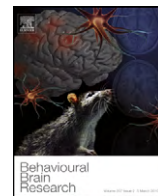




Contents lists available at ScienceDirect

## Behavioural Brain Research

journal homepage: [www.elsevier.com/locate/bbr](http://www.elsevier.com/locate/bbr)

## Review

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

Lucie H. Salwiczek<sup>a,\*</sup>, Arii Watanabe<sup>b</sup>, Nicola S. Clayton<sup>b</sup><sup>a</sup> Department of Physiological Sciences, UCLA, 621 Charles E Young Drive South, Los Angeles, California 90095, USA<sup>b</sup> Department of Experimental Psychology, University of Cambridge, Downing Street, CB2 3EB Cambridge, UK

## ARTICLE INFO

## Article history:

Received 28 January 2010

Received in revised form 5 June 2010

Accepted 9 June 2010

Available online 19 June 2010

## Keywords:

Episodic-like memory

What-where-when memory

Hippocampus

Event-based memories

Deferred imitation

Source knowledge

## 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.

© 2010 Elsevier B.V. All rights reserved.

## Contents

1. Introduction .....	222
2. Review episodic memory in birds .....	222
2.1. Western scrub-jays .....	222
2.1.1. Content: what-where-when memory .....	222
2.1.2. Structure: the integrated representation of what-where-when memory .....	224
2.1.3. Flexibility .....	224
2.2. Other avian models .....	225
2.2.1. Black-billed magpie .....	225
2.2.2. Black-capped Chickadee ( <i>Poecile atricapillus</i> ) .....	225
2.2.3. Pigeons ( <i>Columba livia</i> ) .....	226
2.3. Discussion episodic memory models .....	227
2.3.1. Episodic-like memory in corvids and parids .....	227
2.3.2. Short retention intervals versus long retention intervals .....	228
2.3.3. Episodic-like memory versus one-trial learning .....	228
3. Developmental models for pre-verbal children .....	229
3.1. Event-based memories in toddlers .....	229
3.2. Deferred imitation .....	229
3.3. Source knowledge .....	230
3.4. Conclusion for development models .....	230
4. Birds as biomedical model for studying the neural basis of episodic memory .....	230
4.1. Revision of the of the bird brain nomenclature .....	230
4.2. Hippocampus .....	231
4.3. Conclusions about the avian brain model .....	231

\* Corresponding author. Tel.: +1 310 625 8202; fax: +1 310 206 9184.

E-mail address: [luciesalwiczek@ucla.edu](mailto:luciesalwiczek@ucla.edu) (L.H. Salwiczek).

5. Final remarks .....	232
References .....	232

## 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].

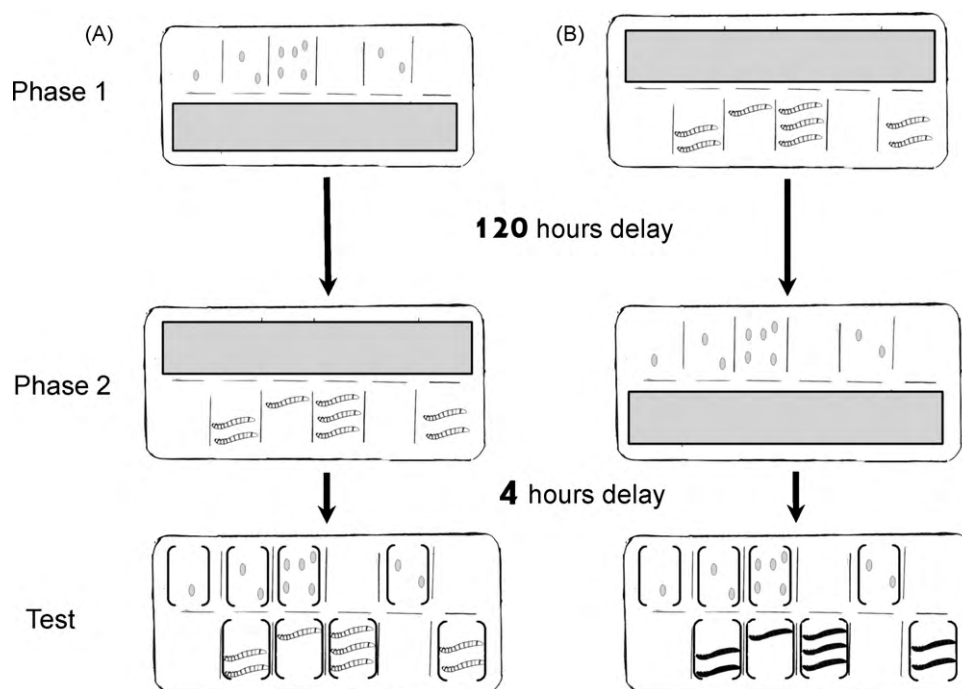
### 2.1. Western scrub-jays

In the wild, Western scrub-jays scatter-hoarded 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



**Fig. 1.** Testing the content criterion of episodic-like memory by Western scrub-jays with the food caching 'what-where-when' memory paradigm. Having received a series of training trials in which the birds could cache and recover peanuts and wax worms, the birds received an interleaved trial procedure: In phase 1 they cached peanuts in one side of a caching tray and then in phase 2 wax worms in the other side of the tray 120 h later (A) or vice versa (B). For testing their memory 4 h later, the birds then were given the opportunity to search in both sides of the tray. The brackets indicate the fact that the food caches were not present at recovery in order to test for memory. The open symbols represent fresh wax worms, the black symbols illustrate rotten wax worms, and the grey filled circles denote peanuts. The grey bar indicates the side of the tray that was blocked by a Plexiglas strip (the unavailable cache site) during each of the two caching events. Adapted from [8].

tag to find their preferred food without actually remembering the contents of the cache sites.

To establish that the jays did remember the content of their respective cache sites, Clayton and Dickinson [18] manipulated the relative preference of a given food type at the time of recovery. They relied on the 'specific satiety effect' that eating one type of food selectively reduces the incentive value of this specific food type, while it does not interfere with eating any other kind of food [19,20]. For example, when a person has eaten a large portion of fish and chips, his/her stomach might feel stuffed to the rim and not able to accept any further piece of fish or chips – and yet still might appreciate some Chocolate Mousse for dessert. Thus Clayton and Dickinson [18] provided their jays with two equally preferred food types during caching, namely peanuts and dog food kibbles. Shortly before the recovery phase, the jays received either powdered peanuts or powdered dog food kibbles and were allowed to eat until satiation; thereafter the birds could retrieve their cached items. The jays preferentially searched for the food type they had not received during the prefeeding phase thereby demonstrating that they did remember which particular foods they had cached where.

**2.1.1.2. When component.** Following Tulving's definition [1,21], it is the 'when' component that is critical to episodic and episodic-like memory. While there are numerous studies demonstrating that animals can learn from past experience, it is episodic memory which is the only kind of memory to be explicitly located in the past; and not only in the past per se, but the individual needs to be aware that it is in its own past. Thus it is this 'when' component that makes two otherwise identical what-where combinations unique.

**2.1.1.2.1. Forgetting.** This ability for separately remembering timely discrete but otherwise similar if not identical events are taken for granted in humans; however, it has been argued that rather than mentally travelling back in time the birds might have

used the strength of the respective memory traces in order to know when to search where for the particular food items. The basic idea is that the age of the memories could cue when to search where during recovery in two ways: in spontaneous forgetting and in directed forgetting [for detailed discussion, see [22]].

Spontaneous forgetting refers to our everyday experience that memories acquired long time ago are usually less accurate due to increased forgetting with time. Thereby not only specific information gets lost, but more and more details about the whole event. For the scrub-jays, this would suggest that they might not only forget the content of particular caches but also the specifics of the caching site, and consequently that their accuracy during retrieval would decline over time.

Clayton and colleagues addressed this question by having a control group, called Replenish group, as well as their experimental groups [4,23,24]. As described previously, the Replenish group's insects never degraded, and these birds consequently could retrieve palatable insects, which they preferred to peanuts, after short or long time interval had elapsed since the caching phase. Since the Replenish group preferentially retrieved insects at both retention intervals (RIs) while the Degrade group changed their retrieval patterns (see above), these inverse preferences of the latter was due to learning (that insects degrade) and episodic recall rather than forgetting. The Replenish group also proved that the jays could locate the respective caching sites after 5 days just as accurately as after 4 h [23]. Thus it is more than unlikely that memory decay explains the scrub-jays' performance in the various caching tasks.

The direct forgetting account [25] argues that the scrub-jays forget the caching sites of insects more rapidly than those of peanuts since half of the time, i.e. on all trials with long delays, they have a negative experience of finding degraded insects. As a result, the jays might spend less time on caching insects, and these 'shallower' memories get more easily lost over time. In response Clayton and co-workers argued they could test this account with a 'ripen-

ing paradigm' rather than the previous 'degrading paradigm' [22]. During the morning, all birds were allowed to cache first peanuts in one side and subsequently wax worms in the other side of a visuo-spatially trial-unique caching tray. During recovery, half of the birds, the Degrade group, found their wax worm caches to be fresh after 4 h and degraded after 28 h, whereas the remainder birds in the Ripen group experienced the worms to be degraded after the short and palatable after the long RI. The scrub-jays learned the inverse relationship and soon avoided insect cache locations after the short RI, but preferentially retrieved worms after the long RI.

In conclusion, none of the available forgetting accounts (spontaneous, direct) could explain the scrub-jays' performances in these experiments, however there are other possible accounts of the birds' observed changes in cache inspections during recovery that must be considered before one can confidently assume that the birds rely on episodic-like memory. One might ask, for example, whether the birds could have used time of day, any physiological state due to circadian rhythms or hunger as cues to guide their memories as, for example, shown in time-place-learning experiments [e.g. [26]]. However, Clayton and co-workers have carefully chosen the RIs in the various experiments. Firstly, intervals as long as 24–124 h definitely require long-term memory (or reference memory respectively), where episodic memory has been located. Secondly, all caching episodes occur at the same time in the morning and recovery trials always at the same time in the afternoon (i.e. 4, 28, 124 h after caching). This experimental design eliminates the possibility that the jays could have taken advantage of any physiological cues linked to time of day since these were kept identical on different trials.

**2.1.1.2.2. Familiarity.** Familiarity, also called 'recency effect', is a special case of distinguishing between older and younger memories. There is, however, growing evidence that familiarity and episodic recall are two distinct cognitive processes, both neurobiologically [27–29] and psychologically [30–32]. Also, the retrieval dynamics differ fundamentally in the two processes [e.g. for humans: [33–35]; for rats: [36]]. Familiarity is an automatic process based on the perceptual features of items (or locations) that enables the individual to distinguish previously encountered stimuli from novel ones without requiring any recollection of the original encounter of the stimuli. Recollection on the contrary is a cognitive process and it supports the retrieval of previously stored memories about prior experiences, such as the temporal, spatial, and content aspects of a caching period.

According to the familiarity account, the scrub-jays in the Degrade group could associate searching in the wax worm tray on the 4 h trials with the trays that appear to be relatively familiar (i.e. have been seen only recently), and associate searching in the peanut tray when the trays have not been seen for 124 h and are therefore comparatively less familiar. To investigate whether the scrub-jays' decision was based on the automatic process of relative familiarity, Clayton and Dickinson [23] modified their previous caching paradigm with two trays for two food types into an interleaved trial procedure with one tray for both food types. They covered one side of the tray with a transparent strip of Plexiglas to make these caching sites unavailable so that the birds could cache the provided food type only on the accessible side of a tray. The birds then got their trays back in the morning of the fifth day (i.e. after 120 h) with the previous caches covered and the previously inaccessible caching sites open for caching the second food type. The critical feature in this interleaved procedure is that it removes the differential relative familiarity of the tray because the temporal pattern of exposures to the tray is always the same regardless of whether peanuts or worms had been cached first, 124 h ago or just recently (4 h ago). Just like before, the jays spontaneously searched for insects after 4 h, while they searched predominantly for peanuts after 124 h. This pattern of recovery confirmed that the scrub-jays

did not rely on relative familiarity of trays, but remembered specific caching episodes in terms of where they had hidden which food item how long ago. Subsequent studies further established that the scrub-jays show similar performance when two perishable food types were used, each of which decayed at different rates [24].

### 2.1.2. Structure: the integrated representation of what-where-when memory

The memory of what-where-when in a single event is a necessary but insufficient component of episodic-like memory [37]. When humans recall a specific event they remember all components in one flash. In other words, what, where, and when are not stored separately but encoded together as one 'gestalt image', and consequently recalling one component elicits the retrieval of the others. A consequence of this integrated representation is that when retrieving one component the other two are automatically reactivated too. Thus it is this integrated structure that enables the discrimination between similar episodes that occurred at different times and possibly different places.

To create trials with identical food items (what) in different trays (where) cached at different times (when) Clayton and co-workers [38] allowed the birds to cache peanuts and worms in one tray on one day, and the same two food items in a second tray on day 4. Only then did the jays get a chance to retrieve their caches from both trays. The RIs had been chosen such that the insect were now unpalatable in the first tray, but still edible in the second tray. If the birds had stored the time separately from what and where they would have associated the caching of worms (and peanuts respectively) with a temporal tag, and the memory recovery would retrieve temporal tags for both the long and short RIs. The search pattern for both trays should be the same. The birds, however, searched preferentially for worms in the second tray and for peanuts in the first tray. Consequently they must have been able to retrieve the specific 'when' together with the specific tray and the particular items cached in that particular tray.

In the wild this integrated representation is actually important for scrub-jays in their everyday social life [for reviews see [39,40]]. Scrub-jays have developed sophisticated cache-protection strategies to minimise the chance that their caches are stolen by other individuals [e.g. [41–45]]. In terms of memory, it is particularly intriguing that the birds recall which particular individual was watching which specific caching event and protect their caches according to who has seen what. The birds can only do so if they are able to instantly recall all features about this specific caching event, including 'who' was watching 'when'.

### 2.1.3. Flexibility

Tulving [1,21,46] has suggested episodic memory to be declarative in nature, a cardinal feature that it shares with semantic memory. Clayton and colleagues [37] argued that declarative memories rely on flexible utilisation of the memorised information, and these memories consequently could be updated when new information is acquired.

In terms of the caching paradigm, this means that if the birds acquired new information about the food items after they had actually hidden them then the jays would be able to incorporate this new knowledge during recovery but only if their episodic-like memory is declarative, namely it is flexible in nature such that new information can be incorporated into the memory system allowing previous information to be updated accordingly. To test this idea, Clayton and Dickinson [18] designed an experiment where the birds had the opportunity to cache two food items in two trays, and were then allowed to retrieve food A from tray A and food type B from the other tray. As a result, tray A contained only food type B, and tray B only food type A. To test whether the jays remembered

the changed content of the different trays Clayton and Dickinson [18] utilized again the specific-satiety effect and pre-fed the birds with one of the two food types. Since the bird searched for food A in tray B if they had been with B, and vice versa, they argued that the scrub-jays could only solve this task by mnemonic updating.

Although semantic memory is distinct from episodic memory, semantic memory can still be employed during episodic recall. This means, for scrub-jays, that they learn the rule that insects have a specific degrading rate, and store this as semantic knowledge. During a caching event they combine this knowledge with the integrated representation of the specific what and where and when of a unique caching episode to decide when they retrieve which food item as described above. If their episodic recall is indeed flexible then the birds should be able to include knowledge, e.g. about changed degrading rates of the cached insects, into their recovery strategies, even if they learnt about this change in degrading rates *after* they already cached the insects. During a new series of trials scrub-jays learnt that mealworms perish within 28 h after caching, while crickets are edible 1 day and degraded 4 days after caching [47]. When tested after 3 days, a RI not used during training trials, the scrub-jays searched preferentially for worms, indicating they expected worms to be palatable, while they – as expected – avoided cricket sites after 4 days (Fig. 2). The critical full test design took 6 days. On day 1–3 the birds were allowed to cache peanuts and crickets in one tray at any one time. Day 4 meant a 3 day RI to day 1, and Day 5 a 3 day RI to the caching episode on day 2; on both trials the birds consequently retrieved crickets first. But against their previous training (i.e. semantic knowledge) the insects had been degraded. Therefore, the birds could learn during these two recovery episodes that the degrading rates of the insects had increased. As predicted by the declarative nature of their memories, the jays incorporated this new knowledge into their searching pattern during recovery on day 6, i.e. 3 days after caching on day 3: they now avoided the cricket sites and first looked for peanuts.

In summary, Clayton and co-workers studied Western scrub-jays extensively over the last 10 years and provided numerous lines of evidence that these birds are capable of episodic-like memory, in that they not only store the content of their cache memory in terms of what happened, when, where, in an integrated representation, and one that can also be used flexibly to update their memories when new information becomes available even long after the initial information was encoded.

## 2.2. Other avian models

Although these pioneering studies on Western scrub-jays have sparked a considerable number of mammalian studies [see this issue [5–7]], there is surprisingly little research in other birds. In fact only three other species have been reported to have a what-where-when memory, namely magpies, black-capped chickadees, and pigeons, although results on pigeons are contradictory.

### 2.2.1. Black-billed magpie

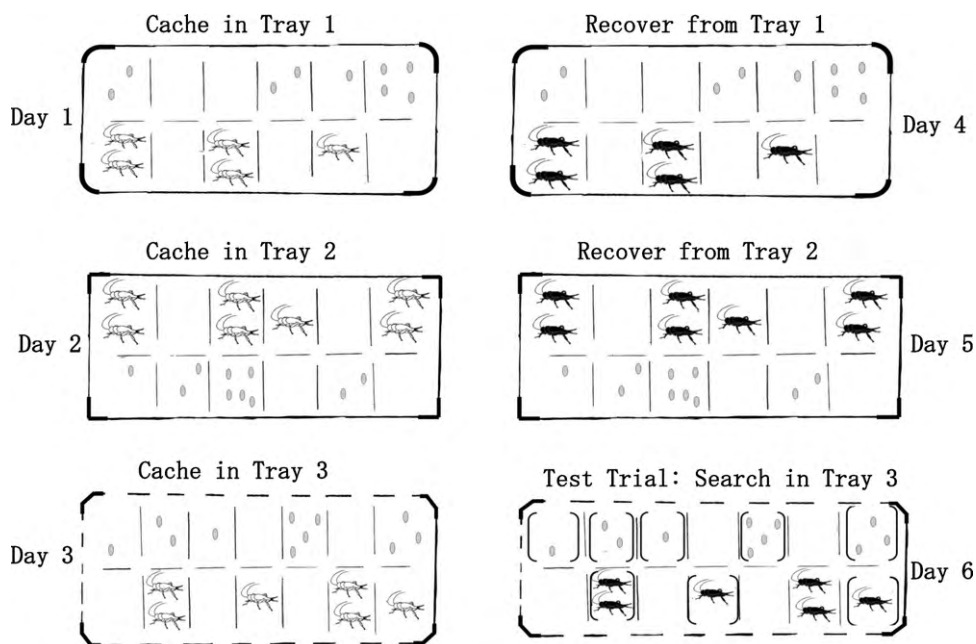
Magpies are, like its cousin the Western scrub-jay, opportunistic hoarders of a range of food types that might degrade over time [48]. Zinkivskay et al. [10] focussed in this first study on the content (what-where-when) only. Rather than using two differently preferred food types, of which the more preferred one degrades, Zinkivskay and colleagues used only one type of food to get around the problem that individuals might differ in their food preferences. Half of the food pellets, composed of scrambled eggs, were dyed red and offered in one bowl at one side of the testing array, while the remaining pellets were dyed blue, and offered in a bowl at the other side of the testing arrays. Six magpies were allowed to cache equal amounts of red and blue food pellets in an area of 150 cm × 130 cm area with landmarks. The birds could then retrieve their cached

items either in the afternoon on the same day (after 4 h) or on the next day (28 h later). Items were made 'unpalatable' by replacing them with wooden beads of the same size and colour after a certain time interval, while the other pellets remained untouched. Palatable items were retrieved consistently above chance, while the percentage of wooden beads (i.e. not palatable items) retrieved dropped dramatically over trials.

To eliminate any visual and olfactory cues Clayton and co-workers always removed the food items for the critical test, as is standard in psychological experiments on memory. In this study, however, the food pellets and beads remained in place during the critical test trial, and thus the magpies could have found the edible pellets guided by visual or olfactory cues from either type of items. Zinkivskay et al. [10] consequently included two control trials. Firstly a probe trial: the setup was the same as in the testing trials, except that items now had been removed before the birds' respective retrieval trials. The birds' performance remained the same as with items present, namely that the magpies mainly searched at the locations of [removed] edible items. Secondly, the birds received a foraging task that tested whether the present items (pellets, wooden beads) gave away their condition (edible, inedible) and/or location. Therefore researchers hid pellets and/or beads in previously preferred caching locations as well as outside preferred hiding locations without the birds watching them. When the magpies were then allowed to search the experimental area, 5 of the 6 individuals could not find any item at all hidden by the researcher, and one bird found only one wooden bead. From performance on both control trials, Zinkivskay et al. [10] concluded that their magpies could not have used any cues from the items present at the test trials and therefore that the birds must have relied on their memory of what they had cached where and how long ago. Future work will have to clarify the exact nature of the 'when' component (e.g. specifically controlling for time of day), as well as to test the magpies' what-where-when memory on its structure and capacity to be flexibly deployed.

### 2.2.2. Black-capped Chickadee (*Poecile atricapillus*)

Feeney and colleagues [11] argued that episodic-like memory might be a more general ability among food-caching species, rather than being restricted to the corvids (magpies and jays), particularly if there is a selective pressure on food-caching animals to memorise the specific details of individual caching episodes in terms of what happened where and when [11]. Black-capped chickadees store a variety of food types and retrieve them after varying intervals after caching [for review see [49]]. They memorise multiple hiding locations [50] and they are able to remember caching locations for at least 28 days [51]. Since their chickadees did not consistently cache in the provided experimental board, the researchers themselves hid food in the holes in a wooden board, and allowed their chickadees to find sunflower seed during a first inspection phase in some holes and mealworms in other holes; some holes remained empty. The birds could return to the board after either a 3 h or a 123 h RI and search again for the food items. After the short RI both types of food could be found in edible form in the same locations as during the inspection phase, while after the 5 day RI the mealworms were rotten. The birds showed 'what-where' memory and preferentially searched for their preferred food (mealworms) at locations where they had encountered them during the inspection phase. The chickadees, however, failed to change their search behaviour according to the elapsed time; they recovered their preferred food after the short as well as the long RI. The authors favoured two reasons to explain this result. Firstly, in contrast to the scrub-jays, the chickadees did not hide their food themselves but found the items placed in the holes; it might be possible that memorising locations of found food relies on a different cognitive process than that of actively cached food, and only the latter results in an integrated memory of



**Fig. 2.** Flexibility criterion of episodic-like memory by Western scrub-jays with the food caching 'what-where-when' memory paradigm. The jays cached peanuts and crickets in caching Tray 1 on Day 1, and then again in Tray 2 on Day 2, and finally in Tray 3 on Day 3. The birds were given the opportunity to recover the caches they had hidden in Tray 1 on Day 4, and in Tray 2 on Day 5. For testing their memory on Day 6 the jays were allowed to search in Tray 3. The brackets indicate the fact that the food caches were not present at recovery on Day 6 in order to test for memory. The open symbols represent fresh cricket caches, the black symbols represent rotten cricket caches, and the grey filled circles represent peanut caches. Adapted from [8].

what-where-when. Secondly and more importantly, the wooden board had been placed on the ground like the ice-cube trays for the scrub-jays. Chickadees, however, usually store their food in shrubs and trees rather than on the ground.

Feeney et al. [11] therefore made their experimental setup more ecologically valid for their chickadees. They removed the wooden board and equipped the testing aviary with 4 artificial trees. The tree branches contained holes with unique landmarks. Like the previous experiment, in phase 1 the birds found food items (worms) in some holes of two trees, and another food type (sunflower seeds) in some holes of the other two trees; some cavities remained empty. During phase 2, either 4 h or 28 h after phase 1, the birds returned to the aviary with all holes open. Contrary to experiment 1 (wooden board on the ground) in this 'tree design' the chickadees searched the worm location significantly more often after the 4 h RI than after the 28-h interval. Thus in this second, more species-adequate experimental setup the chickadees demonstrated a what-where-when memory. Like in the magpies this publication needs follow up studies to clarify the nature of the 'when' component and study structure and possible flexibility of the chickadees' what-where-when memories.

### 2.2.3. Pigeons (*Columba livia*)

Contrary to the previous studies on wild species that emphasised the ecological validity of the employed paradigms, pigeons have been domesticated some 5–10,000 years ago [52] and do not hoard food. They are a popular subject for comparative psychologist to study animal learning and cognition, are comfortable in laboratory settings, and easily trained to peck on touch-screens to receive a food reward.

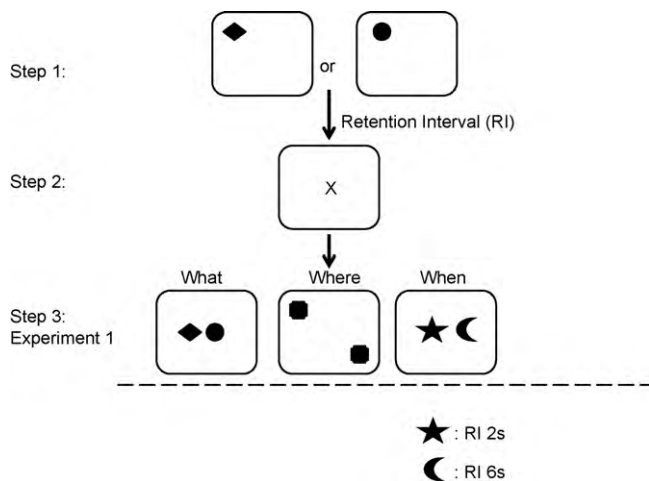
**2.2.3.1. Asking an unpredicted question.** Zentall and co-workers [13] developed a different approach to study episodic-like memory to circumvent two major concerns. Firstly they argued that humans often do not remember exactly when a specific event occurred. Secondly they questioned extensive training procedures, because if

the individual knows in advance what question it will be asked, it can prepare for it. In other words, every time a jay, for example, eats or hides a worm or a peanut it could 'tell' itself to remember this because it will be asked the next day. In the moment of giving the answer the person or animal do not need to travel back in time but simply recall what it aimed to remember. To circumvent these problems Zentall and co-worker developed a paradigm to ask pigeons unexpected questions about their recent behaviour.

In phase 1, the pigeons first learnt in a matching-to-sample training procedure that by pecking on a red light they can report that they had just previously pecked on the screen, while pecking on a green light meant they had just refrained from pecking on the screen. In a differential autoshaping procedure during phase 2, the pigeons were exposed to a series of blue and yellow hues; blue was not followed by food and thus pigeons did not peck at this key, while yellow was followed by a food reward and pigeons tended to peck on this key even without their pecking having any consequences. On test trials yellow or blue was presented first followed by a choice between red and green. In other words the pigeons were first made to peck (yellow) or not (blue), and then were given the opportunity to report what they had just done (red: pecked; green: did not peck). Pigeons performed above chance level from the very beginning of the test trials which excluded the possibility that they learnt correct answers in the course of all trials.

Although pecking the yellow hue was not necessary but reinforced, the birds could have developed a semantic-like rule. Thus the pigeons underwent another differential matching-to-sample procedure using novel stimuli, i.e. a circle and 'no stimulus' (called 'dark response key'). The pigeons quickly learnt to peck on the circle and not to peck the dark response key. Again it took them only 4 trials before they were choosing the respective key to report if they just had pecked or respectively the green stimulus if they did not.

The time intervals (RI) between stimulus presentations were very short, only in the range of up to 4 s. Thus another explanation could be that the birds still feel the sensation from having



**Fig. 3.** Schematic of the design of the experiment 1 to test What, Where, When memory in pigeons. Step 1: presentation of stimulus to be remembered. Step 2: presentation of cross (X) in the centre of the screen after a retention interval (RI) of either 2 s or 6 s. Step 3: one of three possible screens turned up to test the pigeons' memory of what, where, when. What: both initial items were presented in the centre. Where: two symbols different from step 1 appeared, one at the location where the initial sign had been. When: two items were presented, different from previously seen items, each representing one RI. Adapted from [12].

just pecked (or the lack of thereof) and used the presence/absence of this motor after-effect to guide their choices between red and green stimuli. To test this, Singer and Zentall [53] replaced the response 'pecking versus not pecking' by pecking 'right or left', so that the proprioceptive cue (pecking) became identical for both responses. Again the birds' performance was quickly significantly above chance.

Zentall and co-workers ran a final control experiment to eliminate the possibility that one of the keys used in all phases of the experiment might have taken away the surprise, and instead prepared the pigeons that they will be asked a question. But even when eliminating this possibility to use cues rather than memory, the birds performed above chance level. In sum Zentall and colleagues [14] concluded that their approach might not be as stringent as Tulving's episodic memory definition for humans and in turn Clayton and co-workers definition of episodic-like memory for non-human animals, but they provide a non-caching approach which behaviourally separates semantic, rule-based decisions from remembered episodes.

**2.2.3.2. Asking an unpredicted questions and structure of memory.** Like Zentall et al. [13], Shettleworth and colleagues [12] tested pigeons on the unexpected question paradigm that Zentall had developed. Importantly this is the only study that tested the structural criterion of episodic-like memory in another animal species aside from the scrub-jays.

In experiment 1 (see Fig. 3) they trained pigeons in a series of delayed-matching-to sample tasks and tested whether their pigeons remembered what, when and where in an integrated, bound-together fashion or all three features independently.

The pigeons first saw one of two items in one out of eight possible locations at the periphery of the monitor (step 1). Then after a RI of either 2 s or 6 s a 'X' showed up in the centre (step 2). When the bird pecked at this 'X' one of three possible screens (step 3) turned up for (a) what memory: both initial items were presented in the centre, (b) where memory: two symbols different from step 1 appeared, one at the location where the initial sign had been, and (c) when memory: two items were shown, different from previously seen items, each representing one RI. After block training and random presentation of what, where and when trials, the birds entered

the critical two-test phase. They now went through steps [a] to [c] on the first trial, but on the successive trial [a] was skipped and the 'X' was presented again before another (unpredictable!) alternative appeared. The assumption was that once the birds reliably answered the three respective questions, they must have encoded the three characteristics of a given episode since the pigeons did not know which of these questions (a–c) will be asked on part two of the two-phase trials.

The results favoured the interpretation that the pigeons had memorised the three components independently for two reasons. Firstly, on the two-phase tests, performance on phase 1 was not correlated to performance on phase 2, which contradicted the possibility that information about the different characteristics were encoded in a bound fashion. Secondly, after having been trained on blocks of just one kind of content (acquisition phase) performance dropped as soon as the birds received the first block of trials combining what, where and when, although loss of accuracy mainly affected the when component [for detailed discussion see [12]].

While experiment 1 relied on extensive training a second experiment aimed to study spontaneous binding of what-where-when components (for details see [12]), which was expected to reveal itself from the very beginning of the training sessions. Unfortunately the authors abandoned the when component and continued with what and where tasks only. In short, experiment 2 replicated the previous finding and pigeons' performance again did not show any signs of spontaneously linking the identity of an item to the location of its presentation. All together pigeons seem to store what, where and when memories independently rather than in an integrated fashion.

### 2.3. Discussion episodic memory models

Although not numerous in terms of different avian species studied the bird literature tackles some thorny issues that are not easily resolved but have far-reaching consequences in research, namely the extent to which episodic-like memory is prevalent specifically in food-hoarding species or more widely distributed in other species of birds; and the crucial and actual function of the when-component of episodic-like memory.

#### 2.3.1. Episodic-like memory in corvids and parids

With scrub-jays and magpies there is now good evidence for episodic-like memory in corvids, and at least in some parids (chickadees). All three species hoard perishable and non-perishable food items, although to different degrees. This raises the question whether episodic-like memory might be a trait specific for food-hoarding species; this however is highly unlikely. Episodic memory is more likely a general trait that can develop under different selective pressures whenever it is advantages for the owner in its natural and/or social environment.

We already suggested further candidates in nature who might benefit from the ability to remember the 'what, where and when' of individual past episodes. For example nectar-feeding bats and hummingbirds could increase food intake when they use a given flower's individual nectar secretion rate to time their respective revisiting schedule [8,38]. Other potential candidates were brood parasitic species like cowbirds (*Molothrus spec.*) [54,38]. Female cowbirds could return to the appropriate nest site at the ideal time to lay their eggs by keeping track of the hosts' nests current status.

In this review we described how black-capped chickadees performed just as well in the food-finding paradigm ([11], experiment 2) as Western scrub-jays and magpies did in food-storing paradigms. Therefore the chickadees' performance in this study refutes the possibility that the action of storing is essential for forming a what-where-when memory; hence it is very likely that

episodic-like memory is a rather generally applicable cognitive capacity.

Nevertheless, to answer these questions requires comparative studies on caching and non-caching species. For example, episodic-like memory might have been particularly advantageous for food-stores while their respective non-caching close relatives might lack this mental capacity, at least for those for whom the loss in caching was not secondary [55]. The same argument holds for comparisons of food-storers living at different latitudes; since the harsher conditions further north (higher latitudes) will put a greater selective pressure on successful retrieval of edible items, food-storing species in comparatively moderate climates should perform worse than species living in higher latitudes [for reviews see e.g. [56,49]].

It is therefore premature to draw too many conclusions about the generality of these findings in birds as a whole given that data are only currently available for three avian species, of which only one, the Western scrub-jay, has been studied thoroughly to date. But further comparative studies on corvids, on parids, and on other avian and non-avian candidates, could provide interesting clues as to the circumstances under which episodic-like memory evolved, as well as revealing the degree of elaboration that birds – and possibly other animals – can achieve. And since similarity arising as a result of convergence need not lead to identical solutions [e.g. [57]], comparative studies could help to analyze if different mnemonic mechanisms exist for solving what-where-when reference memory tasks, or whether memory in different groups may have similar functional properties without necessarily relying on the same neuro-architecture (see Section 4).

### 2.3.2. Short retention intervals versus long retention intervals

To comply with the concept of human episodic memory and to avoid misconceptions, episodic-like memory tasks for corvids and parids have chosen RIs ranging from several hours to several days, to guarantee that they test (declarative) long-term memory [1,21]. Studies in pigeons, however, dispute the necessity of very long delays and use RI no longer than 6 s. This approach is mainly inspired by two arguments.

Firstly the necessity of long retrieval delays is questionable since the recall of an incident that happened just minutes ago still qualifies as personal past experience, hence episodic memory [14]. It seems more important to distinguish whether animals use rule-based learning, i.e. semantic memory ('to know' facts) or indeed episodic memory, i.e. to remember a personal event spontaneously. Secondly Baddeley extended his previous three component model of working memory by a component termed 'episodic buffer' [58]; some researchers view the episodic buffer as "integral component of both working and reference memory" [[14], p. 97]. Furthermore short RI might be perfectly legitimate, since nothing enters long-term memory that has not been processed, temporally stored and possibly manipulated in short-term memory (including the episodic buffer).

The function of the 'episodic buffer' is to actively create a unitary multi-dimensional representation from information stored in different codes (e.g. visual, phonological, semantic) originating from different sensory (visual, auditory, tactile, etc.) and mnemonic (episodic, semantic) memory stores [58,59]. Although the episodic buffer has some aspects in common with Tulving's description of episodic memory and seems important for the transfer of information between working and reference memory, it is definitely different from episodic memory itself; episodic buffer is a temporal, limited capacity attentional storage with an active binding function [60,61]. On the other hand, episodic memory is a long-term memory without specific temporal constraints; and it stores memories rather than creates or manipulates information. One has, of course, to be aware that memory never is an exact copy or

'video' of the past, and the process of any kind of remembering is a re-constructive process in which bits of information from various sources are pieced together [62,63]. Nonetheless the working memory component 'episodic buffer' is clearly different from episodic memory [58,60,61] and will have to be tested in specific ways, that differ from paradigms testing episodic recall and episodic-like memory.

At the heart of the problem lies the old question what is important to behaviourally demonstrate in non-verbal species in order for the scientific community to be convinced that the species in question (or animals in general) possesses the cognitive ability others have claimed to be uniquely human; this is, however, different from the question of what really defines the cognitive process concerned. There is no doubt that remembering an event which happened just minutes ago can be episodic in nature. However, in behavioural tasks on animals a very short RI will blur the important dissociation between working and long-term (reference) memory. This is why long delays were used in the scrub-jay studies, and why in the pigeon research unexpected questions preferably would be have been asked across time delays of hours or days in order to unambiguously demonstrate long-term memory where episodic memory has been located.

In fact a marginal RI might even undermine testing the working memory component of the 'episodic buffer'. This intermediary "mental modelling space" [[60], p. 1738] requires some working time. Its function is to actively create a unitary multi-dimensional representation of the past, thereby taking into account information from different memory subsystems, each with their own coding styles, including current new information and possibly (but not necessarily) semantic memory. Far too short testing intervals might interfere with this creational process in one way or another (e.g. memory interference), and possibly explain that pigeons demonstrated independent memories for what, where, and when [12] in short-term memory tasks. It does not mean that pigeons are not capable of forming integrated what-where-when memories in long-term (episodic) memories.

### 2.3.3. Episodic-like memory versus one-trial learning

Several other authors have disputed the importance of long time intervals in episodic and episodic-like memory tasks though for again other reasons. For example, it has been argued that time might just work as "occasion setter to distinguish one experience from another similar experience" [[64], p. 221], which resembles the everyday experience that one episode follows another. The time aspect is consequently not seen as the memory of the episode but a recollection of the temporal organisation of experiences [66]; the time component could possibly be removed completely by replacing it with a 'which component' that defines the experience as unique [64,65].

New approaches are always welcome particularly when animal models are necessary, for example, to develop drugs for treatments of cognitive impairments. However, so far success in drug development for episodic memory deficits is rather disappointing [67]. We see the major reason in limitations in the validity of behavioural tasks that might resemble the assessment of episodic recall but do not demand the kind of information recalled in episodic memory as outlined by Tulving [e.g. [1,2,15,21,46,68]] or Clayton, Dickinson and co-workers [e.g. [4,23,24,37,38]]. This might hold true for tasks that do not include a when component, as well as for tasks with too short RI (see above). Here we will exemplify our scepticism by means of associative learning, i.e. an originally inconsequential stimulus acquires significance by being paired with another stimulus and in turn causes a change in an animal's behaviour [69].

For an episode to be temporally unique and its retrieval not to rely on a semantic-like rule through extensive training, the what-where-when of this episode must be memorised in one single



exposure. Some researchers have suggested that one-trial learning [70], like taste aversion learning, trace conditioning [71], fear conditioning [72] or alike might thus qualify as a long-term memory comparable to episodic-like memory. We, however, disagree for the following four reasons that should have become obvious from our studies on scrub-jays: such associative learning accounts (1) do not imply that animals need to mentally represent the various contents, or to connect them in an integrated structure as outlined for episodic-like memory, (2) they also do not require the individual to remember an event as part of their own, personal past, (3) it also does not matter whether the individual had acquired this knowledge by eavesdropping or by experiencing the illness itself and (4) the individual neither needs to recall the location where it became ill or consumed the item nor how long ago; actually such conditioning tasks do not implement any temporal component. For example, in taste aversion learning, when one feels ill after ingestion of a certain flavour, this particular taste becomes associated with the internal malaise, and consequently an individual will reject any further consumption of food carrying this flavour or even smell independent of when the association has been acquired.

Thus we argue that even if we were to accept that single-trial associative learning might enable an organism to memorise what, where, and when of a unique event, this leads at best to semantic memory (knowledge of facts) that does not demand episodic recall, and remembering can rely on relative familiarity rather than recollection [54]. We know so far of no mammalian or avian study that proves otherwise.

### 3. Developmental models for pre-verbal children

Adult humans, with proficient language skills, can report on their memories and mental states, while infants cannot. Babies start without language, and from birth to year one, language comprehension (understanding of language) develops before language production with about a 5 month delay in between the two. Furthermore each of the four main components of language (i.e. phonology, semantics, grammar, and pragmatics) has its own developmental periods [73]. Since babies and toddlers understand more than they are able to say, the non-verbal caching and item-finding paradigm is an ideal task to study the trajectory of episodic memory development. Such tasks would also provide a comparative approach, bridging the gaps between studies of human episodic cognition and that of other animals.

#### 3.1. Event-based memories in toddlers

Growing evidence demonstrates shared course of development, possibly due to shared subserving brain areas, of episodic remembering, theory of mind and prospection, all of which emerge around the age of 4 years [e.g. [68,73–81]]. Russell and Thompson [82] utilised the food caching paradigm as a non-verbal technique for studying event-based memory in 2-year-old infants as possible precursors for episodic memories.

As outlined in detail above Clayton and Dickinson [18] investigated what the scrub-jays remembered about specific caching events in terms of keeping track of which caches had been recovered and which remained intact. The important idea of the experiment was that the tray which would have formed a stronger association with the preferred non-prefed (*different*) food, through caching and recovery, only contains the less preferred prefed (*same*) food at the time of the test and vice versa. Therefore, if the jays were solving the task through an associative strategy, they would search more in the tray containing the *same* food. On the other hand, jays using a mnemonic process should be able to successfully locate the *different* food in the appropriate tray. The jays showed

the latter behaviour after delays of both 4 h and 172 h. In short, the associative account cannot explain the scrub-jays' ability to accurately recover from intact sites containing their desired food caches, and to keep track of which caches they have already recovered previously.

Russell and Thompson [82] modified the above experiment to test children aged between 14 and 25 months by replacing caching and recovery of food with placement and removal of toys. In this study, an experimenter placed a toy in each of the two boxes while the child watched. One of the toys was immediately removed by a second experimenter. After a delay of 20 min or 24 h, depending on the assigned group, the child was told to go and find the toy. Only the oldest group (22–25 months) could find the toy more frequently than predicted by chance. In fact, performance by the youngest group (14–17 months) was significantly below chance in the 20-min delay group. Russell and Thompson suggest that these unsuccessful children were using an association strategy when trying to solve the task. The incorrect box had formed a stronger association with the toy because the children saw it interacting with the toy on two occasions, during placement and removal, while they saw the correct box with the toy on one occasion only, during placement. This explanation is consistent with the observation that children in the 24-h delay group of the same age was at chance level because the association would have weakened over the delay period. The results from the middle group (18–21 months) were also at chance under both delay lengths. Improved performance in the oldest group (22–25 months) implies that by around their second birthday, children abandon the incorrect associative strategy and switch to a mnemonic strategy. This is in parallel to the behaviour shown by the scrub-jays, who also seem to solve the task through non-associative means.

Although the experiment by Russell and Thompson [82] was not specifically designed as a test for episodic-like memory, it involves the ability to distinguish two different events, placement and removal, that occurred at different locations (*where* and possibly *what*). It also illustrates how the tasks used in comparative studies can be modified to test pre-verbal children. Apart from this study, which was directly inspired by the work on jays, a number of alternative approaches have been taken by developmental researchers to investigate episodic memory in children using methods with minimal reliance on verbal report. Some have overlapping elements with the episodic-like memory work.

#### 3.2. Deferred imitation

One popular method used to test children's memory is deferred imitation. In a typical experiment, children watch a model, usually an adult experimenter, perform particular actions to a target object. They are brought back to the same setting at a later time and are instructed to reproduce the previously observed actions. An example of this approach is demonstrated by Meltzoff [83] who showed that 14-month-old children imitate the action of turning on a light-box with their forehead. Because imitation of such an unnatural action is unlikely to be the result of simply learning the affordance of the object, these children were, possibly, recalling the modelled action. Evidence for deferred imitation of actions directed to target objects is observed in children as young as 6 months [84]. Six-week-old babies also show imitation of simple facial expressions, such as tongue protrusion and mouth opening [85].

It has been argued, however, that some actions may not require declarative memory when reproducing them, and if so this is problematic for tests of episodic memory given that episodic memory is part of the declarative system. Mandler and McDonough [86] mention two ways in which deferred imitation is possible using procedural memory. Firstly, subjects could develop an association between the object and the target behaviour through sensorimotor

learning. In this process, target behaviours are elicited automatically upon presentation of the object. Secondly, sight of the objects could act as priming for a cognitive set (object + action), in a similar mechanism to the word-completion tasks. One way to solve these problems is to involve sequences of actions. Thus, in addition to performing the right actions, the imitator needs to recall the correct order in which they had occurred. McDonough et al. [87] found that when given such a sequential task involving three actions (e.g. turning on a blow dryer, placing a balloon in the air stream, and tilting the dryer to create the Bernoulli effect), amnesic patients could not reproduce the actions any more than the inexperienced control group, indicating that the task involves declarative rather than procedural memory.

The type of a deferred imitation task also affects the age at which children can pass it. For example, Hayne et al. [88] found that of the two age groups (12-month and 18-month olds) that showed deferred imitation, only the older group was able to recall the demonstrated action sequence when the target object used during recall was different from that used during the demonstration. Therefore, children's memory becomes more flexible with age as they develop an ability to make use of generalised retrieval cues, whereas younger children can only show deferred imitation under limited settings.

Deferred imitation experiments are related to episodic-like memory in that sequential tasks also require a temporal element by testing memory for the relationship between each action ("what happened when?"). In addition, some studies of deferred imitation overlaps with those of episodic-like memory in investigating flexibility of the memory by testing whether children or animals can use information about the previous action or event and apply it under different conditions (e.g. when the target object changes, or when their food preference changes). What deferred imitation does not involve is the *where* component. However, note that the spatial element may still be playing a role during such a task, as suggested by Clayton and Russell [89]. This would be easily testable by modifying the task such that the actions are performed at different locations.

### 3.3. Source knowledge

Another approach taken by some researchers to study episodic memory in children involves two other forms of complex cognition, namely theory of mind and source knowledge. Perner argues that an understanding of how one's recollection of experiences can represent real past experiences is a critical pre-requisite for episodic memory [90]. In support for this claim, there is evidence that free recall scores of experienced events are related to performance on questions that tap into source knowledge [91,92,75]. For example, in a study by Perner and Ruffman [75], children were asked to study a set of pictures and later questioned what they were. Number of items correctly named under free recall positively correlated with their performance on separate source knowledge questions, including how-do-you-know (e.g. "How do you know the contents of a box? Did you see or were you told?"), know-guess (e.g. "Did you know or guess the answer?"), and when-learned (e.g. "Have you always known the answer or did you just learn it?") tests. Additional experiments have shown that these correlations only emerge with directly-experienced events, where children studied and placed the picture cards in a box, but not with indirectly-experienced events, where they were blindfolded during placement and were later informed what were printed on the cards [92]. Not all types of theory of mind tasks correlate with event recall, however. Both Naito [91] and Perner et al. [92] found no significant relationship between false-belief tasks and free recall. Therefore, introspective ability about self, in particular, seems to be the important component of event memory. This is consistent with Tulving's [68] emphasis on

the role of self-knowledge, or auto-noetic consciousness, in episodic memory.

Besides acting as a test for introspective abilities, source memory questions also examine a similar idea to that used in episodic-like memory tasks, namely that if the owner of episodic memory can re-experience a past event, he should be able to extract some basic information, which could be but not necessary what, where, and when, about the event that were available to the author of the memory at the time the event occurred.

It should be noted that all of the source memory questions mentioned above require a verbal response from the subject and so strictly-speaking they are not non-verbal tasks, and therefore cannot be assessed in infants or non-linguistic animals. However, such questions would be easy to convert into non-verbal tasks. For example, Clayton and Russell [89] suggest such a non-verbal task that requires subjects to report on the modality they used to sense the stimuli by asking a question equivalent to "did you see it or hear it?"

### 3.4. Conclusion for development models

Studying episodic-like memory from a developmental perspective has important implications for both developmental and comparative research, particularly when considering the claims that episodic memory emerges at or soon after the age of four [e.g. [74,75]]. Studies using non-verbal tasks can address the question of whether children under the age of four are incapable of episodic recall or whether they simply cannot share their episodic memories in the absence of language. Furthermore, the relationship between episodic-like memory and episodic memory can be inferred by studying the relative timing at which such memories develops in young children. If both types of memories emerge at around the same age, this would suggest that the two are highly related in nature and therefore episodic-like memory tasks may be valid non-verbal tests for episodic memory. On the other hand, if children can pass tasks of episodic-like memory before the age of four, then this would suggest either that episodic-like memory may be a necessary, but certainly not a sufficient, component of episodic memory or that the tasks are showing episodic memory ability in children through non-verbal means. Thus, future studies on episodic-like memory in children would shed light on whether or not episodic-like memory really reflects the behavioural criteria for episodic memory, stripped of its phenomenology and thus empirically tractable in non-verbal animals and young children, or whether it is fundamentally different from episodic recall.

## 4. Birds as biomedical model for studying the neural basis of episodic memory

When combining recent advances in avian neuroscience with a neuro-ethological approach [93] as outlined for food-caching species the study of birds can critically facilitate insights into brain function and underlying development and maintenance of cognition in general and episodic memory in particular. In the remaining section we shall – only very briefly – exemplify the new understanding of the avian brain, and sketch selected similarities between the avian hippocampus and the human hippocampal formation as functional homologues in processing and retaining episodic memory and spatial information [for reviews see [94,93]].

### 4.1. Revision of the of the bird brain nomenclature

There is still the assumption that the laminar organisation of the mammalian brain is a structural requirement for enhanced cognitive abilities [95], and that the neocortex is obligate for higher cognitive and executive functions. This evolution-based model

of brain organisation [96], that dominated throughout the 20th century, goes back to the German Ludwig Edinger [97] and fellow comparative neuro-biologists and neuro-anatomists [98–100], who described the vertebrate brain evolution as a progressive and unilinear development from fish to mammals [101]. Since bird-brains lack both a laminar organisation and a neocortex, they were not expected to solve cognitively highly complex tasks. However, by now a wealth of behavioural studies has well established that birds, corvids in particular, are en par with primates in cognitive tasks like object permanence, tool use and tool manufacturing, causal reasoning, theory of mind, flexibility, prospection and most importantly episodic memory [see above; for review see also [42]]. Thus the nuclear avian pallium supports comparable cognitive abilities, and for some species more advanced capacities, than the laminar mammalian brain.

The Avian Brain Nomenclature Consortium [101–103] initiated a paradigm shift to eliminate these misconceptions [101]. After about 6 years of online discussions on the Avian Brain Nomenclature Exchange website and several meetings of experts, the Consortium presented a new terminology of the bird brain that reflects the current understanding of the avian brain organisation and its homologies with mammals [101–103], i.e. the brains of distantly related species tend to be derived from the same embryonic tissue found in the common ancestor.

#### 4.2. Hippocampus

In general all forms of declarative long-term memories depend on the hippocampal formation [e.g. [70,104]]; since its unique anatomy allows for a rapid formation of crossmodal associations the hippocampal formation plays a crucial role in encoding personally experienced events and their spatial–temporal context [for overview see [105]]; consequently bilateral damages have been reported to be associated with remarkable deficits in anterograde amnesia for personally experienced events [106]. However, despite intense research the function of the hippocampus is still far from understood. Nevertheless, with the new view on the avian brain and the use of validated ethological paradigms like outlined for scrub-jays and children, we have powerful tools to study how the hippocampus is involved in declarative (semantic and episodic) memory and what distinguishes this type of memory from non-hippocampal memory.

Human brains show lateralization in spatial cognition as do the brains of homing pigeons and chicks [for review on lateralization see [107]]. For example during lesion studies the right hippocampus was preferentially involved in the representation of global environmental space, whereas only the left hippocampus has been sensitive to local landmarks for navigation [108]. Although there are few indications for lateralization in mammals [e.g. [109]], the lateralization of the avian hippocampus seems to be convincingly similar to humans [for review see [107]].

Furthermore, in humans and in birds (see also e.g. rats: [110], fish: [111], snakes: [112]) the hippocampus enlarges with experience when spatial memory plays a crucial role in it. To give only one human example, licensed London taxi drivers are required to undergo extensive training for about 2 years and to pass stringent police examinations before being licensed to operate. When comparing brains of these taxi drivers to age-matched non-taxi drivers, significant differences in gray matter volume were only found in the hippocampus [113]. Patient TT, a licensed London taxi driver who had sustained bilateral hippocampal damage, revealed some more details on the function of the hippocampal formation, i.e. that it was not required for general orientation in the city, knowledge of landmarks, or their spatial relationships, but necessary for facilitating navigation in places learned long ago, particularly where complex large-scale spaces are concerned, and success-

ful navigation required access to detailed spatial representations [114].

As expected the hippocampus of food hoarding species is larger than compared to close relatives that do not store food [for review see [115]]; the advantage of an enlarged hippocampus to the food-storing species lays in an resulting increased memory persistence [116]. Young birds that have been prevented from food hoarding or experience of spatial memory intensive tasks also have smaller hippocampi compared to same-aged food hoarding conspecifics [117–120]. Lesion studies demonstrated that hippocampal impairment disables cache retrievals [121,122] and retrieval after 3 h but not after only 15 min [123].

Particularly interesting are studies on the hippocampus of Western scrub-jays. Since cognitive traits and their underlying neural substrates are shaped by natural selection [124], the ecological rational predicted that Western scrub-jays (*Aphelocoma californica*), classified as only moderate food cachers [125] compared to the more specialized Clark's nutcracker, should have a comparatively smaller hippocampus. Pravosudov and de Kort [126], however, reported that the relative hippocampal volume of the scrub-jays was among the largest of all eight investigated corvid species included in their paper. This relatively large hippocampus compared to other corvids does not come as a real surprise, since Western scrub-jays have been shown not only to engage in food storing per se, but in episodic-like memory as well as future planning, and other cognitively highly advanced tasks (e.g. [8,39,44,127,128]).

Finally the hippocampus is most vulnerable during ontogeny in both humans and birds. Neuropsychological and magnetic resonance imaging methods disclosed strikingly similar patterns in prematurely born infants [129]. A study of adolescents born preterm compared to full-term demonstrated that the preterm group had significantly smaller hippocampal volumes bilaterally, despite equivalent head size, and suffered specific deficits in certain aspects of everyday memories and learning abilities.

Similarly, birds nutritionally deprived early in ontogeny developed reduced hippocampal volume due to fewer hippocampal neurons, and also performed worse on cache retrieval tasks as well as on a spatial version of an associative learning task. On the other hand performance of scrub-jays in a control group tested on two colour versions of an associative learning task, which are thought to be hippocampus-independent [122,130], did not deteriorate. Actually the differences in hippocampus structure and spatial memory performance between nutritionally deprived and control scrub-jays persisted well after the birds gained nutritional independence and were offered ad libitum food [131].

#### 4.3. Conclusions about the avian brain model

Our scant comparison is by far not exhaustive, but hopefully it provides a flavour of the functional as well as some mechanistic similarities between the avian and mammalian hippocampus. Even more intriguing similarities have been established between the caudolateral nidopallium (NCL) in the avian telencephalon (fore-brain) and the mammalian dorsolateral prefrontal cortex (PFC) in cognitive (“executive”) function as well as connectivity, neurochemistry and physiology [for detailed reviews see [132–135]]. In any way, we see birds as a highly promising biomedical model to study episodic-like memory and episodic recall with the respective underlying brain areas from an evolutionary, mechanistic, development, functional and comparative perspective to pinpoint the selective forces that drive mental system towards higher cognitive functions, and the neural machinery necessary for these cognitive abilities, to understand the benefits and vulnerabilities of these systems during ontogeny in both birds and men.

## 5. Final remarks

Western scrub-jays have been shown to be a promising species for investigating complex cognitive capacities. The focus of this review paper was on episodic-like memory, and we have summarised numerous studies that establish beyond doubts that scrub-jays are capable of episodic-like memory. In the 10 years since the first publication by Clayton and co-workers a few other bird species have been shown to be capable of a what-where-when memory (the content criterion), but these studies are only in their infancy in that most of them have not tested the other criteria namely structure and flexibility and none have tested all three criteria.

While studies of episodic recall in adults are mainly based on verbal reports, babies and toddlers are just in the process of language acquisition. Also pre-school children have not acquired full verbal skills to adequately share their knowledge and experiences. Non-verbal animal tasks like the caching and finding paradigm that have been established to test episodic memory can reliably test young children who have not yet developed sufficient linguistic proficiency and, as such, we can study the ontogenetic trajectory from the first traces of components of episodic memory to fully developed episodic recall.

Finally adequate animal models enable us to study the neurobiological mechanisms of episodic memory. Despite this advantage, birds have been used rather rarely as a model system for studying higher cognitive function. We hope that our brief overview of the remarkable amount of convergence in human and avian brain regions such as the hippocampus illuminates the potential of avian model systems for cognitive neuroscience, particularly when the behavioural components are so well characterised as outlined for episodic memory.

## References

- [1] Tulving E. Episodic and semantic memory. In: Tulving E, Donaldson W, editors. Organisation of memory. New York: Academic Press; 1972. p. 381–403.
- [2] Tulving E. Origin of autonoesis in episodic memory. In: Roediger HL, editor. The nature of remembering: essays in honor of Robert G. Crowder. Washington, DC: American Psychological Association; 2001. p. 17–34.
- [3] James W. The principles of psychology. Dover Publications Inc. 1890 (December 1957).
- [4] Clayton NS, Dickinson A. Episodic-like memory during cache recovery by scrub jays. *Nature* 1998;395:272–4.
- [5] De Vito LM, Eichenbaum H. Distinct contributions of the hippocampus and medial prefrontal cortex to the “what-where-when” components of episodic-like memory in mice. *Behav Brain Res*, this issue.
- [6] Easton A, Eacott MJ. Recollection of episodic memory within the medial temporal lobe: behavioural dissociations from other types of memory. *Behav Brain Res*, this issue.
- [7] Crystal JD. Episodic-like memory in animals. *Behav Brain Res*, this issue.
- [8] Salwiczek LH, Dickinson A, Clayton NS. What do animals remember about their past? In: Menzel R, editor. Cognitive Psychology of Memory. Vol. [1] of Learning and memory: a comprehensive reference, 4 Volumes. Byrnes J, editor. Oxford: Elsevier; 2008, pp. 441–459.
- [9] Clayton NS, Salwiczek LH, Dickinson A. Episodic memory. *Curr Biol* 2007;17:R189–91.
- [10] Zinkivskay A, Nazir F, Smulders TV. What-where-when memory in magpies (*Pica pica*). *Anim Cog* 2009;12:119–25.
- [11] Feeney MC, Roberts WA, Sherry DF. Memory for what, where, and when in the black-capped chickadee (*Poecile atricapillus*). *Anim Cog* 2009;12:667–777.
- [12] Skov-Rackette SI, Miller NY, Shettleworth SJ. What-where-when memory in pigeons. *J Exp Psychol Anim B* 2006;32:345–58.
- [13] Zentall TR, Clement TS, Bhat RS, Allen J. Episodic-like memory in pigeons. *Psychon B Rev* 2001;8:685–90.
- [14] Zentall TR, Singer RA, Stagner JP. Episodic-like memory: pigeons can report location pecked when unexpectedly asked. *Behav Process* 2008;79:93–8.
- [15] Tulving E. Concepts of memory. In: Tulving E, Craik FIM, editors. The Oxford handbook of memory. Oxford: Oxford University Press; 2000. p. 33–43.
- [16] Crowder RG. Remembering experiences and the experience of remembering. *Behav Brain Sci* 1986;9:566–7.
- [17] Curry RK, Peterson AT, Langen TA. Western Scrub-Jay. In: Poole A, Gill F, editors. The birds of north America, vol. 712. Philadelphia: The Birds of North America, Inc; 2002. p. 1–35.
- [18] Clayton NS, Dickinson A. Memory for the content of caches by scrub jays (*Aphelocoma coerulescens*). *J Exp Psychol Anim B* 1999;25:1–10.
- [19] Dickinson A, Balleine B. Motivational control of goal directed action. *Anim Learn Behav* 1994;22:1–18.
- [20] Dickinson A, Balleine B. Motivational control of instrumental action. *Curr Dir Psychol Sci* 1995;4:162–7.
- [21] Tulving E. Elements of episodic memory. Oxford: Clarendon Press; 1983.
- [22] de Kort SR, Dickinson A, Clayton NS. Retrospective cognition by food-caching western scrub-jays. *Learn Motiv* 2005;36:159–76.
- [23] Clayton NS, Dickinson A. Scrub jays (*Aphelocoma coerulescens*) remember the relative time of caching as well as the location and content of their caches. *J Comp Psychol* 1999;113:403–16.
- [24] Clayton NS, Yu KS, Dickinson A. Scrub jays (*Aphelocoma coerulescens*) form integrated memories of the multiple features of caching episodes. *J Exp Psychol Anim B* 2001;27:17–29.
- [25] Roper KL, Zentall TR. Directed forgetting in animals. *Psychol Bull* 1993;113:513–32.
- [26] Biebach H, Gordjin M, Krebs JR. Time-and-place learning by garden warbler (*Sylvia borin*). *Anim Behav* 1989;37:353–60.
- [27] Aggleton JP, Brown MW. Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behav Brain Sci* 1999;22:425–89.
- [28] Aggleton JP, Brown MW. Interleaving brain systems for episodic and recognition memory. *TICS* 2006;10:455–63.
- [29] Wheeler MA. Episodic memory and autothetic awareness. In: Tulving E, Craik FIM, editors. The Oxford handbook of memory. Oxford: Oxford University Press; 2000. p. 597–608.
- [30] Mandler G. Recognising: the judgement of previous experience. *Psychol Rev* 1980;87:252–71.
- [31] Jacoby LL, Dallas M. On the relationship between autobiographical memory and perceptual learning. *J Exp Psychol Gen* 1981;3:306–40.
- [32] Kelley CM, Jacoby LL. Recollection and familiarity. In: Tulving E, Craik FIM, editors. The Oxford handbook of memory. Oxford: Oxford University Press; 2000. p. 215–28.
- [33] Yonelinas AP. Components of episodic memory: the contribution of recollection and familiarity. *Phil Trans Royal Soc Lond (B)* 2001;356:1363–74.
- [34] Yonelinas AP, Kroll NEA, Quamme JR, Lazzara MM, Sauve M-J, Widaman KF, et al. Effects of extensive temporal lobe damage or mild hypoxia on recollection and familiarity. *Nat Neurosci* 2002;5:1236–41.
- [35] Yonelinas AP, Otten LJ, Shaw KN, Rugg MD. Separating the brain regions involved in recollection and familiarity in recognition memory. *J Neurosci* 2005;25:3002–8.
- [36] Fortin NJ, Wright SP, Eichenbaum H. Recollection-like memory retrieval in rats is dependent on the hippocampus. *Nature* 2004;431:188–91.
- [37] Clayton NS, Bussey TJ, Dickinson A. Can animals recall the past and plan for the future? *Nat Rev Neurosci* 2003;4:685–91.
- [38] Clayton NS, Griffiths DP, Emery NJ, Dickinson A. Elements of episodic-like memory in animals. *Phil Trans Royal Soc Lond (B)* 2001;356:1483–91.
- [39] Clayton NS, Dally JM, Emery NJ. Social cognition by food-caching corvids. The Western scrub-jay as a natural psychologist. *Phil Trans R Soc Lond (B)* 2007;362:507–22.
- [40] Emery NJ, Dally JM, Clayton NS. Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Anim Cog* 2004;7:37–43.
- [41] Emery NJ, Clayton NS. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* 2001;414:443–6.
- [42] Emery NJ, Clayton NS. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* 2004;306:1903–7.
- [43] Dally JM, Emery NJ, Clayton NS. The social suppression of caching in Western scrub-jays (*Aphelocoma californica*). *Behaviour* 2005;142:961–77.
- [44] Dally JM, Emery NJ, Clayton NS. Food-caching western scrub-jays keep track of who was watching when. *Science* 2006;312:1662–5.
- [45] Stulp G, Emery NJ, Verhulst S, Clayton NS. Western scrub-jays conceal auditory information when competitors can hear but cannot see. *Biol Lett* 2009;5:583–5.
- [46] Tulving E, Markowitsch HJ. Episodic and declarative memory: role of the hippocampus. *Hippocampus* 1998;8:198–204.
- [47] Clayton NS, Yu KS, Dickinson A. Interacting cache memories: evidence for flexible memory use by western scrub-jays (*Aphelocoma californica*). *J Exp Psychol Anim B* 2003;29:14–22.
- [48] Birkhead TR. The magpies: the ecology and behaviour of black-billed and yellow magpies. London: Poyser; 1991.
- [49] Shettleworth SJ. Spatial memory in food-storing birds. *Phil Trans R Soc Lond (B)* 1990;329:143–52.
- [50] Crystal JD, Shettleworth SJ. Spatial list learning in black-capped chickadees. *Anim Learn Behav* 1994;22:77–83.
- [51] Hitchcock CL, Sherry DF. Cache pilfering and its prevention in pairs of black-capped chickadees. *J Av Biol* 1995;26:187–92.
- [52] Blechman AD. Pigeons: the fascinating saga of the world's most revered and reviled bird. New York: Grove Press; 2006.
- [53] Singer RA, Zentall TR. Pigeons learn to answer the question “where did you just peck?” and can report peck location when unexpectedly asked. *Learn Behav* 2007;35:184–9.
- [54] Griffiths D, Dickinson A, Clayton NS. Episodic memory: what can animals remember about their past? *TICS* 1999;3:74–80.
- [55] de Kort SR, Clayton NS. An evolutionary perspective on caching by corvids. *Proc R Soc B* 2006;273:417–23.

- [56] Vander Wall SB. Food hoarding in animals. London: University of Chicago Press; 1990.
- [57] Salwiczek LH, Wickler W. Birdsong: an evolutionary parallel to human language. *Semiotica* 2004;151:163–82.
- [58] Baddeley AD. The episodic buffer: a new component of working memory? *TICS* 2000;4:417–23.
- [59] Rudner M, Rönnerberg J. The role of the episodic buffer in working memory for language processing. *Cognitive Process* 2008;9:19–28.
- [60] Baddeley AD, Wilson BA. Prose recall and amnesia: implications for the structure of working memory. *Neuropsychologia* 2002;40:1737–43.
- [61] Baddeley AD. Working memory. *Curr Biol* 2010;20:R136–40.
- [62] Bartlett FC. Remembering. Cambridge, UK: Cambridge University Press; 1932.
- [63] Schacter DL, Addis DR. The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Phil Trans R Soc B* 2007;362:773–86.
- [64] Eacott MJ, Easton A, Zinkivskay A. Recollection in an episodic-like memory task in the rat. *Learning Memory* 2005;12:221–3.
- [65] Eacott MJ, Norman G. Integrated memory for object, place, and context in rats: a possible model of episodic-like memory? *J Neurosci* 2004;24:1948–53.
- [66] Eichenbaum H. The hippocampus and episodic memory: cognitive and neural mechanisms. *Neuropsychopharmacology* 2005;30(Suppl. 1):1–37.
- [67] Sarter M. Animal cognition: defining the issues. *Neurosci Biobehav Rev* 2004;28:645–50.
- [68] Tulving E. Episodic memory and autoevidence: uniquely human? In: Terrace HS, Metcalfe J, editors. *The missing link in cognition: self-knowing consciousness in man and animals*. New York: Oxford University Press; 2005. p. 3–56.
- [69] Pearce JM. Animal learning and cognition. 3rd ed. Psychology Press; 2008.
- [70] Morris RGM. Episodic-like memory in animals: psychological criteria, neural mechanisms and the value of episodic-like tasks to investigate animal models of neurodegenerative disease. *Phil Trans R Soc Lond (B)* 2001;356:1453–65.
- [71] Runyan JD, Dash PK. Inhibition of hippocampal protein synthesis following recall disrupts expression of episodic-like memory in trace conditioning. *Hippocampus* 2005;15:333–9.
- [72] Dumas S, Halley H, Lassalle J-M. Disruption of hippocampal CA3 network: effects on episodic-like memory processing in C57BL/6J mice. *Eur J Neurosci* 2004;20:597–600.
- [73] Ruben RJ. A time frame of critical/sensitive periods of language development. *Acta Oto-Laryngologica* 1997;117(2):202–5.
- [74] Nelson K. Emergence of autobiographical memory at age 4. *Hum Dev* 1992;35:172–7.
- [75] Perner J, Ruffman T. Episodic memory and autoevidence: developmental evidence and a theory of childhood amnesia. *J Exp Child Psychol* 1995;59:516–48.
- [76] Povinelli DJ, Landry AM, Theall LA, Clark BR, Castille CM. Development of young children's understanding that the recent past is causally bound to the present. *Dev Psychol* 1999;35:1426–39.
- [77] Povinelli DJ, Simon BB. Young children's understanding of briefly versus extremely delayed images of the self: emergence of the autobiographical stance. *Dev Psychol* 1998;34:188–94.
- [78] Atance CM, O'Neill DK. The emergence of episodic future thinking in humans. *Learn Motiv* 2005;36:126–44.
- [79] Prencipe A, Zelazo PD. Development of affective decision making for self and other. *Psychol Sci* 2005;16:501–5.
- [80] Russell J, Alexis D, Clayton NS. Episodic future thinking in 3- to 5-year-old children: the ability to think of what will be needed from a different point of view. *Cognition* 2010;114:56–71.
- [81] Clayton NS, Russell J. Looking for episodic cognition in animals and young children: prospects for a new minimalism. *Neuropsychologia* 2009;47:2330–40.
- [82] Russell J, Thompson D. Memory development in the second year: for events or locations? *Cognition* 2003;87:B97–105.
- [83] Meltzoff AN. Infant imitation after a one-week delay: long-term memory for novel acts and multiple stimuli. *Dev Psychol* 1988;24:470–6.
- [84] Collie R, Hayne H. Deferred imitation by 6- and 9-month-old infants: more evidence for declarative memory. *Dev Psychobiol* 1999;35:83–90.
- [85] Meltzoff AN, Moore MK. Imitation, memory, and the representation of persons. *Infant Behav Dev* 1994;17:83–99.
- [86] Mandler JM, McDonough L. Long-term recall of event sequences in infancy. *J Exp Child Psychol* 1995;59:457–74.
- [87] McDonough L, Mandler JM, McKee RD, Squire LR. The deferred imitation task as a nonverbal measure of declarative memory. *PNAS USA* 1995;92:7580–4.
- [88] Hayne H, Boniface J, Barr R. The development of declarative memory in human infants: age-related changes in deferred imitation. *Behav Neurosci* 2000;114:77–83.
- [89] Clayton NS, Russell J. Looking for episodic memory in animals and young children: prospects for a new minimalism. *Neuropsychologia* 2009;47:2330–40.
- [90] Perner J, Kloos D, Stottinger E. Introspection & remembering. *Synthese* 2007;159:253–70.
- [91] Naito M. The relationship between theory of mind and episodic memory: evidence for the development of autoevidence consciousness. *J Exp Child Psychol* 2003;85:312–36.
- [92] Perner J, Kloos D, Gornik E. Episodic memory development: theory of mind is part of re-experiencing experienced events. *Infant Child Dev* 2007;16:471–90.
- [93] Suzuki WA, Clayton NS. The hippocampus and memory: a comparative and ethological perspective. *Curr Opin Neurobiol* 2000;10:768–73.
- [94] Colombo M, Broadbent N. Is the avian hippocampus a functional homologue of the mammalian hippocampus? *Neurosci Biobehav Rev* 2000;24:465–84.
- [95] Montagnini A, Treves A. The evolution of mammalian cortex, from lamination to arealization. *Brain Res Bull* 2003;60:387–93.
- [96] Ariëns Kappers CU, Huber CG, Crosby EC. Comparative anatomy of the nervous system of vertebrates, including man. New York: Hafner; 1936.
- [97] Stahnisch FW, Ludwig Edinger (1855–1918). *J Neurol* 2008;255:147–8.
- [98] Edinger L. Untersuchungen zur Vergleichenden Anatomie des Gehirns. Vol. 1–5. Moritz Diesterweg: Frankfurt/Main. 1888–1903.
- [99] Edinger L. Vorlesungen über den Bau der nervösen Zentralorgane des Menschen und der Tiere: fuer Aezte und Studierende. Nabu Press; 2010 (reprint; paperback).
- [100] Edinger, L. The relations of comparative anatomy to comparative psychology (1908). Kessinger Publishing, LLC; 2009 (reprint, paperback).
- [101] Jarvis ED, Güntürkün O, Bruce L, Csillag A, Karten H, Kuenzel W, et al. Avian brains and a new understanding of vertebrate brain evolution. *Nat Rev Neurosci* 2005;6:151–9.
- [102] Reiner A, Perkel DJ, Mello CV, Jarvis ED. Songbirds and the revised avian brain nomenclature. *Ann New York Acad Sci* 2004;1016:77–108.
- [103] Reiner A, Perkel DJ, Bruce LL, Butler AB, Csillag A, Kuenzel W, et al. The Avian Brain Nomenclature Forum: a new century in comparative neuroanatomy. *J Comp Neurol* 2004;473:E1–6.
- [104] Squire LR, Zola-Morgan S. The medial temporal lobe memory system. *Science* 1991;253:1380–6.
- [105] Hartley T, Bird CM, Chan D, Cipolotti L, Husain M, Vargha-Khadem F, et al. The hippocampus is required for short-term topographical memory in humans. *Hippocampus* 2007;17:34–48.
- [106] Spiers HJ, Burgess N, Hartley T, Vargha-Khadem F, O'Keefe J. Bilateral hippocampal pathology impairs topographical and episodic memory but not visual pattern matching. *Hippocampus* 2001;11:715–25.
- [107] Bingman VP, Gagliardo A. Of birds and men: convergent evolution in hippocampal lateralization and spatial cognition. *Cortex* 2006;42:99–100.
- [108] Kahn MC, Bingham VP. Lateralization of spatial learning in the avian hippocampal formation. *Behav Neurosci* 2004;118:333–44.
- [109] Kawakami R, Shinohara Y, Sugiyama H, Shigemoto R, Ito I. Asymmetrical allocation of NMDA receptor epsilon2 subunits in hippocampal circuitry. *Science* 2003;300:990–4.
- [110] Nilsson M, Perfilieva E, Johansson U, Orwar O, Eriksson PS. Enriched environment increases neurogenesis in the adult rat dentate gyrus and improves spatial memory. *J Neurobiol* 1998;39:569–78.
- [111] Salvanes AGV, Moberg O, Braithwaite VA. Effects of early experience on group behaviour in fish. *Anim Behav* 2007;74:805–11.
- [112] Roth ED, Lutterschmidt WL, Wilson DA. Relative medial and dorsal cortex volume in relation to sex differences in spatial ecology of a snake population. *Brain Behav Evol* 2006;67:103–10.
- [113] Maguire EA, Gadian DG, Johnsrude IS, Good CD, Ashburner J, Frackowiak RSJ, et al. Navigation-related structural change in the hippocampi of taxi drivers. *PNAS USA* 2000;97:4398–403.
- [114] Maguire EA, Nannery R, Spiers HJ. Navigation around London by a taxi driver with bilateral hippocampal lesions. *Brain* 2006;129:2894–907.
- [115] Smulders TV. A multi-disciplinary approach to understanding hippocampal function in food-hoarding birds. *Rev Neurosci* 2006;17:53–69.
- [116] Biegler R, McGregor A, Krebs JR, Healy SD. A larger hippocampus is associated with longer-lasting spatial memory. *PNAS USA* 2001;98:6941–4.
- [117] Clayton NS, Krebs JR. Hippocampal growth and attrition in birds affected by experience. *PNAS USA* 1994;91:7410–4.
- [118] Clayton NS. Comparative studies of food-storing, memory, and the hippocampal formation in Parids. *Hippocampus* 1995;5:499–510.
- [119] Clayton NS. Development of memory and the hippocampus: comparison of food-storing and nonstoring birds on a one-trial associative memory task. *J Neurosci* 1995;15:2796–807.
- [120] Clayton NS. The neuroethological development of food-storing memory: a case of use it, or lose it. *Behav Brain Res* 1995;70:95–102.
- [121] Krishinskaya NL. Some complex forms of feeding behaviour of nutcracker *Nucifraga caryocatactes*, after removal of old cortex. *Zh Evol Biokim Fiziol* 1966;2:563–8.
- [122] Sherry DF, Vaccarino AL. Hippocampus and memory for food caches in black-capped chickadees. *Behav Neurosci* 1989;103:308–18.
- [123] Shiflett MW, Smulders TV, Benedict L, DeVoogd TJ. Reversible inactivation of the hippocampal formation in food-storing black-capped chickadees (*Parus atricapillus*). *Hippocampus* 2003;13:437–44.
- [124] Healy SD, de Kort SR, Clayton NS. The hippocampus, spatial memory and food hoarding: a puzzle revisited. *TREE* 2005;20:17–22.
- [125] Balda RP, Kamil AC. The ecology and evolution of spatial memory in corvids of the southwestern USA: the perplexing pinyon jay. In: Balda RP, Pepperberg IM, Kamil AC, editors. *Animal cognition in nature*. London: Academic Press; 1998. p. 29–64.
- [126] Pravosudov VV, de Kort SR. Is the Western scrub-jay (*Aphelocoma californica*) really an underdog among food-caching corvids when it comes to hippocampal volume and food caching propensity? *Brain Behav Ev* 2006;67:1–9.
- [127] Raby CR, Alexis DM, Dickinson A, Clayton NS. Planning for the future by Western scrub-jays. *Nature* 2007;445:919–21.

- [128] Raby CR, Clayton NS. Prospective cognition in animals. *Behav Proc* 2009;80:314–24.
- [129] Isaacs EB, Lucas A, Chong WK, Wood SJ, Johnson CL, Marshall C, et al. Hippocampal volume and everyday memory in children of very low birth weight. *Pediatr Res* 2000;47:713–20.
- [130] Hampton RR, Shettleworth SJ. Hippocampus and memory in a food-storing and in a nonstoring bird species. *Behav Neurosci* 1996;110:946–64.
- [131] Pravosudov VV, Kitaysky AS, Omanska A. The relationship between migratory behaviour, memory and the hippocampus: an intraspecific comparison. *Proc R Soc B Sci* 2006;273:2641–9.
- [132] Reiner A. Is prefrontal cortex found only in mammals? *Trends Neurosci* 1986;9:298–300.
- [133] Güntürkün O. Avian and mammalian “prefrontal cortices”: Limited degrees of freedom in the evolution of the neural mechanisms of goal-state maintenance. *Brain Res Bull* 2005;66:311–6.
- [134] Güntürkün O. The avian ‘prefrontal cortex’ and cognition. *Curr Opin Neurobiol* 2005;15:686–93.
- [135] Kirsch JA, Güntürkün O, Rose J. Insight without cortex: lessons from the avian brain. *Conscious Cog* 2008;17:475–83.