going to do this weekend? If you can answer these questions, you are probably doing so by casting your mind back in time to subjectively re-experience events this morning, and imagining scenarios that you might enact this weekend. This ability to consciously both re-live past events and imagine future ones is referred to as mental time travel (Tulving, 1993, 2002; Suddendorf and Corballis, 1997) and unlocks one from being ‘stuck in time’ and living solely in the present moment. The backward travel component is known as episodic memory (Tulving, 1993, 2002), and the forward travel component has been referred to as episodic future thinking (Atance and O’Neill, 2001).

Episodic memory, a well studied and still evolving concept in human psychology (Tulving, 1972; Baddeley, 2001; Morris, 2001), is currently defined in terms of what it stores (information about personally experienced events in particular places at particular times in the past—‘what, where and when memory’) and how it is experienced (a conscious and vivid recall of these events). Eye-witness memory is a good example of episodic memory. The conscious experience of being transported back to the time when an event took place has been termed ‘autonoetic’ (self-knowing) consciousness by Tulving (1985, 2002) because of the direct personal knowledge of the recalled experiences, and the resulting sense of ‘self’ existing in the past.

Phenomenologically, episodic future thinking feels very similar to episodic memory except, of course, that it is not experienced as being in the past or constrained by exactly what happened (or what one remembers happened). Instead, episodic future thinking allows imagination and rehearsal of any number of possible scenarios that might be encountered in the future. Episodic memory may underlie the capacity to perform episodic future thinking and it has even been suggested that it is just an adaptive design feature of the future planning system, because there is no apparent selective advantage in recalling the past without influencing current or future behaviour (Suddendorf and Corballis, 1997; Suddendorf and Busby, 2003b). Episodic future thinking is now beginning to receive more attention in human psychology research including being defined in similar, but future-directed, terms to episodic memory (Atance and O’Neill, 2001; Suddendorf and Busby, 2005).

In considering whether animals mainly ‘live in the present’, the critical issue would seem to be whether they possess something similar to human episodic memory and/or episodic future thinking. It is these abilities that, uniquely, appear capable of enabling mental time travel. For example, humans have other long-term memory systems but, interestingly, none of these appear to be specifically concerned with consciously re-experiencing the past. Of these long-term memory systems, only one other appears to be consciously experienced (‘explicit’ or ‘declarative’). This is the semantic memory system, a memory for facts characterised by the ability to know something without remembering the event/s at which that knowledge was acquired. ‘People eat cornflakes for breakfast’ would be an example of a semantic memory which need not be tied to any particular consciously recalled event. ‘I had a bowl of Golden Grahams at home this morning’ would be an episodic memory. Semantic memory, therefore, does not convey information about past events, but provides facts and knowledge that can be used in the present (e.g. Tulving, 2002; Squire, 2004).

Alongside these explicit long-term memory systems, there are ‘implicit’ or ‘non-declarative’ memory systems related to processes such as habituation, priming, simple classical conditioning, certain forms of non-associative learning, and habit and skill learning (Fig. 1). These systems appear to influence behaviour without any conscious awareness that they are being accessed (Seger, 1994; Shanks and St John, 1994; Hampton and Schwartz, 2004; Squire, 2004). Therefore,
they would be of little use in facilitating mental time travel. Neither would short-term or working memory which, while being consciously accessible in humans, usually holds information for only a few seconds or minutes (Baddeley, 1996).

The ability to measure time intervals, or to associate particular actions or happenings with certain times of day, or to remember the order in which events took place, also need not imply an ability to consciously recall or anticipate specific events. Researchers have put forward a number of theories as to how humans and animals may be able to time short intervals without requiring the ability to re-experience when the time interval began, or to ‘mark’ that event on a subjective time scale. Internal clocks or pacemakers, the performance of behavioural sequences, or the strength of decaying memory traces are putative candidate mechanisms that could allow interval timing without any true subjective concept of time (Gibbon, 1991; Killeen and Fetterman, 1993; Staddon and Higa, 1999; see Roberts, 2002). Comparison of relative familiarity, or of the strength of memory traces, may help animals to discriminate the order of past events. Internal circadian oscillators may function as cues with which events occurring at particular times of day can become associated. All of these processes may thus allow efficient measurement of time and use of time-related cues without implying an ability to travel mentally in time (Roberts, 2002).

Given the above, we suggest that when the Brambell Committee raised the possibility that animals largely live in the present, they were making implicit reference to the importance of conscious episodic memory (and future planning) in human experience, and to the possibility that some, many or all animals do not possess these cognitive systems. Since our ability to consciously recall countless things that have happened to us during our lives, or to anticipate those that might happen in future, is such a central part of human experience (some estimate that over 50% of adult conversation is about past or potential future events (Szagun, 1978)), it is difficult to imagine life without this ability, even if we are trying to imagine this for another species such as a chicken or pig. Nevertheless, a number of scientists believe that mental time travel is indeed likely to be the preserve of human beings alone, and that, as the Brambell Committee implied, animals are ‘stuck in time’ (e.g. Köhler, 1927; Tulving, 1983, 2002; Suddendorf and Corballis, 1997; Roberts, 2002). Furthermore, we do not need to rely on imagination of what this might be like because, for many human amnesic patients, the absence of episodic memory is a reality. We now consider what it is like to live life in the present, and

---

**Fig. 1.** Putative long-term explicit (consciously experienced or declarative) and implicit (non-conscious or procedural) memory systems and associated neural structures. Based on Squire (2004).
whether the absence of episodic memory is likely to be compatible with effective functioning and survival.

3. Absence of episodic memory in humans: what is it like and how does it affect normal function?

By studying memory disorders to work out what is likely to be going on during normal mnemonic processes, case studies of amnesic patients have been instrumental in progressing our understanding of human memory (Tulving, 2002; Manns, 2004; Rosenbaum et al., 2005). Many patients have been studied over the last century or so, including two particularly well researched individuals, HM and KC (Corkin, 2002; Rosenbaum et al., 2005), who we will focus on here. These two cases cannot give a complete overview of work in this area, or of our knowledge of human memory in general which is based on a much larger and diverse literature. Nevertheless, they are representative of findings from other cases, and shed some light on the issues we are considering here.

HM became amnesic in 1953 following surgical resection of the medial temporal lobes, known to play a critical role in memory processes, to treat intractable epilepsy (Scoville and Milner, 1957). KC became amnesic in 1981 after a motorcycle accident left him with closed head injuries including extensive damage to the medial temporal lobes (Tulving, 2002; Rosenbaum et al., 2005). Following these traumas, both patients showed severe anterograde amnesia evidenced by an inability to acquire new episodic knowledge. In KC’s case, this episodic amnesia also extends back to before the time of his accident (retrograde amnesia) leaving him with virtually no episodic memory of any event in his life (Rosenbaum et al., 2005). HM remembers some things that occurred before the operation, but his memories appear to be semantic rather than episodic; few if any personal details can be provided to embellish a recalled event (Corkin, 2002; Steinvorth et al., 2005).

What is it like to live without episodic memory? Rosenbaum et al. (2005) provide a brief but illuminating account of KC’s daily life. He is guided through activities by reminders from family members or by written notes, for example one on the microwave door telling him to go upstairs after breakfast for his daily exercise routine. He is able to take part in various activities, including playing pool and chess, playing card games on the computer, and playing the organ. He watches television and has particular favourite programmes. In fact, his daily life appears similar to that of many contemporaries, except that he is unable to remember or re-experience any single event that has happened to him or that he has witnessed. For example, he claims never to have met researchers who have visited him up to eight times a year over many years and, when told about the events of September 11th, reacts as if hearing about them for the very first time (Rosenbaum et al., 2005).

An important finding from studies of human amnesics is that the lack of episodic memory appears to have a significant effect on episodic future thinking (Atance and O’Neill, 2001). Thus, when asked what he will be doing later on in the day, KC is unable to give an answer. He reports that his mind goes blank; he cannot imagine his future in just the same way that he cannot recall his past (Tulving, 1985, 2002). Another amnesic, DB, also has great difficulty visualising future events that will happen to him, although he is able to anticipate future public issues and events. Klein et al. (2002) argue that his relatively intact semantic memory allows for this ‘semantic future thinking’ while his damaged episodic memory prevents imagination of future personal events.

Like other amnesics with impaired episodic memory, both KC and HM are ‘stuck in time’, living in the present. They cannot remember what happened to them in the past, except in the last
few minutes, and they cannot plan ahead. They both require considerable assistance to live successfully in the modern world, and yet they are both quite capable of participating in a variety of activities, finding their way around in familiar environments, and learning new skills and certain sorts of information. How can this be? It appears that their profound lack of episodic memory dissociates from the preservation of a number of other learning and memory abilities.

HM’s short-term working memory appears to be intact; he can hold in mind information to be used in ongoing activities. He can learn motor skills (e.g. to draw a line between images using mirror reflection to guide movements), even though he has no conscious recollection of previous testing sessions or of any familiarity with the tasks. He is capable of perceptual learning (e.g. learning to read mirror-reversed words) and priming tasks in which words that are incidentally encountered in a list influence subsequent responses on word-stem or phrase completion tasks, despite a lack of conscious awareness that they were seen before. His language shows relatively minor impairments, and he is capable of a certain degree of semantic learning, for example about the spatial arrangement of the house where he lived following his operation, and about people who have become famous since that time (Corkin, 2002; O’Kane et al., 2004). This may result from prolonged exposure to repeated information over time, and contrasts with his markedly reduced ability to recall facts about significant, but ‘one-off’, public events occurring since his operation (Corkin, 2002; Steinvorth et al., 2005).

KC retains similar non-episodic memory abilities. For example, he has successfully learnt how to use computers to carry out a variety of tasks despite denying that he has ever worked with them before. Interestingly, this knowledge seems to be held in a rather rigid form suggesting a simple form of ‘stimulus-response’ learning where any change to the cueing conditions can lead to a failure to respond appropriately. He also retains a considerable body of semantic information from the time prior to his accident, ranging from factual knowledge of geography, history, maths and other ‘school subjects’, to information about the location of his house and summer cottage and the shortest route between them. Furthermore, his ability to understand the intentions and feelings of others indicates an intact ‘theory of mind’, suggesting that this form of high level cognitive functioning is also preserved (Tulving, 2002; Rosenbaum et al., 2005). Although not the subject of systematic research, it also seems likely that his basic motivational processes are intact and that changes in motivation to eat, drink, sleep and so on guide his behaviour into the future, using semantic and implicit memory systems to allow selection of appropriate behaviours to achieve these goals in the absence of episodic future thinking.

A final issue to consider is the impact of a lack of episodic memory on an individual’s self identity. An absence of autobiographical memory might reasonably be expected to severely limit the capacity for a self concept. Indeed, HM does not know his age or the colour of his hair. He has no awareness of his fame and the impact that he has had in medical and scientific circles. He has no memory of the 53 years that have passed since his operation, and therefore would be expected to fail to recognise the image he sees in a mirror. However, Corkin (2002) reports that he appears unfazed by seeing his reflection, and speculates that he may recognise the image as familiar due to repeated exposures and updating over the years. She further suggests that HM’s remote memories of things that happened prior to his operation may provide the foundations for a self concept, and notes that HM has consistent beliefs, desires and values that confer a distinctive personality which may also provide the basis for a self identity. He may thus have a rudimentary self concept, although this is likely to be qualitatively different to that experienced when episodic memory is intact.

The evidence from HM, KC and other amnesic patients indicates a dissociation between episodic and other types of learning and memory processes; much can still be achieved in the
absence of episodic memory. This suggests that particular memory systems may be linked to particular neural structures (e.g. Squire, 2004; Fig. 1). For example, Squire and Zola (1998) suggest that the autobiographical nature of episodic memory may require both intact medial temporal and frontal lobes, and hypothesise that damage to frontal lobes may impair episodic but not semantic memory in amnesic patients such as KC. The involvement of the frontal lobes in episodic retrieval is also emphasised by Tulving (2002) who points out that the importance of these evolutionary recent structures for mental time travel supports his notion that this ability may not exist in non-human species in which frontal lobe structures are much less well developed (Deacon, 1990).

Overall, the evidence from HM, KC and other amnesic patients suggests that the absence of episodic memory brings with it significant challenges to coping with modern daily life, including a deficit in episodic future planning. However, these are to some extent offset by the retention of other learning and memory abilities that may be sufficient to allow successful survival, at least in species that live in less complex environments. Animals might, therefore, be able to function without the capacity for mental time travel, just as the Brambell Committee suggested. However, this does not necessarily mean that they do indeed lack these abilities. In the next two sections we review evidence for the existence of episodic memory and future planning in animals.

4. Evidence for episodic memory in animals

A clear definition of episodic memory is required in order to identify the type of evidence needed to demonstrate its existence. Human episodic memory, as mentioned earlier, is usually defined in terms of its ‘what–where–when’ content, and in terms of the vivid conscious awareness that characterises recall of an event in the past (Tulving, 1993). This latter subjective component is obviously of key importance from an animal welfare perspective. However, it is currently impossible to study in the absence of agreed non-linguistic indicators of conscious experience in animals. Consequently, scientific research in this area has concentrated on features of episodic memory that are more amenable to empirical investigation, with different researchers taking different approaches.

4.1. What, where and when (www) memory

Clayton and co-workers (Clayton and Dickinson, 1998, 1999; Clayton et al., 2001a,b, 2003a,b,c) have focused on the ‘what–where–when’ (www) characteristics of episodic memory (Tulving’s original (1972) definition), and identify three behavioural criteria that need to be satisfied in identifying its existence (Clayton et al., 2003a). First, the content of episodic memory must encode not just what happened and where it happened, but also when it happened. The ‘when’ component is important as it clearly distinguishes episodic memories (‘remembering’) of specific personal experiences, from semantic memories (‘knowing’) of facts about the world. Semantic memories can be retrieved without recall of the time and location at which they were acquired. Thus animals experiencing a number of trials or events, as in many animal learning studies, need not remember any of these individual trials, and yet still acquire a semantic representation of the factual information (e.g. A predicts B) presented in the trials. Single-trial learning might conceivably involve episodic encoding of the original event (Schwartz et al., 2002), but also need not (see later). For example, Morris (2001) argues that one-trial poison avoidance learning may be a form of implicit associative learning that requires no recall of the original stimulus. Furthermore familiarity based recognition, rather than episodic recall, may
account for learning about single events in the past (e.g. as in delayed-match-to-sample or object recognition memory tasks) and need not require any conscious recall of previous encounters with the now ‘familiar’ stimulus (Griffiths et al., 1999; Eichenbaum et al., 2005; see later).

Clayton et al.’s (2003a) second criterion of structure requires that the ‘what’, ‘where’ and ‘when’ of an episodic memory are not simply retrieved individually, but in a bound form such that retrieval of one component activates retrieval of the others and results in a unique representation of each temporally and spatially defined event. The final criterion is flexibility. This requires that episodic information can be used in a declarative way. In other words it is not tied to a specific behavioural response but can be used flexibly in conjunction with newly acquired semantic or episodic information to yield new or different behavioural responses.

Clayton and co-workers’ influential studies of food caching and retrieval behaviour in western scrub jays provide evidence to satisfy each of the above criteria. In an early study, birds were allowed to cache waxworms, a preferred but perishable food, in one half of a foraging tray, and peanuts, a less-preferred but non-perishable food, in the other. Birds in one group cached waxworms first (at 0 h) followed by peanuts (at 120 h), while birds in the other group cached peanuts first (0 h) followed by waxworms (120 h). Previously, half of the birds in each group (Degrade) were trained that waxworms remain fresh and edible after 4 h, but degrade and become inedible after 124 h, while the other half (Replenish) were trained that waxworms remain edible after both 4 h and 124 h. In both cases, peanuts remained edible after both time intervals. In probe retrieval trials (with no food in the trays) at 124 h, birds were allowed to search for food. Birds in the Replenish group searched in the half of the tray where they had cached waxworms irrespective of whether they had cached these 4 h or 124 h earlier. However, birds in the Degrade group searched in the waxworm half of the tray only if they had cached them 4 h previously. If they had cached them 124 h earlier, they searched in the peanut half of the tray (Clayton and Dickinson, 1998, 1999).

These results indicated that birds could use information about ‘where’ and ‘when’ they had cached the different food types (‘what’), coupled with (semantic) information about the degrading properties of their favoured food, to guide their retrieval decisions. Birds that had not experienced degrading waxworms always searched for this food. But birds that had learnt that waxworms degrade over 124 h switched to retrieving the less-preferred peanuts if they had cached the worms 124 h previously. This www memory was demonstrated across several days rather than just a few hours. Clayton et al. (2003a,b) argue that it is unlikely that interval timing clocks started by each caching episode, and not episodic-like memory, were responsible for the findings, because interval timing has not been demonstrated across such lengthy intervals. Because caches were in different halves of the same tray, the tray was equally familiar irrespective of the order in which caches were made and hence the task could not be solved on the basis of relative familiarity. However, it is possible that, rather than retrieving an episodic-like memory of the caching event, the jays’ behaviour was more simply explained by a decay in the strength of the memory trace (forgetting) for waxworms cached longer ago. Indeed, Staddon and Higa (1999) have proposed an interval timing mechanism based on memory trace strength. Searching might therefore have been guided simply by the strength of retrieved memory traces. However, birds could be trained to search for waxworms only after a long interval and not after a short interval (de Kort et al., 2005). This result could not be explained in terms of simple forgetting, and was used by de Kort et al. (2005) to argue that forgetting was unlikely to be a general mechanism underlying the jays’ behaviour.

These findings appear to satisfy the content criterion for episodic memory. They also suggest that the ‘what’, ‘where’ and ‘when’ components are bound together to allow an integrated
memory or structure of the caching event. To test this more formally, Clayton et al. (2001a,b) investigated whether birds could discriminate between two temporally distinct events in which they performed the same action (caching peanuts and preferred mealworms) at different locations (trays). Birds that had learnt that mealworms decay over 24 h were allowed to cache peanuts in one half of tray A and mealworms in the other half at time 0. A day later they did the same in tray B. Four hours later they were allowed to search in both (empty) trays. Fig. 2 shows how www memory of the caching events might be structured. If seeing the empty trays triggered retrieval of the ‘where’ memory (trays A and B) on its own, or if the ‘where’ memory was only linked to the ‘what memory’ (peanuts and mealworms), then the birds would be unable to select the tray with the preferred non-degraded mealworms. Only if the ‘where’ memory was linked to both the ‘what’ and ‘when’ (how long ago) memories, would the birds be able to search in the correct tray. The birds showed the correct response of searching for mealworms in tray B indicating that they had integrated representations of ‘what’, ‘where’ and ‘when’ allowing each caching episode to be stored as a unique episodic-like memory.

The third criterion of flexibility was demonstrated in a study which showed that new semantic information on how quickly caches perish, acquired in the middle of a cache-retrieve session, could be used by scrub jays to alter their subsequent retrieval decision (Clayton et al., 2003a,b). This indicates that the birds were able to use the encoded information at caching in a flexible declarative way and to integrate it with new knowledge resulting in a changed behavioural response. Overall, the scrub jay experiments provide compelling evidence for the existence of www memory. Clayton and Dickinson (1998) referred to this as ‘episodic-like’ memory because they acknowledged that their studies could not shed light on the conscious experience of recollection, which is the other key component of human episodic memory.

Other researchers have adapted Clayton and co-workers’ approach for other species. Bird et al. (2003) studied rats in a radial maze task. Rats were trained to carry pieces of preferred cheese or less-preferred pretzel to the end of the arms of the maze (caching) and to retrieve them later. Rats retrieved cheese earlier than pretzels showing memory for the type of food they had cached (‘what’) and ‘where’ they had cached it. When divided into two groups and trained that cheese degrades after either 1 h or 24 h, neither group made earlier visits to pretzel cache locations than to cheese cache locations during trials when they should have anticipated that the cheese had degraded, thus providing no evidence for www memory.
Babb and Crystal (2005) also studied rats in an eight arm radial maze using a different procedure. Rats visited the maze in the morning (‘caching’) with chocolate pellets (preferred food) available at the end of one arm, normal pellets (less-preferred) available in another three, and the other four arms closed. On days with a short retention interval, rats revisited the maze 0.5 h later with all eight arms open and normal pellets available at the end of the four arms which had been closed during ‘caching’. Exactly the same procedure was followed on days with long retention intervals, except that revisits were in the afternoon, 4 h after ‘caching’, and the original chocolate baited arm was replenished. Rats learnt to revisit this arm more during the 4 h than the 0.5 h trials. A subsequent stage of the experiment involved devaluing chocolate pellets by associating them with sickness induced by an injection of LiCl. The rats then showed a decrease in visits to the chocolate arm after the 4 h trials which, the authors claim, could only occur if they had www memory. However, it is possible that the rats were solving the task using a time-of-day linked rule, ‘if tested in the afternoon, revisit chocolate arm’. This was ruled out in a subsequent experiment (Babb and Crystal, 2006a), and a further study (Babb and Crystal, 2006b) showed that rats could learn about when and where to seek two different preferred foods (what: grape and raspberry), specifically avoid the one which was devalued between ‘caching’ and retrieval, and transfer this learning to two completely new preferred foods (chocolate and banana). These studies provide evidence for www memory in rats (Roberts, 2006).

Hampton et al. (2005) used similar methods to test rhesus monkeys. In each trial, monkeys were initially allowed to learn the location of preferred and less-preferred food hidden in two of three sites in a room (‘caching’). They showed a clear preference for retrieving the preferred food up to 25 h after this initial learning. They were then trained that the preferred food degraded after 25 h. There was little evidence that they subsequently learnt to avoid the preferred food when foraging for it 25 h as opposed to 1 h after the initial ‘caching’ experience. Although this study provided no evidence for www memory, the authors note that certain experimental procedures, such as testing all monkeys at both the 1 h and 25 h interval and hence potentially introducing interference effects, might have been responsible for the negative results.

Recently, Skov-Rakette et al. (2006) investigated the extent to which what, where and when components of pigeon memory are bound together. Pigeons were trained on computer screen match-to-sample tasks requiring matching on the basis of sample identity, location on the screen, and time since it was shown. Results indicated that pigeons could learn all three tasks together, but that while there was evidence for independent feature memories, there was no evidence for any integration of these into a bound www memory.

It is worth noting that in the studies of Bird, Babb, Crystal, Hampton, Skov-Rackette and colleagues, all ‘caching’ or sampling events occur at time A and decisions have to made subsequently at times B or C while in Clayton, Dickinson and colleagues’ studies, caching events occur at different times (A or B) and decisions have to be made at one time (C). In the latter studies, decisions could be made on the basis of elapsed time since the caching events, or on the basis of a representation of times A and B in time space. In the former studies, however, since caching occurs at one time only, decisions are more likely to be made on the basis of elapsed time only.

4.2. Recollection as a characteristic of episodic memory

Different approaches to the study of episodic memory in animals have been taken by other researchers. Eichenbaum et al. (2005) concentrate on the distinction between recollecting an experience, as in an episodic memory, and simply perceiving that experience as familiar. For
example, recognising someone as familiar without having any recollection of when and where you met them before. They argue that recollection is a rapid onset phenomenon during which details of the event come flooding back, as when suddenly remembering when and where it was you previously met that person, whereas familiarity memories are gradual and progressive. Recollection also allows experience of the temporal flow of an event, sequences in which things happened, rather than simply whether the event happened or not. Finally, recollection should allow the discrimination of different events that share the same elements. Eichenbaum et al. (2005) thus view the properties of recollection memory to be intrinsic components of episodic memory. They also argue that recollection is mediated by the hippocampus (Eichenbaum and Cohen, 2001), while familiarity learning may be dependent on other structures such as the perirhinal cortex (Brown and Aggleton, 2001).

Tests of recollection vs. familiarity memory for odours were carried out in rats by observing the ratio of ‘hits’ (correct identification of previously encountered odours) to ‘false alarms’ (incorrect identification of new odours as if they had been previously encountered) and plotting these as receiver operating characteristic (ROC) curves (Fig. 3). Familiarity memory appears to be characterised by a signal-detection process that produces a smooth curvilinear relationship between false alarms and hits. However, human studies indicate that recollection memory produces an unexpectedly high number of hits in the absence of any false alarms, perhaps reflecting the threshold-like all-or-nothing quality of episodic recollection (Yonelinas, 2001). Rat ROCs showed indications of both recollection and familiarity processes. When hippocampal lesions were applied, the ROCs lost the recollection component, supporting the idea that rats may
indeed have hippocampally dependent recollection-like memories (Fortin et al., 2004). Another study showed that memories for the temporal order of odour presentation are also dependent on a functional hippocampus, and in its absence only familiarity memory (i.e. ‘have I encountered this odour before or not?’) is preserved (Fortin et al., 2002).

The above tasks involved ‘what’ and ‘when’ components, but not a ‘where’ component. Eichenbaum et al. (2005) tackled www memory using an odour discrimination task involving presentation of a sequence of different odours, each at a different location. Rats were able to learn to visit the earlier presented stimulus first in test trials, though it appeared that they relied more on odour information than spatial information. Once again, this ability was shown to be dependent on an intact hippocampus (Ergorul and Eichenbaum, 2004). A final study showed that rats have the ability to track and discriminate two sequences of odours involving overlapping elements. For example if trained on the sequences ABCDEF and WXCDYZ, they can correctly select the 5th element (E or Y) according to which elements the sequence started with (AB or WX), despite the fact that this element follows the ambiguous 3rd and 4th elements (CD). This ability to track sequences was again shown to be hippocampally dependent (Agster et al., 2002). Eichenbaum et al. (2005) argue that the above characteristics (recollection, temporal organisation, ability to separate events with overlapping elements) are all features of episodic memory, and hence that these studies indicate its existence in rats and, as in humans, its dependence on a functional hippocampus. Again, the existence of conscious episodic recollection could not be addressed in these studies.

4.3. Single-trial learning

A recent set of studies on rodents has attempted to use spontaneous one-trial learning tasks to address a potential criticism of some of the above studies. This is that animals need to be trained on many of the tasks used, sometimes extensively, such that semantic learning and memory of contingencies may allow the tasks to be solved using rule-based strategies rather than episodic-like memory. Dere et al. (2005a) adapted the object recognition test (Ennaceur and Delacour, 1988) which capitalises on the spontaneous tendency of laboratory rats and mice to investigate a new object more than a familiar (remembered) object. They devised a simple test requiring no training in which animals first encounter one set of objects (set A) in an open field for 10 min. Fifty minutes later, they encounter another set of different objects (set B) for 10 min. Fifty minutes after this, they encounter examples of both the ‘recent familiar’ (set B) and less recent ‘old familiar’ (set A) objects, some of which are in their original positions, and some of which have been moved. They found that both rats and mice show more interest in the ‘old familiar’ objects, suggesting an ability to encode temporal information, and also spent more time investigating ‘new familiar’ objects that were presented in new locations relative to those that were in the same location as before (though the reverse was observed in rats for ‘old familiar’ objects). They concluded that rats and mice establish an integrated www memory (Dere et al., 2005b; Kart-Teke et al., 2006). However, it seems likely that this task could be solved on the basis of familiarity rather than requiring an episodic-like memory of the two encounters with the objects and, as for some of Eichenbaum’s studies, it focuses on short-term memory rather than the longer-term memory (of at least several hours) under which episodic memory is usually categorised (Squire, 2004).

Another set of studies using single-trial events was carried out by Schwartz et al. (2002, 2004, 2005) on a western lowland gorilla called King. King communicates with humans using cards bearing symbols or pictures. He can select appropriate cards to indicate events that happened to
him up to 24 h earlier, such as what foods he ate and who gave him these foods (Schwartz et al., 2002). He can also use them to identify novel objects or the person who performed a novel act (Schwartz et al., 2004), the (reverse) order in which he ate different foods and, to a limited extent, the location in which an event took place (Schwartz et al., 2005), all after a 5–10 min retention interval. The authors argue that because the witnessed events are discrete and, at the time of recall, lack any obvious correspondence to the current situation, King is likely to be using episodic-like memory of past events to tackle the tasks. However, all the results are based on recognition of the appropriate cards presented and may thus depend on familiarity rather than episodic-like memory. Furthermore, the 5–10 min retention intervals again reflect short-term memory processes rather than long-term memory, and the studies have not yet tackled situations requiring integration of ‘what’, ‘where’ and ‘when’ information.

4.4. Distinguishing whether information has been stored episodically or semantically

Zentall (2005, 2006) raises the issue of how the encoding of information into memory may affect whether it is episodically or semantically stored and retrieved. He suggests that some pieces of information may be committed to memory with the knowledge that they will be used in the future. Therefore, they may be stored in a semantic form which does not require mental time travel for their retrieval. For example, if one knows that one will need to remember where the car is parked, this information may be encoded semantically (e.g. by storing information about the floor number on which the car is parked). The ‘find the car’ task can then be solved using this semantic information rather than episodic recall of driving the car to the parking space, getting out, checking for landmarks, etc. Zentall thus argues that animals that repeatedly perform tasks involving acquisition of information for use in the future (e.g. cache-retrieval tasks) may encode this information semantically. He suggests that a better test of episodic memory, increasing the need for the animal to actively delve into its past, is to unexpectedly ask it to provide information about past events. Successful responding in this case is less likely to be due to ‘pre-prepared’ semantic coding of the information.

Zentall et al. (2001) trained pigeons to report what they had just been doing. They pecked on a red key if they had recently pecked at a stimulus, and pecked a green key if they had recently refrained from pecking. In a second phase of the experiment, they were autoshaped to peck at one stimulus (a yellow key that was always followed by food) and not at another (a blue key that was never followed by food). When they were performing well on this task, they were unexpectedly asked to report on what they had just done. A yellow or blue key was presented and immediately followed by a choice of the red or green key. The pigeons pecked the red key (‘I have just pecked’) more after they had pecked at the yellow key, and pecked the green key (‘I have refrained from pecking’) more after they had refrained from pecking the blue key. Similarly, dolphins show an ability to respond to the command ‘repeat what you just did’, even when the preceding action was relatively novel or uncommon (Mercado et al., 1998). Successful performance in these tasks may require animals to travel back in time, albeit only a few seconds in these studies, to recollect what they were just doing.

4.5. Summary

It is clear that different views of the defining characteristics of episodic memory lead to different ways of investigating whether animals have this facility. Studies of www memory focus on the ability of animals to store integrated representations of events in terms of what, where and
when they happened. Studies of recollection seek evidence for information processing abilities that capture the phenomenal qualities of recalling an event (e.g. rapid onset, temporal organisation or ‘flow’). Single-trial learning and ‘unexpected recall’ studies try to rule out the possibility that semantic learning processes underlie apparent episodic-like memory. Each approach has its own set of strengths and problems.

While many issues remain to be resolved, cleverly designed experiments are beginning to provide evidence that certain features of episodic memory may not be the sole preserve of humans. It is possible, perhaps likely, that some species, due to their behavioural ecology, were more predisposed to evolving such abilities. Cache-recovering birds are one example but many species, including common domestic species such as pigs and sheep, may benefit from an ability to recall when and where food patches were last encountered, integrate this with information about the type of food encountered and the replenishment rates of such food, and use a type of www memory to organise foraging trips to capitalise on the most productive patches and avoid the least productive ones (cf. Henderson et al., 2006). For example, pigs appear to be able to use ‘what’ and ‘where’ information about more and less-preferred food to organise their foraging behaviour (Held et al., 2005). It may thus be possible to take the next step and ask whether this important domestic species can also use ‘when’ information.

Ultimately, however, it could be argued that the key question from an animal welfare perspective is whether animals have recollection-like experiences, rather than whether they can encode precisely when in time a particular event happened. It is the ability to re-experience events per se that is likely to impact most on emotional state and welfare, even if that experience cannot be tied to a specific time in the past, or even identified as being in the past (as sometimes appears to be the case in post-traumatic stress disorder (PTSD) patients who report experiencing vivid flashbacks of traumatic events as if in the present moment (see later)). Studies of the phenomenology of recollection may thus be particularly relevant for future animal welfare related research.

5. Evidence for episodic future planning in animals

In contrast to research on episodic-like memory, there have been fewer studies of episodic future planning. Suddendorf and Corballis (1997) proposed a framework for research in this area which they named the Bischoff-Köhler hypothesis after its three proponents (Köhler, 1927; Bischof, 1985; Bischoff-Köhler, 1985; cited by Suddendorf and Corballis, 1997). This states that animals other than humans are unable to anticipate future (motivational) states and hence cannot mentally travel forward in time, but instead are constrained to behaving according to current states alone. For example, anticipatory behaviour (e.g. approach a food source, freeze or hide) that is directly related to the presence of a learnt cue predicting arrival of a particular reinforcer, cannot reasonably be concluded to result from episodic thinking about a future event. The animal is behaving in accord with its current motivational or emotional state (e.g. hunger, fear) and not in anticipation of a future state. A key requirement in studying episodic future planning is therefore to demonstrate that behaviours are based on anticipation of future mental or motivational states and are not simply a response to current ones.

Prominent examples of apparent future planning come up against this problem. For example, chimps preparing tools in advance of a hunting trip may be responding to their current state of hunger, and so may be exhibiting an initial step in a sequence of foraging behaviours rather than showing insightful future planning (Suddendorf and Corballis, 1997; Roberts, 2002; Clayton et al., 2003a). Other apparently adaptive anticipatory behaviours may be species-specific legacies
of natural selection. Examples include birds showing preparatory behaviour prior to migration, squirrels storing nuts in the autumn, pigs and chickens building nests prior to birth. A parsimonious explanation is that these behaviours are somehow ‘hard-wired’ and not a cognitive response to mental time travel into the future (Suddendorf and Corballis, 1997; Roberts, 2002; Suddendorf and Busby, 2005).

The inability of many animals to demonstrate ‘self control’, delaying an immediate response for a small reward in favour of a delayed response for a larger one, is often interpreted as indicating a limited ability to anticipate the future (Roberts, 2002). However, there are sound ecological reasons for why animals may be selected to prefer a guaranteed smaller reward in the short-term rather than a more uncertain larger reward in the future (Stephens and Anderson, 2001; Zentall, 2005, 2006). Furthermore, some studies do indicate that, under the right conditions animals can reverse this preference (e.g. chickens, Abeyesinghe et al., 2005). This may indicate some ability for episodic future thinking although, if so, it is only for a few seconds into the future, clearly tied to current motivational state, and hence would not be considered by some as strong evidence (Clayton et al., 2003a).

Despite these challenges, there is some evidence for episodic future planning in animals. Perhaps the most convincing evidence comes from studies of western scrub jays. Caching is competitive and caches may be pilfered by other jays. Emery and Clayton (2001) showed that scrub jays appear to be able to alter their caching behaviour in anticipation of the future state of their cache, namely whether it is likely to be pilfered or not. Birds cached food either in the presence or absence of another watching bird. After a 3 h retention interval they were allowed to recover their caches (always in private). Some re-caching occurs during cache recovery, and birds that had cached their food in the presence of another bird were more likely to re-cache it at a new site during recovery than those who had cached in private. Critically, this was only observed in birds that had had experience of pilfering another jay’s cache. There was also evidence that birds which had performed sequential caching in two different trays, one in private and one in the presence of another jay, showed more re-caching of food from the tray in which they had been observed to cache.

Together these findings indicate that scrub jays can combine information about their previous experience of pilfering and about whether or not they were watched when caching food, to alter their cache recovery behaviour. Their use of re-caching suggests that they may anticipate future stealing of their cache by another bird. A potential alternative explanation is that the presence of a watching competitor at caching somehow devalues the food that is being cached (an ‘evil eye’ effect, e.g. Tomasello et al., 2003), and therefore it becomes a less attractive food source and is subsequently re-cached rather than recovered and eaten. However, there was no evidence that food cached in the presence of another bird was recovered less. If anything the opposite was the case in some experiments (Emery and Clayton, 2001). Overall, these experiments indicate that scrub jays may be able to anticipate a change in the future state of their food caches, and perhaps show something similar to episodic future planning. Studies of visual perspective taking by primates in a competitive context might also be interpreted in this way, a subordinate who sees a dominant animal watching where food is being hidden may anticipate the future behaviour of the dominant and avoid that food, although the time course of these studies is usually a few minutes rather than hours (Hare et al., 2000, 2001). A recent study has provided further evidence for episodic future planning in western scrub jays. Raby et al. (2007) demonstrated that after birds had experienced which of two foods they would be lacking at breakfast-time in two different locations, they showed location-appropriate compensatory food storage in preparation for next day’s breakfast. In all cases, further studies are required to see whether the animals can anticipate...
changes that are not relevant to their current motivational states and behave accordingly; the true test of the Bischoff-Köhler hypothesis.

McKenzie et al. (2005) used the methods of Bird et al. (2003) to investigate whether rats caching cheese at the end of the arms of a radial maze might also anticipate the future state of their caches. Over a series of caching and retrieval trials, they trained the animals that the cheese stored at specific cache sites would always be pilfered (or, in separate experiments, substituted for less attractive food, or degraded with quinine). Their hypothesis was that if the rats cached food with the anticipation of recovering it at a later time, they should cease to cache at sites where food disappeared or became degraded. However, if rats had no anticipation of future retrieval, their caching behaviour would not change. The results supported the latter interpretation. Interestingly, rats did modify their retrieval behaviour and showed avoidance of visiting the arms where food was removed, but this did not affect their subsequent caching behaviour. The authors conclude that there was no evidence for anticipation of the future state of caches in this memory task (retention intervals were 45 min).

Baker and Anderson (1995) found similar results for black-capped chickadees, but Hampton and Sherry (1994) did find that repeatedly depleted cache sites on one side of an aviary came to be used less often than those on the other side, although this could have been due to the development of a semantic memory devaluing the depleted side and hence decreasing both caching and retrieval. Clayton et al. (2005) investigated this issue further and found that scrub jays selectively decreased caching of perishable items when these items were consistently found to be degraded or pilfered on cache retrieval. They suggested that the memory of caching becomes associated with the rewarding or punishing state of food (fresh, absent or degraded) at retrieval, and that this bound memory influences future caching behaviour. In this sense, it could be argued that no anticipation or future planning is needed for this effect, but rather the memory retrieved at the point of caching influences behaviour.

Zentall (2005, 2006) has taken a different approach to investigating the possibility of forward planning by focusing on whether short-term working memory tasks are guided either by representations of information that has already been encountered or by representations of the (future) response that is to be made. He argues that the latter would indicate that animals can hold anticipatory or prospective representations and hence are not stuck in the present. Data from studies of delayed conditional discrimination or match-to-sample tasks, and radial maze performance provide some evidence that prospective information is used to guide choice. For example, Edwards et al. (1982) trained pigeons on different delayed-match-to-sample tasks with different outcomes. A hue matching task used red and green colours such that a correct match to a red sample gave one reward (e.g. peas) and a correct match to a green sample gave another reward (e.g. corn), while a line orientation matching task using two line stimuli also gave either peas (vertical) or corn (horizontal) in response to correct matches. The pigeons were then tested on a transfer task where the sample and match were from different categories (e.g. sample = hue; match = line). Pigeons tested under conditions where the ‘correct’ response was predicted by the reward (e.g. sample = red; match = vertical; reward = peas) performed better than those tested with the reverse contingencies. This indicated that an anticipatory representation of the reward, or its motivational or hedonic value, was being used to solve the task.

Similar findings come from radial maze studies in which there is evidence that rats switch from using memories of arms that have already been visited, to guide choice during early visits, to using representations of arms that are yet to be visited, to guide choice during later stages (Cook et al., 1985). Again, this suggests a future based encoding of information, even if the time
frame in which this information is held is short, usually a few seconds, and hence likely to be a feature of working memory (cf. Clayton et al., 2003a).

Just as for episodic memory, different researchers have used different empirical and theoretical approaches to investigate whether animals may possess something similar to episodic future planning. The framework provided by the Bischof-Köhler hypothesis is particularly challenging requiring experiments to demonstrate that animals can make flexible (and not ‘hard-wired’) decisions that are based on anticipated future (motivational) states rather than current ones, and hence can be thought of as true future planning, divorced from current cues and circumstances. Data indicate that scrub jays, primates and pigeons may have some representation of future conditions (sometimes only seconds into the future) involving the current motivational context (feeding-related). Although this does not satisfy the Bischoff-Köhler hypothesis, it should be possible to devise tasks which start to separate current and future states (Suddendorf and Busby, 2005). Furthermore, from an animal welfare perspective, evidence that animals do have representations of the future is in itself important, even if these representations are tied to current motivational states.

6. Mental time travel, consciousness and welfare

Do animals live in the present? The evidence that we have reviewed indicates that some species show behaviour consistent with the capacity for mental time travel, even though alternative interpretations are often difficult to rule out completely. What are the implications for their welfare and for those species in which these abilities appear to be lacking? In addressing this question, we first need to consider the conscious experience of mental time travel.

6.1. Mental time travel and conscious experience

It is the conscious component of episodic memory and future planning that is likely to have most impact on the animal’s emotional state and welfare, and that was probably foremost in the minds of Thorpe and the Brambell Committee when they raised the question of whether animals live in the present. However, as is made clear by many researchers, this aspect of mental time travel is currently not accessible to study in animals (Clayton et al., 2003a; Eichenbaum et al., 2005), leading to arguments about whether any of this research can really identify an animal equivalent of human episodic memory (Suddendorf and Busby, 2003a,b; Clayton et al., 2003c), and to the careful use of terms such as ‘episodic-like’ and ‘www’ memory.

Consciousness has been defined in a variety of ways and, as argued in a previous paper (Mendl and Paul, 2004), it is phenomenal or feelings consciousness (e.g. Block, 1996; MacPhail, 1998; primary-process consciousness, Panksepp, 2005) that is likely to be the most important from an animal welfare perspective in that it refers to the capacity for basic awareness of feelings, sensations, and emotions. Episodic memory is also likely to require access consciousness, allowing mental representations to exert control over reasoning, reporting or action (Block, 1996), and it may even provide a basis for self consciousness (MacPhail, 1998; Damasio, 2000), an awareness of oneself as a unique thinking, feeling individual. Thus, the occurrence of episodic memory may be linked to a variety of different types of phenomena construed under the ‘consciousness’ label.

Opinions differ as to whether episodic-like memory in animals is accompanied by one or more of these types of consciousness. Some (e.g. MacPhail, 1998; Rolls, 1999) suggest that language is critical to the development of consciousness and therefore that other animals do not have
conscious experiences, and hence could not experience human-like episodic memory. Suddendorf and co-workers argue that if animals can combine mental representations in flexible ways, reflect on their own cognitive processes, measure time, and possess a self concept, these ‘pre-requisite’ capacities would predispose them to experience human-like episodic memory. The strategy they therefore advocate is to study aspects of cognition that require these capacities such as language, metacognition, theory of mind and sense of self. In the absence of such capacities they doubt that animals do consciously experience episodic recall (Suddendorf and Corballis, 1997; Suddendorf and Busby, 2003b). Others are more sanguine (cf. Panksepp, 2005). For example, Morris’ (2001) view is that the hippocampal system is likely to be involved in the encoding, storage and private recollection of episodic memories in non-human animals. Eichenbaum et al. (2005) acknowledge that it is impossible to know the subjective experiences of other animals, but argue that because animals exhibit defining features of episodic memory which, as in humans, are hippocampally dependent, they therefore also experience conscious episodic memory: ‘if it quacks like a duck, and walks like a duck, it’s a duck’.

In addition to theoretical and personal views on animal consciousness, there is increasing interest in empirical approaches that may make some headway in addressing this issue. For example, Seth et al. (2005) and Edelman et al. (2005) list a number of properties of human (visual) consciousness (e.g. neural signatures, thalamo-cortical involvement, sensory binding) that may be shared by other animals. Panksepp (2005) argues that affective consciousness is an intrinsic property of brain systems involved in emotional behaviour. Studies of blindsight indicate that macaque monkeys, like humans, may have at least two levels of visual processing, one of which may be consciously accessible (Cowey and Stoerig, 1995). The apparent ability of some primates and dolphins to report on their state of knowledge, in particular a state of ‘uncertainty’ when insufficient perceptual information is present, has been taken as evidence that they may be able to consciously monitor their own cognitions and hence discriminate between ‘knowing’ and ‘not knowing’ (‘metacognition’, e.g. Smith et al., 2003).

This latter area of research has also been extended to ask whether animals can or cannot report on the quality of their memory (‘metamemory’) and hence, by implication, whether the memory trace in question is or is not consciously accessible. Studies of rhesus monkeys, chimpanzees and orang-utans suggest that individuals behave as if aware of whether they can or cannot remember the answer to a task by either seeking further information at the time of the task (Call and Carpenter, 2001; Hampton et al., 2004), showing an ‘uncertain’ response leading to a safe but less rewarding pay-off (Smith et al., 1998), or opting to take or decline a memory test (Hampton, 2001). A study of pigeons failed to reproduce the latter result (Inman and Shettleworth, 1999). Other research relevant to memory processes comes from studies of trace conditioning in which a cue predicts an air puff to the eye presented a few hundred milliseconds later. Successful trace conditioning in humans requires conscious awareness of the temporal link between the cue and the air puff because amnesic people, who report no conscious memory of the temporal relationship, fail the task (Clark and Squire, 1998). Hippocampal damage affects trace conditioning in animals indicating hippocampal dependence of this task, and raising the possibility that intact animals that can perform the task also consciously experience memory of the events (Schacter, 1998). Although we cannot be certain about the subjective experience of other species, these research approaches offer a promising way forward, and suggest that representations in memory might be consciously experienced, at least in some species and for some types of memory task.
6.2. Implications of the presence and absence of mental time travel for emotion, suffering and welfare

On the basis of the evidence and arguments presented in this paper, it is conceivable that conscious experience of mental time travel may exist in some non-human species. The picture is likely to become clearer as research in this young area develops, hypotheses and criteria for proof become clearer, and more species are investigated. However, at present, we also cannot rule out the possibility that many species live their lives largely in the present moment. In this final section, we consider how the presence or absence of mental time travel might impact on animal welfare. In doing so, we again refer to human research. Although this may invite the criticism of anthropomorphism, we argue that we are motivated to ask questions about the mental lives of animals, and in fact about animal welfare, precisely because of our own subjective experiences, and therefore it is reasonable to consider what we can learn from our own species. In fact, humans are really the only models we can turn to in this endeavour, and it is notable that contemporary researchers, including animal welfare scientists, are actively seeking parallels between humans and animals in their studies of emotion, cognition, consciousness and mind (e.g. Clark and Squire, 1998; Call and Carpenter, 2001; Smith et al., 2003; Desiré et al., 2002; Harding et al., 2004; Paul et al., 2005).

If animals mainly live in the present, they would not be able to ruminate on past events, be they positive or negative, and therefore to experience any suffering generated by episodic memories of, for example, a painful event or the loss of a companion. Indeed, patient KC is unable to re-experience the events of his younger brother’s accidental death which happened a few years prior to his own accident. Likewise, he has only a ‘dry’ semantic memory of the fact that a potentially lethal chemical spill occurred near his home causing his family to evacuate for a week, and he has no conscious memory of a painful fall that left him with a broken knee. Because he cannot re-experience these events, they appear to carry limited emotional impact (Rosenbaum et al., 2005).

Animals living in the present might also lack the capacity to experience intensely distressing human phenomena such as PTSD. Good episodic memory of a traumatic event may predispose people to develop PTSD (Casi et al., 2005), and the disorder is characterised by a vivid and intrusive re-experiencing of the event, or of warning signs of that event (Ehlers et al., 2002). However, some PTSD patients may not be aware that the traumatic memory is of the past, and instead experience it as actually happening in the present (Ehlers et al., 2004). This would not be classified as a true episodic memory in terms of Tulving’s (2002) definition, as it would not involve a sense of experiencing oneself in the past (autonoetic awareness). However, such an experience would be highly relevant in welfare terms, despite its lack of www information. PTSD patients may also experience the emotions and sensations associated with an event without recalling the event itself, only later recognising a cue that likely triggered these responses (‘affect without recollection’; Ehlers and Clark, 2000). Therefore, animals that lived in the present might, assuming some capacity for consciousness, still be capable of experiencing the emotional components of traumatic events despite an inability to travel mentally in time and recall the events episodically.

In accordance with these speculations, it is notable that KC shows some capacity for emotional learning. For example, despite failing to consciously recognise researchers that he has met many times before, he appears comfortable and relaxed in their presence and more prepared to talk and ask questions than with ‘true’ strangers (Rosenbaum et al., 2005). Other studies have also demonstrated intact emotional learning in the presence of episodic amnesia. A classic
example from the early 20th century is provided by the physician Eduard Claparède who concealed a pin in his palm before shaking the hand of an amnesic patient. Subsequently, the patient refused to shake his hand despite having no conscious recall of the event (Claparède, 1995). Recent studies have confirmed the ability of amnesic patients to discriminate appropriately between people with whom they have had staged positive or negative encounters, even though they have no conscious memory of these (Tranel and Damasio, 1993). There is also evidence that amnesic patients can show more complex emotional learning, such as that required to solve the Iowa Gambling Task (Bechara et al., 1994) which involves tracking the relative positive and negative rewards provided by different card decks (Turnbull and Evans, 2006). Emotional learning mechanisms may involve sub-cortical systems that remain relatively preserved in the presence of frontal and medial temporal lobe damage, hence allowing a dissociation from the loss of episodic memory.

So, the absence of episodic memory need not preclude emotional learning and memory, and hence the ability to experience emotional reactions and to show appropriate behavioural responses to cues associated with emotionally significant events in the past. Animals with no episodic memory should thus be capable of experiencing negative emotional states induced by cues. Their inability to link these emotional responses to a specific recalled event might in itself be distressing (‘I’m afraid but I don’t know why’), but might also render the emotional responses less vivid or intense (as for KC’s responses to discussions about his brother’s death), and would preclude conscious recall and brooding on the relevant events either in the presence or absence of cues (see also Mendl et al., 2001). In this respect, any suffering would likely last only as long as a relevant cue was present, and could not be perpetuated or re-induced by further rumination about past events and about one’s own condition, core cognitive components of human depression (Watkins and Teasdale, 2004).

What about emotional responses to events in the present that require no mental time travel? Are these blunted in the absence of episodic memory? KC is able to report on his current emotional state but his emotional repertoire seems, anecdotally, to be somewhat limited (Rosenbaum et al., 2005). HM appears to be impaired in his ability to detect or report on painful sensations, and on states such as hunger and thirst. However, this deficit is unlikely to be related to his lack of episodic memory, but instead is probably caused by damage to the amygdala, an important emotional processing centre (Phelps and LeDoux, 2005), that occurred during his operation (Hebben et al., 1985). Another amnesic AC, though described as ‘emotionally flat’, reports subjective reactions to emotional video clips that do not differ from normal subjects except that he shows no negative feelings in response to a ‘sadness’ clip (Chapelle et al., 1996). Overall, there is limited systematic research on the subjective emotional experience of amnesics. Although there are some suggestions that they may experience ‘blunted’ emotional reactions, this may be the result of brain damage to emotional processing centres such as the amygdala, and unrelated to loss of episodic memory. On current evidence, therefore, animals with no episodic memory would be expected to have largely intact emotional responses to events in the present.

If so, could experience of these events influence long-term stress or mood states, and general stress responsiveness? Although there appears to be no systematic study of this issue in humans, there is no obvious reason why, for example, events in early life or repeated stressful experiences should not impact on the functioning of stress response systems (e.g. Weaver et al., 2004; de Kloet et al., 2005a,b; Herbert et al., 2006) in animals with no episodic memory. Conscious recall of events is not an obvious prerequisite for such events to exert cumulative effects on these systems, and associated emotional or mood states. Animals could thus show physiological and...
emotional indicators of chronic stress and depression-like conditions, and of enhanced stress responsiveness and generalised anxiety, even if they were unable to recall the events that had altered their baseline state.

An ability to consciously imagine one’s own future and to model various situations in anticipation of achieving a goal or avoiding a problem brings with it clear adaptive advantages (Suddendorf and Busby, 2003b; Mendl and Paul, 2004). Humans and animals lacking this ability are thus likely to be impaired in their capacity for conscious planning. For example, emotions may be involved in making risky decisions, either as immediate states that reflect the uncertainty involved in a decision (anticipatory emotions) or as imagined future states (anticipated emotions) that may occur consequent on the decision taken (e.g. Bechara et al., 1997; Loewenstein et al., 2001). An inability to mentally travel forward in time would impair emotion-based decision making processes that rely on imagining future scenarios. However, it should not interfere with other ‘forward-planning’ mechanisms. For example, semantic associations between learned locations of food sources and motivational states (hunger) related to those resources may allow effective preparatory and ‘goal-directed’ behaviour without any conscious imagining of the forthcoming hunt or foraging trip.

Future mental time travel also renders the subject vulnerable to pre-occupation with future events and associated anxiety and worry which, in humans, can become clinical conditions that severely affect emotional state and quality of life. An absence of episodic future thinking may protect animals from such states. However, anxiety is still likely to occur when in the presence of cues or situations that have been associated with unpleasant events in the individual’s (or species’) past, or if the animal’s baseline state has become one of high vigilance due to the cumulative effects of past events. Any resulting suffering will be temporally linked to the presence of cues and likely to fade rapidly when they are removed, but also to be prolonged if cues are chronically present.

If a lack of episodic memory severely limits an individual’s capacity to form a self concept, what implication does this have for their ability to suffer? As has been discussed before, the difference between having or not having a self concept probably equates to the difference between experiencing “I feel pain” as opposed to “this is painful” (Bekoff, 2002; Mendl and Paul, 2004). At the time of the pain, suffering is likely to be similarly intense in both situations. The fact that the pain is being experienced by ‘me’, a person with a clear self identity, rather than just ‘being experienced’ may have little impact on the subjective sensation itself. However, the capacity to recall the painful experience and to worry about it in the future, is likely to affect suffering (Lea, 2001). Therefore, it is not the presence or absence of a self concept per se that is likely to impact on the ability to suffer, but the presence or absence of the capacity for mental time travel.

A final point concerns the sensory nature of episodic memory and future planning which, in humans, is generally thought of in visual, and sometimes auditory, terms. Other sensory modalities (e.g. smell, pain, taste) appear more difficult to consciously re-experience or imagine (though it is claimed that they may be re-evoked by some PTSD patients (Ehlers et al., 2004)). This might be a protective mechanism in the case of sensations such as pain. If this is also the case in other species, then the capacity for mental time travel might be limited by the extent to which a particular species relies on vision and hearing. On the other hand, it may be that conscious re-evocation of smells, tastes and even pain, occurs in other species that depend more on these sensations, allowing mental time travel that would be qualitatively different from the human experience.
7. Conclusions

The Brambell Committee suggested that animals mainly live life ‘in the present’, and that this may have significant (and beneficial) effects on their experience of suffering. Recent evidence contradicts their suggestion, indicating that some species may indeed be able to travel mentally in time including, particularly relevant for animal welfare, having recollection-like experiences of the past, and cognitive representations of the future. However, we cannot rule out the Brambell Committee’s premise especially because evidence suggests that, even without episodic memory or future planning, many species would likely have sufficient cognitive mechanisms in place to function successfully. Past experiences could still impact on the emotional state of such animals via (implicit) learning of associations between cues and emotional events, and via cumulative effects altering stress response mechanisms and baseline stress or mood states. Emotional responses, including future-directed anxiety would be temporally bound by the presence of relevant stimuli or cues and, therefore, potentially short-lived. What such animals would miss would be the beneficial consequences of being able to use previous experience or forward thinking to plan and organise future behaviour, and the detrimental consequences of being able to brood, ruminate on, and worry about the past and future and so to extend, perhaps greatly, the duration of emotional impact of any stimulus or cued memory. One could also speculate that something like the human experience of ‘boredom’ might arise more readily in animals that had subjective experience of existing in time, and hence of having time to fill stretching into the future. The potential influence of mental time travel on animal welfare is thus great, though the actual influence remains to be determined. It is also clear that absence of mental time travel by no means releases animals from many effects of the environment, including the past environment, on their emotional state. Recent interest in this area, and resulting new techniques, mean that answers to the Brambell Committee’s question of whether animals live in the present, and what consequences this has for their welfare, may soon be attainable.

Acknowledgements

We thank the UK Biotechnology and Biological Sciences Research Council for supporting ESP.

References

Babb, S.J., Crystal, J.D., 2006a. Discrimination of what, where and when is not based on time of day. Learn. Behav. 34, 124–130.


Clayton, N.S., Dickinson, A., 1999. Scrub jays (aphelocoma coeruleus) remember the relative time of caching as well as the location and content of their caches. J. Comp. Psychol. 113, 403–416.


