

**The end to a ‘timeless memory’: A look at episodic memory in animals and its implications for welfare**

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*Allison traveled to the University of Toronto Mississauga to hear Professor Nicky Clayton (Cambridge University) speak, and returned to Guelph buzzing with enthusiasm for Clayton’s exciting cognitive research. For her paper, Allison chose the ambitious topic of what human-like episodic memory could mean for animal welfare.*

**Introduction.**

When humans travel backwards in subjective time it is referred to as episodic memory because it involves the memory of past episodes (Zentall, 2005). Episodic memory is defined as the conscious recollection of unique personal experiences (Tulving, 1983). It is largely believed to be a trait unique to humans since it requires integration of self, subjective sense of time, and auto-noetic consciousness (the subjective experience as a whole, or the ‘feeling of remembering’), which are not conclusively known to exist in animals (Tulving, 2001; Dere et al, 2006). Further, experiencing consciousness, the capacity for basic awareness of sensations, feelings, and emotions, has been suggested to require language (Mendl & Paul, in press). Thus, difficulties arise when attempting to answer whether animals have episodic memory.

With spoken language, humans can answer questions about past personal experiences. For example, do we remember someone, or only recognize them. It is possible to recognize someone as familiar without actually remembering how you know them. This is because recognizing relies on semantic (factual) recall and can be learned with repeat encounters or trials (associative learning). Habits and memory for facts and rules are generally not tied to personal experiences (Zentall, 2005). However, recollection (episodic recall) is an integrated memory of the person, where, and when you met (what-where-when), (Clayton et al, 2001), and requires one to travel backwards in time in order to retrieve the memory (Zentall, 2005). Eichenbaum and Fortin (2005) state that memory based on familiarity is characterized by a continuous incremental retrieval depending on the strength of the memory, whereas episodic recall is characterized by an all-or-none retrieval of items along with circumstances of prior experience. Thus, episodic memory is vivid and involves the replay of events in the sequence that they were experienced. Today, the perirhinal cortex is thought to be the key brain region responsible for familiarity learning (Brown & Aggleton, 2001), and the hippocampus as the site of memory retrieval (Eichenbaum & Cohen, 2001). For the above reasons, evidence of associative learning (i.e. conditioning) is not sufficient evidence of episodic learning.

In previous years, people with brain injuries have enabled the discovery of critical brain regions and their corresponding functions. Most famously, KC and HM proved to be valuable tools for investigation into the brain regions required for storage and recollection of memories. The patients suffered from damage to the medial temporal lobe causing anterograde amnesia, and from the time of trauma, were incapable of acquiring new episodic memories. While still retaining the ability to communicate via verbal language, these patients can report about a memory (i.e. tell you facts), but cannot remember. They also state that they understand factual tomorrow, but cannot imagine it (Clayton, Oct 2006). Episodic memory and imagination for future are collectively termed ‘mental time travel’. The mental time travel hypothesis has been argued to be exclusive to humans and even crucial to hominid evolution (Clayton et al, 2003).

Episodic recall hinges on auto-noetic consciousness and a sense of subjective time (Kart-Teke et al, 2006). Currently it is not possible to assess episodic memory in animals as there are no accepted behavioural markers of conscious experience (Clayton et al, 2001). In 1965, the Brambell Report addressed the overall welfare issues of animals used in production. Within this report it was implicated that animals were stuck in the present and had improved welfare as a result (Brambell, 1965). Today, it is still believed by many that animals are devoid of a sense of subjective time and can remember only the facts of a past event, not a personal experience (Kart-Teke et al, 2006). Thus, animals are often said to have the capability of semantic memory, and not episodic memory; that they are fixed in a ‘timeless memory’.

For many years, studies of animal memory have focused on requiring the animal to retrieve information on a single feature of an episode without distinguishing between episodic recall of events and semantic knowledge. These tests of memory may require repeated training, thereby eliminating trial-uniqueness and enabling potential solving of the task based on relative familiarity (Clayton et al, 2003). Recent studies have begun to address the issue of episodic memory in animals directly. This paper will review such findings of Dr. Nicky Clayton and colleagues in light of the direction in which they have taken the concept of episodic memory in animals and its relevance to welfare.

### ***The approach***

With the problem of assessing a subjective experience in an animal, the older accepted definition (by Tulving (1972): episodic memory ‘receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events’) is re-examined to establish behavioural criteria for ‘episodic-like’ memory in animals (Clayton et al, 2003). With this new term, there is no implied subjective experience of the past (Schwartz et al, 2004).

The three components that emerged as defining properties of episodic recall are content, structure and flexibility. Content is the recollection of what happened, where, and when, on the basis of past experience, with ‘when’ acting as the crucial component to episodic memory. If you can remember what and where, but not when, then it is not impossible that you are experiencing familiarity based on the associative principal. As well, retrieving these components individually does not suffice as episodic recall. Thus, the second criterion of episodic recall is structure, an integrated representation of what-where-when. Flexibility, the final requirement, ensures that episodic memory can be used in a declarative framework, or according to a system of rules, and modified in conjunction with new information to potentially result in a novel behavioural response (Clayton et al, 2003). When attempting to discover if animals possess the capability of integrating these components, and therefore fulfilling the behavioural criteria of episodic-like memory, Clayton looks to examples in nature where this type of memory would be advantageous. This ethological approach leads to food-caching species, which hide food for future consumption and therefore must rely on a keen memory.

The Western scrub jay (*Aphelocoma coerulescens*) is a food-caching species belonging to the Corvid family (e.g. crows, rooks), known to be extremely intelligent and have highly developed sociocognitive skills (Clayton & Dickinson, 1998). When brain to body weights are plotted against each other, the scrub jay falls close to chimps, although they are rarely viewed in the same light by humans (Emery, Oct 2006). Corvids rely on spatial memory to recover previously stored caches and steal others caches (Dally et al, 2006). Studies have found that the hippocampus is larger relative to body size in these birds than in other species less reliant on spatial memory for their fitness (Lucas et al., 2004). Therefore, the scrub jay is a reasonable choice when looking for a time in nature that it would be beneficial to exhibit episodic-like memory.

### ***The experiments***

Clayton & Dickinson (1998) sought to answer whether scrub jays would remember the location of two food items that were cached under trial-unique conditions. First, birds were trained that two types of food, a naturally preferable but perishable wax-worm or a less-preferred but non-perishable peanut, each degrade over a certain time. They were allowed to cache both food types in a variety of spatial locations and return after different amounts of time had elapsed. Birds were found to visit cache sites containing wax-worms when cache-recovery intervals were short, and recover the non-perishable peanuts when these intervals were long. Results indicate that scrub jays modify their behaviour according to the duration of time passed and are therefore capable of using integrated information about what (food type), where (cache site), and when (time since caching) to recover their preferred food type from cache sites. Thus, scrub jays meet the behavioural criteria defined for episodic-like memory.

More recently, Clayton and colleagues show that when caching individuals were observed by conspecifics they were later more likely to re-cache those sites which the observer potentially had a good look at, as measured by the proximity of cache site to the observer (Dally et al, 2006). Birds were allowed to cache in private or in the presence of an observer bird and compared for differences in re-caching behaviour with controls, observed birds that, upon recovery, were not being watched by the original observer, but instead by a stranger conspecific. This study then combines episodic-like memory and social affiliation by making the observer birds of a known relationship, having either subordinate, dominant or partner status. Results reveal that the scrub jay has episodic-like memory and social relationships accompanied by affiliative behaviour, as the most re-caching occurred when the observer was dominant, and the least when in front of their partner or in private (Dally et al, 2006).

### ***Validity***

Early results for integrated what-where-when memory have been shown to be reproducible within (Clayton & Dickinson, 1998; 1999; 2006) and across species (Ergorul & Eichenbaum, 2004; Kart-Teke et al, 2006; Schwartz et al, 2005), thus giving the overall results of episodic-like memory existing in animals both high internal and external validity.

For example, Ergorul & Eichenbaum (2004) adopt Clayton's research question, but test it with a newly developed procedure for rats. Rats were trained to remember unique episodes, and by combining odor and spatial cues were able to make decisions on the order of events. By successfully testing the rats within a format unlike that in which they were trained, this study went on to show that the memory expression was flexible.

Kart-Teke et al (2006) integrated a novelty-preference paradigm with the temporal order memory for objects at a specific time point to test if Wistar rats have episodic-like memory. By displaying a preference for a 'recent familiar' object over an 'old familiar' object in a new location, these rats demonstrate the content, structure, and flexibility required for true episodic memory. With a lowland gorilla that used picture cards to correctly identify what food he had been given, by whom, and in which order, Schwartz et al (2005) was able to demonstrate episodic-like memory. This study is promising as it uses human language, however, was limited in scale and the structure component required for episodic memory.

### ***The implications***

The establishment of episodic memory in non-human species is likely to have profound welfare implications. Evidence that animals have representations of the past implies that experiences are not necessarily acute, but can be relived, causing the weight of a single negative experience to be greater. However, true episodic memory requires that an element of consciousness exist and this is likely to have the biggest impact on welfare (Mendl & Paul, in press).

Supporters of animal welfare believe that animals have sentience, or that they are conscious beings, in spite of the inability to communicate subjective experience through human language. Therefore, with evidence of episodic-like memory in animals it becomes reasonable to discuss whether animals are also subject to feelings linked to the capability of mental time travel, such as anxiety and worry. It is not doubted that the ability to experience episodic memory and mental time travel would contribute to adaptive fitness by increasing the efficiency of experience based learning and memory. However, seemingly hyper-efficient learning and memory could potentially lead to anxiety disorders, as seen in human victims of post-traumatic stress disorder (PTSD) who experience a severe and ongoing reaction to previously experienced psychological trauma, such as war.

For example, one study suggests that without the guidance of adult bull elephants, young adult males may act abnormally, as in the case of when orphaned male elephants unexpectedly killed over 40 white rhinoceros (Slotow, 2000). Specifically, the violent acting out of male elephants seen years after the initial implicated trauma could be considered a form of post traumatic stress disorder (Bradshaw et al, 2005). Recent theories, like that of elephant hyperaggression involving the effects of a previously broken family structure, can only be considered in conjunction with evidence for episodic memory in animals. Thus, if animals are assumed to possess human-like

episodic memory and all of its attached components, additional welfare questions, like the incidence of PTSD, arise.

It is interesting to consider the welfare of animals that are stuck-in-time when the implication of this is an inability to recover personal memories of past events (Zentall, 2005). Thus, an aversive situation that was experienced chronically would be no worse for welfare than the same situation experienced acutely. In other words, the negative emotions associated with the aversive situation would only last the duration for which any salient cues were present (Mendl & Paul, in press). It would be impossible for animals that live in the present to be able to dwell on the events of the past or foresee problems of the future. Here, it is again helpful to use testimonials of humans with brain injuries, to gain a linguistic report of what it might be like to be stuck in the present. KC reports on the events of his younger brother's death with apparently limited emotion (Corkin, 2002), and provides evidence that without episodic memory, the emotional attachment to a memory is impaired and hence, the power of the memory itself. Therefore, animals that could not relive an experience would likely only be capable of retrieving and acting upon only factual information of the experience.

### ***The criticisms***

Early documents like the Brambell Report recognize that the way people view animals' intelligence plays a large factor in their treatment, for example, when considering ruling legislation. The establishment of human-like episodic memory in animals could promote change in how the public views the use and management of animals. However, it should be mentioned, that cleverness does not correlate to consciousness (Mendl, 2004). Intelligence should not be equated with the capability to suffer. As humans, we are anthropomorphic in nature, and are more readily able to transfer human-like emotions to animals that we can see ourselves in, such as chimpanzees and apes (Emery, Oct 2006). We tend to use cognitive abilities as an indicator for an animal's potential to feel pain and suffering (Mendl, 2004). But cognition and consciousness are very different. Cognition is the acquiring, processing and storage of information, while consciousness refers to awareness of feelings, thoughts and emotions (Mendl & Paul, 2004).

Similarly, studies on patients with the neurological condition of 'blindsight' implicate that attention and consciousness can be related, but are not necessarily one and the same thing. Blindsight is a condition where damage to the primary visual cortex or its afferents, cause the individual to report that they are subjectively blind, in spite of retaining the ability to detect, discriminate, and localize visual stimuli presented in areas of their visual field (Kentridge et al, 2004). Using blindsight patient GY, Kentridge et al (2004) successfully show that attention may be a necessary precursor to visual awareness, but it is not a sufficient one. With evidence that neurological processes exist on multi-levels, the potential remains that episodic-like memory in animals could occur on a level without true consciousness.

Criticism for the lack of identification of key brain structures responsible for episodic-like memory led Ergorul & Eichenbaum (2004) to subsequently address the issue of episodic-like memory in rats and the suspected involvement of the hippocampus. Bilateral hippocampal-lesioned rats were compared to sham-operated controls and tested in a task of integrated memory for which they were equally proficient at during pre-surgery testing. Their results suggest that rats do exhibit memory for what-when-where and that this is critically dependent on the hippocampus. Interestingly, the lesioned rats made the correct object choice significantly less often than chance. They were inclined to visit the more recently presented and rewarded place, thereby showing learning. Thus, although these results support that rats have episodic-like memory as defined by Clayton, they also support that there are multiple levels in the memory process, and the possibility that only some require consciousness.

Many of the studies assessing episodic-like memory in other species have failed (Roberts & Roberts, 2002), and those successful have fallen to criticism, mainly as they can be explained in alternative manners such as using a sense of time passed since exposure, or strength of a memory trace (Eichenbaum & Fortin, 2005, Eacott et al, 2007). The ability to time durations is not the same as being able to travel back in time to recovery a unique memory (Zentall, 2005). An alternate explanation of Clayton's own work was that scrub jays were continually updating semantic knowledge of the current world, and thus, would know what food is where and whether it has degraded (Schwartz et al, 2005). This would be important for real-world scenarios as when trees are found felled or barren, or when predators move dens. Thus, it is suggested that re-caching behaviour based on duration of time since cached is more like remembering where you put your keys than remembering who stole your keys (Schwartz et al, 2005).

Recently, Eacott et al (2007) suggested that the 'when' component of what-where-when memory, should be replaced with 'which'. They support their case with examples of human memory for timing of events, which is often poor and found to be dissociable from episodic memory. However, only the employed methodology used in species other than birds, not the idea that there could potentially be episodic memory in animals, is critiqued. Rather, Eacott suggests a new protocol for successfully testing episodic-like memory in rats that relies on their innate preference for novelty.

Evidence that animals fulfill the operational definition of episodic-like memory does not answer of whether there exists human episodic memory in animals and these implications are most relevant to animal welfare. Although animals may show learning from past experiences, this does not confirm an ability to retrieve past episodes (Zentall, 2005). Unfortunately, it is impossible to directly test episodic memory in an animal as long as its definition lacks accepted behavioural criteria. Tulving (2001) would agree that no evidence yet supports that animals have autonoetic consciousness or episodic memory.

These arguments are ongoing, and although evidence is strongly in support of certain non-human animals having the defining properties of content, structure, and flexibility,

doubt remains as to whether this is the equivalent of human-experienced episodic recall.

### **Conclusion**

In conclusion, the overall aim of Clayton and colleagues to determine if animals are capable of mental time travel and episodic-like memory was successfully met through careful experimental design that maximized natural caching behaviour in scrub jays. New potential welfare issues arise with respect to the establishment of human-like episodic memory in animals, most notably, potential concern for anxiety disorders, such as PTSD. The capability for episodic memory increases the chance that an animal could relive unpleasant experiences indefinitely, thus having implications for lifetime behaviour and welfare. Finally, if it is established that true episodic memory exists in animals, it also implies that they have an accepted form of consciousness.

Proving that animals experience a subjective state similar to humans is, at least for the moment, impossible. By using components of a widely accepted definition for episodic memory, Clayton is able to identify representational behavioural criteria that can then be tested in animals. The development of these criteria allows testing of what-when-where memory to be transferred across species. In fact, this has been done by several researchers and will likely continue to be assessed across many species.

Through a series of experiments that build on themselves, Clayton and colleagues provide answers to their own critical analyses. The Western scrub jay is a choice experimental species for this research, and relies on natural robust behaviour. As this was ecologically inspired, there was no need for excessive training, or invasive procedures such as surgical lesions to critical brain areas. However, it should be noted that individuals were wild-caught and, not without irony, their proven keen memory for what-where-when may imply compromised welfare from this imposed change in environment. The species is now the focus of a series of experiments in a new ingenious direction of socioaffiliative and reconciliation behaviour in animals which may also prove to have profound welfare implications.

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