

Vulnerable: A photo of flowers of *Delonix regia*, an increasingly rare native of Madagascar, now accessible at the API. (Picture: RBG Kew.)

provide information ranging from the morphology and uses of plant species to the history of plant exploration and the European discovery of Africa.

The RBG Kew has contributed historical material, including maps and papers from David Livingstone's South East Africa Expedition Papers and over 2,000 sheets of Africa-related material from the Director's Correspondence covering early botanical exploration of tropical Africa. Two major works, The Flora of West Tropical Africa and the **Useful Plants of West Tropical** Africa, are now available electronically for the first time, as are more than 1,200 original illustrations from Curtis' Botanical magazine. Other works include La Flora du Cameroun, Flora Zambesiaca and Flowering Plants of South Africa.

Collections soon to be added include watercolour drawings of macrophytes, ethnobotany data, a set of scholarly reference volumes from the eighteenth and nineteenth centuries, the Medbase medicinal and traditional uses database from South Africa and the flora of Ethiopia and Eritrea.

Quick guide

Episodic memory

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What is episodic memory? Endel Tulving coined the term 'episodic memory' in 1972 to refer to our ability to recall specific past events about what happened where and when. Episodic memory is distinct from other kinds of memory in being explicitly located in the past and accompanied by the feeling of remembering, whereas other knowledge that we acquire is purely factual, without any personalised pastness attached to it.

As William James, the famous psychologist, once wrote "Memory requires more than the mere dating of a fact in the past. It must be dated in my past." (James, 1890, p. 650). It is for this reason that Tulving makes the distinction between *remembering* and *knowing*. Each of us remembers what happened when we last went to London, for example, whereas although we know that London is the capital of England we do not remember when this fact was learned.

Some memories are more vivid than others but, even when we do not have a very accurate memory of a particular event, we do know that we experienced the event at some point in our past, even though the memory of the event is current. To do so, we travel mentally back in time to reconstruct and re-experience the event.

Tulving has suggested that the development of civilization and culture was, and is, critically dependent on this awareness of our continued existence in time. With physical time, the past can influence the present, and the present can affect the future, but there is no way in which the future can influence anything that happens in the present. With mental time travel, however, we can go backwards as well as forwards in time in our mind's eye.

For normal healthy humans this ability to reminisce about specific past events is an integral part of our daily lives. We often take it for granted because these episodic memories happen automatically, and often without any deliberate intent to remember. However, not all humans are capable of episodic remembering. Indeed, episodic memory develops relatively late, and is not fully developed until about four years of age. It is also the most fragile kind of memory, the first to be lost in Alzheimer's disease and other debilitating neurodegenerative diseases of the mind.

Mental time travel

Many people have assumed that episodic memory is unique to humans, and that all other members of the animal kingdom are incapable of mental time travel. The point was made most eloquently by Robbie Burns in his lament Ode to a Mouse, where he returns home at dusk to reflect upon the day's events, having accidentally ploughed up the nest of a field mouse and watched the animal run off into the autumn night to perish. Riddled with guilt, he consoles himself with the thought:

Still thou are blest compared w' me! The present only touches thee...

Burns' view of the psychology of the field mouse finds an echo in the words of many current comparative and cognitive psychologists, including Tulving, who define episodic memory, at least in part, in terms of the conscious experience of recollection. This characterization of episodic memory presents an insurmountable barrier to demonstrating this form of memory in animals in the absence of any agreed behavioural markers of conscious experience. So according to this definition, we can never know whether or not

animals other than humans have episodic memory. After all, it should always be remembered that absence of evidence does not constitute evidence of absence.

Episodic-like memory

This dilemma can be resolved to some degree by using Tulving's original definition of episodic memory when referring to animals, according to which he identified episodic recall as the retrieval of information about 'where' a unique event or episode took place, 'what' occurred during the episode, and 'when' the episode happened.

The merit of this definition is that the simultaneous retrieval and integration of information about these three features of a single, unique experience may be demonstrated behaviourally in animals. We refer to this ability as 'episodic-like memory' rather than episodic memory because we have no way of knowing whether or not this form of remembering is accompanied by conscious recollection.

Episodic-like memory by food-caching birds

Until recently there was little or no evidence that animals could recall a specific past experience, nor was there any reason to believe they would need such a memory system in the types of laboratory tasks on which they were tested. Recently, however, we have adopted a different approach by considering cases in nature in which an animal might benefit from the capacity to remember a specific past episode of what happened where and when.

One example concerns the food-caching behaviour of members of the crow family, which hide or cache a variety of perishable foods, such as insects and fruit, as well as non-perishable nuts and seeds, and rely on memory to recover these caches at a later date. In the laboratory, one species of crow, the western scrub-jay, demonstrates remarkable memories for what they have cached on a given day as well as where they hid them. The jays also keep track of how long ago they cached different types of perishable foods that decay at different rates, and they can even discriminate between unique memories of events that have similar 'what' and 'where' contents but ones that occurred at different times.

We have concluded from such observations that the jays form integrated memories about what happened where and when, rather than encoding the information separately (Clayton *et al.* 2003). Furthermore, the jays can also remember whether another individual was present at the time of caching, and if so, who was watching when.

The distribution of episodic-like memory

The discovery that jays have episodic-like memory raises the question of whether other animals are also capable of remembering specific past events. Using a design similar to that employed with the jays, Babb and Crystal (2006) found evidence for episodic-like memory in the humble laboratory rat. Having learned that an attractive food was only available after a certain time had elapsed since they discovered its location, their rats returned to this location only after the appropriate period had passed. Surprisingly, however, monkeys failed to show a comparable sensitivity to the age of their memory in an analogous task.

Alternative approaches

Other students of animal memory have focussed on different criteria for detecting episodic-like memory. For example, studies of human memory suggest that remembering and knowing are subserved by different retrieval processes. In order to retrieve an episodic memory, its strength has to exceed a threshold, whereas simply to know that one has encountered a stimulus before, one has to discriminate whether or not its apparent familiarity arises from a genuine past encounter.

Each of these retrieval processes shows a different sensitivity to varying the payoff costs of being right and wrong. By varying these costs, Fortin and colleagues (2004) demonstrated that the normal rat's ability to recognise odours was governed by a combination of remembering and knowing. Moreover, brain lesions in areas equivalent to brain regions where damage has been reported to produce episodic amnesia in humans changed the sensitivity of their rats to the payoff costs from one reflecting both processes to one characteristic of familiarity alone.

Others have challenged whether the encoding of the 'when' component is central to the concept of episodic-like memory or whether in fact it is the context in which the event occurred that is critical. For example, remembering two meals with the same friend are discriminated in memory by binding each episode to the different contexts provided by the two restaurants.

Eacott and colleagues (2005) exploited this concept of episodic memory by capitalising on the rat's propensity to seek out novelty. Their rats explored two different objects placed in a certain spatial configuration in a particular context, before investigating them again in a different configuration in a second context. Following this episode, the rats were exposed to one of the objects in a different place until they were bored with it, an experience that enhanced their propensity to seek out the other object when returned to the original contexts. This they could only do, however, if they could remember where the objects were located in a particular context during the initial episode. Their success at this task led Eacott and colleagues to argue that the rats recollected the object (what) and its location (where) in a particular context (which) on the basis of unique 'what-where-which' memories.

Robbie Burns revisited

Whatever the precise conception of the content of episodic-like memory, these studies suggest that at least some animals can mentally travel back to their past. However, the concept of mental time travel we introduced at the beginning goes beyond episodic memory, as Robbie Burns alluded to in his original lament. For, when filled with remorse over the fate of the field mouse he concluded that being stuck in the present was a blessing:

But oh I cast my eye on prospects drear, and forwards tho' I canna see, I guess and fear.

This forward-looking aspect of mental time travel is only just beginning to be explored in animals. It may also provide the key to understanding episodic memory's errors: for a memory that reconstructs pieces of the past can also reassemble them into imaginary future scenarios. As Mark Twain noted so judiciously: "My life has been filled with many tragedies, most of which never occurred."

Where can I find out more?

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Essay

All the queen's men

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Humans have an ancient and intimate relationship with honey bees — from the development of beekeeping in prehistoric times up to the recent sequencing of the honey bee genome. Yet, the intimacies of bee sexuality remained obscure and contentious until relatively recently. Their stepwise unravelling is a tale of advances and misconception that, in part, may have stemmed from an all too humanised view of bees.

Humans and bees have had a long lasting relationship that consisted mainly of humans robbing the bees of their honey. This relationship dates back to ancient hunter-gatherer cultures and probably to non-human ancestors. Even in prehistoric times, humans had quite sophisticated techniques for dealing with bees; cave paintings show how ladders and ropes were used to get at the bees (Figure 1) and how smoke was used to calm them. Certainly, by the 3rd millennium BC in ancient Egypt, beekeeping had developed into a fully fledged sophisticated practice, with specialised beekeeping techniques and man-made hives, which have largely remained unchanged over the centuries.

The Egyptians worshipped bees and thought that they stemmed from tears shed by the sun god Ra. As a hieroglyph the bee symbolised lower Egypt (Figure 1).

Successful beekeeping and honey harvesting obviously required a detailed knowledge about bee biology, of their sensory capabilities, their life cycle and how they propagate. But just how detailed did that knowledge have to be? And what aspects did it entail? It turns out that, despite having achieved great sophistication in bee management, humans were, until relatively recently, surprisingly ignorant about essential features of bee biology, in particular bee sex. This may be because, until recently, bees





Figure 1. An ancient love affair.

A cave painting (left) from La Araña Cave in Spain showing Neolithic honey collection using ladders or ropes (With permission from *Letters from the Hive* p12, Bantam Books). A hieroglyph of a bee (right), symbolising Lower Egypt from the tomb of pharao Senusret I, from his 'sedge and bee' title. (From http://commons.wikimedia.org/wiki/ Image:AncientEgyptianRelief-BeeHieroglyph-ROM.png)