



Review

Ten years of research into avian models of episodic-like memory and its implications for developmental and comparative cognition

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ABSTRACT

Episodic memory refers to the ability to remember specific personal events from the past. Ever since Tulving first made the distinction between episodic memory and other forms of declarative memory in 1972, most cognitive psychologists and neuroscientists have assumed that episodic recall is unique to humans. The seminal paper on episodic-like memory in Western scrub-jays (*Aphelocoma californica*) by Clayton and Dickinson [4] has inspired a number of studies and in a wide range of species over the past 10 years. Here we shall first review the avian studies of what-where-when memory, namely in the Western scrub-jays, magpies, black-capped chickadees and pigeons; we shall then present an alternative approach to studying episodic-like memory also tested in pigeons. In the second and third section we want to draw attention to topics where we believe the bird model could prove highly valuable, namely studying development of episodic-memory in pre-verbal children, and the evolution and ontogeny of brain areas subserving episodic(-like) memory.

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1. Introduction

It was in 1972 that Endel Tulving first coined the term ‘episodic memory’ to describe our ability to remember specific events or episodes that happened in our personal past, in contrast to the ability to simply acquire knowledge about the world. To do so he described episodic memory in the information processing terms which were common at that time:

“Episodic memory is an information processing system that a) receives and stores information about temporally dated episodes or events, and about temporal-spatial relations among these events, b) retains various aspects of this information, and c) upon instruction transmits specific retained information to other systems, including those responsible for translating it into behavior and conscious awareness.” [1, p. 385]

Since the time of its introduction the concept of episodic memory has changed considerably. According to Tulving, the major transition in his concept of episodic memory was the “shift from the general idea of “consciousness” that applied to both episodic and semantic memory in 1972 to “autonoetic consciousness” in 1999” [2], namely that “Memory requires more than mere dating of the fact in the past. It must be dated in *my* past.” [3].

When Clayton and Dickinson [4] started their pioneering work with Western scrub-jays (*Aphelocoma californica*), they argued that there are no agreed behavioural markers of consciousness in non-linguistic animals, and consequently it is not possible to empirically evaluate the autonoetic component of episodic memory in animals, or pre-verbal children for that matter. Therefore they returned to Tulving’s original description of episodic memory [1] to ask whether the birds could remember what, where and when of specific past caching episodes, focusing on Tulving’s original description for a memory that “receives and stores temporally dated episodes or events, and about temporal-spatial relations among these events” [[1], p. 385]. They termed this ability ‘episodic-like’ memory to make a distinction between the behavioural and phenomenological criteria for episodic memory, given that the phenomenological aspects that usually accompany conscious recollection in humans are impossible to assess in non-human animals and pre-verbal children.

Their seminal paper on episodic-like memory in Western scrub-jays [4] has inspired a number of studies in a wide range of species over the past 10 years, from primates and rodents to pigeons and passerine birds. The mammalian studies will be discussed elsewhere in this issue [5–7]. Here we shall first review avian studies of what-where-when memory, namely in the Western scrub-jays mentioned above [[4], for recent reviews see [8,9]], and subsequent work in other species of bird, from a fellow corvid, the magpie [10], and another food-hoarding species, the black-capped chickadee [11]. We shall then describe studies on domestic pigeons and present an alternative approach for studying what-where-when memory [12–14]. We will close this section with a discussion of the various approaches to study episodic-like memory. In the second section we suggest that the non-verbal caching and item finding paradigm is an ideal task to study the development of episodic-memory in pre-verbal children. In the final section we want to draw attention to topics where we believe the bird model could prove highly valuable, namely as a biomedical model system to better understand the neural basis of episodic memory.

2. Review episodic memory in birds

Episodic memory is the only memory to be oriented in time [15], and more precisely in subjective time. Since the “subjective experience of having a past event from one’s life projected into the present is not just an additional criterion for defining episodic memory” [[16], p. 566] but critical for the concept of episodic memory, it is essential to demonstrate in animals that they remember when a particular event occurred in the past as well as what happened where on the basis of a single past experience [4].

2.1. Western scrub-jays

In the wild, Western scrub-jays scatter-hoard hundreds of perishable insects that degrade over time, as well as seeds that stay palatable for an almost indefinite time. Clayton and Dickinson [4] exploited this natural behaviour in controlled laboratory experiments, and gave the jays a series of trials in which they were allowed to cache highly preferred insect larvae and less-preferred peanuts in sand-filled ice cube trays. These trays were made visuo-spatially distinct and trial-unique by attaching children’s building blocks (Lego Duplo) to one or two of the sides of the tray. While for one group of birds, the Replenish group, both food types remained palatable throughout the experiment, for the Degrade group the larvae were palatable if the trays were returned after 4 h, but had degraded after 124 h (Fig. 1). The birds in the Degrade group quickly learnt to recover their preferred food after 4 h, but to avoid them after 124 h, when they were no longer palatable, and instead to recover the peanuts that did not degrade [4]. The Replenish group, however, who had never experienced that worms degraded over time, continued to inspect their worm sites before their peanuts sites after both delays, i.e. after 4 h and 124 h. This result is not surprising considering that scrub-jays in the wild can accurately locate their caches even after months [17]. However, the consistent preference of the Replenish group to recover worms even after a long time (124 h) eliminates the possibility that the observed reversal in the Degrade group’s search pattern might be caused by any kind of forgetting due to the long interval between caching trial and recovery trial. Taken together the jays must have recalled what (wax worm, peanut) they have hidden where (location in the tray) and when (4 h, 124 h ago); and they have coherently memorised all three features in one single caching event. This was the “first conclusive behavioural evidence of episodic-like memory in animals other than humans.” [[4], p. 274].

2.1.1. Content: what-where-when memory

Clayton’s co-authors have argued that Clayton and Dickinson’s elegant experimental design is ingenious in its simplicity. Subsequent studies established that scrub-jays remembered each component (what has been cached, where, and when), and that their behaviour was not based on other forms of learning or alternative strategies.

2.1.1.1. What-where component. One still might question whether or not the scrub-jays truly remembered the identity of the different food types they had cached, and argue, for example, that they had cached food items at more memorable or preferred caching sites in the tray; or that the birds could have associated the cache sites with the relative preference for the food stored at that site. If that was the case, the scrub-jays only had to return to (or avoid respectively) the location with the stronger preference or higher valued memory

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