


## ARTICLE OPEN ACCESS

# Episodic Memory in Animals

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## ABSTRACT

Do animals have episodic memory—the kind of memory which gives us rich details about particular past events—or is this uniquely human? This might look like an empirical question, but is attracting increasing philosophical attention. We review relevant behavioural evidence, as well as drawing attention to neuroscientific and computational evidence which has been less discussed in philosophy. Next, we distinguish and evaluate reasons for scepticism about episodic memory in animals. In the process, we articulate three pressing philosophical issues underlying these sceptical arguments, which should be the focus of future work. The Problem of Interspecific Variation asks which differences between humans and animal memory mean that an animal has a variant of episodic memory, and which mean that it has a different kind of memory altogether. The Problem of Functional Variation asks how we should conceptualise the functions of episodic memory and other capacities across species and across evolutionary time. Finally, the Problem of Alternatives asks what, besides episodic memory, might explain the evidence—and how we should evaluate competing explanations.

## 1 | Introduction

You run into an old friend: someone you have not seen in years. Their face evokes a flood of memories. Specifically, it evokes *episodic* memories: rich, detailed memories of specific past events. You do not simply have a vague sense that this person is familiar or recall biographical details about them; you call to mind specific times you and your friend have spent together.

Chimpanzees and bonobos show more interest in photographs of familiar apes than unfamiliar ones, even when they have not seen them in 25 years (Lewis et al. 2023). Bonobos respond more intently to recordings of familiar bonobos than unfamiliar ones, even if they have been separated for 5 years (Keenan et al. 2016). Elephants recognise their keepers even after 13 years apart (Kränzlin et al. 2024). Chimpanzees and Mexican jays

remember solutions to complex tasks they have not faced in years (Jo et al. 2023; Vale et al. 2016).

How alike are these cases? Do these animals experience *episodic memories*? It is tempting to think so, but surprisingly difficult to demonstrate conclusively. Behaviour suggestive of episodic memory is often consistent with other explanations. For example, the apes' behaviour might be explained by a feeling of recognition without their recalling any specific interactions with that individual. Indeed, it is disputed whether *any* non-human animals<sup>1</sup> have episodic memories; many researchers only ascribe 'episodic-like' memory.<sup>2</sup> Some even claim that animals are 'cognitively stuck in time', with no memory of past events (Hoerl and McCormack 2019; Roberts 2002; Suddendorf et al. 2022).

The lack of consensus about episodic memory in animals reflects both limitations in our empirical evidence and

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philosophical issues. These include questions that have occupied the existing philosophical literature: whether behavioural evidence establishes that animals' memories resemble humans' in specific respects, especially phenomenologically. But underlying these questions are deeper philosophical issues which are only beginning to be adequately addressed. We articulate three such philosophical issues. The Problem of Interspecific Variation asks which differences between humans and animals imply that an animal has a variant of episodic memory, and which mean that it has a different kind of memory altogether. The Problem of Functional Variation asks how we should conceptualise functions of episodic memory. Finally, the Problem of Alternatives asks what, besides episodic memory, might explain the evidence—and how we should evaluate competing explanations. Episodic memory is not the only capacity that raises these problems: similar issues arise when we ask whether nonhuman animals—and other nonhuman agents, such as AI systems—share other cognitive capacities with us, including empathy and insightful problem solving (see Boyle 2024). As such, the question of episodic memory in animals can be viewed as a case study which can inform our understanding of nonhuman minds more generally. Resolving these problems in the case of episodic memory would have broad implications for philosophy of science, philosophy of mind, animal ethics, and the sciences of animal minds.

We begin by showing why it matters whether animals have episodic memory (Section 2). Next, we survey several lines of evidence favouring episodic memory in animals, including neurological and computational evidence which is less frequently discussed in philosophy (Section 3). We then distinguish and evaluate four sceptical arguments, highlighting the deeper philosophical questions they raise (Section 4), before turning to the question of what animals might have if not episodic memory (Section 5). Section 6 concludes.

## 2 | Why It Matters

Which species have episodic memory is more than a matter of curiosity. Episodic memory seems central to many important human characteristics, including guilt, nostalgia, and our sense of self. Our relationships are built on memories of key events such as those prompted by familiar faces—the time we met, that holiday we took, the promises we made. We rely on episodic memory for everyday tasks, such as locating our keys.<sup>3</sup> Given its centrality to human cognition, whether animals have episodic memory will deeply shape their minds. This may be ethically significant. It will shape what animals' relationships feel like to them, the kinds of emotions they can have, and the ways their past positive and negative experiences inform their current experience. It might affect their ability to set momentary joys or sorrows in a broader context, and to continue to derive pleasure or pain from past events whether through fond reminiscence, regret, or traumatic flashback. Some traditions also emphasise connections between personal identity, self-understanding, pursuing long-term projects, and episodic memory. If episodic memory is required for these other capacities, this might imply, for example, that painless death is not harmful to animals lacking episodic memory.<sup>4</sup>

Discovering the distribution of episodic memory across the tree of life is also key to using model organisms to understand human memory: such research depends on the underlying mechanisms being relevantly similar (Kaplan 2017). Using rodents to develop dementia treatments, for example (Drummond and Wisniewski 2017), depends on those treatments having similar effects on rodents and humans (Malanowski 2016). Optogenetics research studying memory traces in mice (e.g., Park et al. 2022; Ramirez et al. 2013), much discussed in recent philosophy (Najenson 2021; Robins 2016, 2018), only sheds light on human episodic memory if the memory traces in question sufficiently resemble episodic ones.<sup>5</sup> Reflecting on the animal evidence might also shed light on episodic memory's evolutionary history (Section 4) and undermine standard typologies of human memory (see [Section 5]).

## 3 | The Evidence

This section reviews evidence suggestive of episodic memory in animals. Section 4 considers countervailing considerations.

### 3.1 | Behavioural

Clayton and Dickinson (1998) introduced the most prominent approach to studying episodic-like memory in animals: testing for integrated representations of *What* happened, *Where*, and *When*. Scrub jays cache food, hiding items such as nuts and seeds. By manipulating which caches their subjects were able to access at different times, Clayton and Dickinson showed that scrub jays' retrieval of food items is sensitive to how long ago (*when*) they cached *what* kinds of food, *where*. Subsequent work has shown that jays integrate what–where–when information with other details, such as how quickly different foods degrade (Clayton et al. 2003), and *who* was watching during caching (Dally et al. 2010). Similar memory abilities have been found in a wide range of other animals, including other birds, mammals, and invertebrates including bees and cuttlefish.<sup>6</sup>

The philosophical literature has largely focused on 'what–where–' studies. But another prominent line of behavioural evidence uses 'unexpected questions' to look for *incidental encoding*. Whereas other forms of memory primarily store information likely to be task-relevant, episodic memory stores such a rich array of details that it includes many incidental ones. Pigeons, dogs, rats and dolphins have all completed unexpected question tasks requiring them to access incidentally encoded information.<sup>7</sup> Other studies have investigated animals' storing details of the context in which stimuli were encountered (Basile and Hampton 2017; Crystal et al. 2013; Crystal and Alford 2014) and how they were encountered, for example, via sight or smell (Billard et al. 2020).

Human episodic memory often represents sequences of events within episodes. Likewise, monkeys' reactions when recalling which frame of a video came first suggest they replay the video in order (Zuo et al. 2020); and rats remember sequences of odours (Panoz-Brown et al. 2018). Sheridan et al. (2024)

combine sequence tasks with the unexpected question paradigm.

Many researchers link episodic memory to a broader capacity for ‘mental time travel’, including future-as well as past-related cognition, suggesting evidence of future planning may be relevant. Some suggest that animals cannot plan in ways that anticipate future preferences (Suddendorf and Corballis 1997, 2007; Tulving 2005), but there is evidence suggestive of such planning and other future-oriented behaviour, especially in birds and primates.<sup>8</sup> Views linking episodic memory to mental time-travel, or to simulation of events more broadly, often appeal to the idea that human episodic memory displays distinctive patterns of error. These patterns are taken to show that it does not simply preserve details of past events, but reconstructs past events based partly on general information about events of this kind. Some recent work has searched for similar patterns of error in bees (Martin-Ordas 2024) and cuttlefish (Poncet et al. 2024).

### 3.2 | Neural

There is also relevant neuroscientific evidence, which is less discussed in philosophy.

One approach looks for neural structures which could support episodic memory. In humans, the most famously relevant structure is the hippocampus. All vertebrates have a structure *homologous* to the human hippocampus—derived from a structure in our last common ancestors 500 million years ago—which develops in a similar way, guided by some of the same genes (Murray et al. 2017, 39–55; Sherry 2011). However, having a hippocampus is only weak evidence of episodic memory. First, human episodic memory involves other areas, including the prefrontal cortex, which may be unique to primates.<sup>9</sup> Second, the hippocampus has other functions besides subserving episodic memory, including navigation—a function supported by ‘place cells’, which fire when animals are in a particular location (Moser et al. 2008; O’Keefe et al. 1978). The relationship between hippocampal functions is debated (e.g., Eichenbaum 2017; Huber 2023), but given the primate hippocampus’ changes in shape and location in response to neocortical developments, its function *may* have changed too, such that it enables episodic memory only in humans (Murray et al. 2017, 50–54).

Another approach focuses on the neural underpinnings of performance in the behavioural paradigms above. Several of these are hippocampus-dependent in multiple species, including what-where+ memory, unexpected question tasks, memory for sequences, and birds’ cache memories.<sup>10</sup> Scene-specific memories for objects depend on a common structure in humans and monkeys (Aggleton et al. 2000; Gaffan 1994). Recent work using high-density recording of neurons while chickadees cache and retrieve food has uncovered event ‘barcodes’, distinctive patterns of activity in the hippocampus. These barcodes only occur during caching and shortly before retrieval, not when the bird simply visits the site, suggesting (though this interpretation merits more philosophical discussion) these are not simply

location-linked memories but highly unique memories relating to the caching event (Chettih et al. 2024).

Neuroscientific details can be suggestive in other ways, too. Sharp Wave Ripples (SWRs) are a much discussed example. SWRs involve place cells firing in rapid sequences, often corresponding to routes the animal has taken. This occurs during rest, when the animal pauses at a choice point in a maze, and during sleep, when much memory consolidation takes place.<sup>11</sup> Although this literature focuses on rodents, related phenomena have been found in humans,<sup>12</sup> and SWRs have been found in enough species to suggest their presence in all mammals, and perhaps some birds and lizards (Payne et al. 2021; Shein-Idelson et al. 2016). The functions of SWRs are debated, and they may not solely be implicated in memory ‘replay’ (Ólafsdóttir et al. 2018), but for Corballis (2013), they establish episodic memory in animals.<sup>13</sup>

### 3.3 | Computational

Computational modelling also has an important role to play. Whilst not providing *direct* evidence about the memory capacities of animals, computational methods can supplement behavioural and neuroscientific work, and suggest new hypotheses to explore.

In some cases, computational techniques are crucial to obtaining other types of evidence. For example, to identify the barcodes discussed above, researchers needed to identify when chickadees were finding caches through memory rather than stumbling on them at random. Using a computational model which predicts, based on typical behaviour, when chickadees would find caches randomly, the researchers were able to identify the memory-based retrievals (Applegate and Aronov 2022).

Computational models may be particularly illuminating when they aim to *simulate* cognitive mechanisms, showing how their interaction might give rise to observed behavioural phenomena and thereby suggesting interpretations of the behavioural data. For example, Brea et al. (2023) construct computational models to explore which mechanisms could account for scrub jays’ caching behaviour. Their models involve associative learning interacting with specialised memory mechanisms tracking the ‘age’ of memories, thereby capturing the ‘when’ component of cache memories. In one model, these are combined with a ‘plastic caching’ mechanism that increases preference for caching at a site when food is recovered successfully. This is compared with a ‘mental time travel’ model, in which past caching events are ‘replayed’. The ‘plastic caching’ model fits the behavioural data at least as well as the ‘mental time travel’ model, suggesting that such a mechanism could be sufficient to explain scrub jays’ behaviour. In this case, computational modelling was used to generate and test granular *how-possibly* explanations—detailed hypotheses about which mechanisms could in principle produce the jays’ behaviour.

Models simulating episodic memory can also elucidate its role in other cognitive processes. For example, computational

systems with episodic-like memory components learn more quickly and across longer time intervals than those without—leading some to suggest that rapid learning and learning across temporal distance are among episodic memory's functions (Boyle and Blomkvist 2024; Gershman and Daw 2017). Zeng et al. (2023) compare different memory architectures in AI systems and propose that episodic memory supports rapid learning in at least two distinct ways, which can be distinguished computationally but are difficult to distinguish in biological systems due to overlapping neural bases. Drawing on theories from machine learning, Boyle (2021b) argues that episodic memory plays a crucial role in the encoding and retrieval of semantic memory. Brown (2024) proposes, on similar grounds, that episodic memory enables 'unrestricted learning'—a form of learning which uses detailed representations of past events to generate and test indefinitely complex models of our environment.<sup>14</sup> All of these authors draw on computational ideas to generate how-possibly explanations, articulating how episodic memory could, in principle, support other cognitive operations.

This work has substantial bearing on our central question, because investigating whether animals have episodic memory rests in part on considerations of its *function* (see Section 4.3). Understanding in detail how episodic memory works, and how it contributes to other processes in the mind, is key. The computational work just described can shed significant light on the function of episodic memory, and thereby guide the search for episodic memory in other species (Boyle and Brown 2024). Yet there are delicate questions about the interpretation of computational models, and here philosophers have a role to play.

Some questions concern the relationship between idealised computational models and biological minds (Stinson 2020). When can *how-possibly* explanations give rise to *how-actually* explanations—ones that tell us how biological memory *actually* works (Boyle and Blomkvist 2024)? Computational models differ from biological minds in myriad ways. They are implemented in different hardware; perhaps more importantly, they process information in different ways. For example, many AI systems learn through backpropagation, a process unlikely to occur in biological systems in the same way (Lillicrap et al. 2020). Does this undermine their utility for modelling biological systems? Other questions concern how well specific computational models map onto relevant theories. For instance, Brea et al. (2023)'s models are intended to compare competing theoretical explanations for scrub jays' caching behaviour. A key question then is how well their computational models capture the details of the relevant theories—and, to the extent that they do not, whether this weakens any conclusions we might draw.

Addressing such questions requires philosophical work, drawing on discussions of modelling in philosophy of science and biological plausibility in philosophy of AI, and considering other models of episodic memory and hippocampal function (Cheng et al. 2016; Franklin et al. 2020; Spens and Burgess 2024). Engagement with a computational perspective is a growing, promising trend in philosophy of memory (Aronowitz 2019; Boyle 2021b; Brown 2024; Cheng et al. 2016; Werning 2020), and

will be central to answering the deeper questions about episodic memory in animals articulated below.

## 4 | Sceptical Responses

The evidence above appears to converge on the conclusion that many species have episodic memory. Nevertheless, this remains disputed. In part, this reflects issues in interpreting specific experiments. For example, some tasks might be performed using short-term memory (e.g., Zuo et al. 2020), whereas episodic memory is generally assumed to be long-term. Bees' 'when' memories (Pahl et al. 2007) may, unlike mammals', be limited to recording time of day. But here we highlight four more general sources of scepticism.

### 4.1 | Phenomenological Scepticism

Episodic memory is thought to involve *recollective phenomenology*: a feeling of 're-experiencing' the past event. The following reasoning underpins what we will call 'Phenomenological Scepticism':

P1. Having episodic memory requires having recollective phenomenology.

P2. Demonstrating recollective phenomenology in animals is impossible.

Therefore,

C. Demonstrating episodic memory in animals is impossible.

One might resist P1. The idea can be traced to Tulving, who labelled recollective phenomenology 'autonoesis' (1983, 2005). However, Tulving offered conflicting accounts of autonoesis, and provided little evidence for its being required for episodic memory (Boyle 2021a, 2509–2511). Contemporary researchers who agree that autonoesis is a defining feature of episodic memory also offer conflicting accounts (see Sant'Anna et al. 2024 for review). If its defenders cannot agree on what recollective phenomenology *is*, we might wonder whether there really is a special phenomenology here, let alone whether it is *required* for episodic memory.

Alternatively, one might reject P2. Boyle (2020) argues that recollective phenomenology can be analysed into several components, each of which is empirically detectable. For instance, one aspect of re-experiencing is representing an event's spatial features and temporal structure. We can find evidence for these representational features. Other aspects of animals' phenomenology—including pain and short-term memory—are similarly investigated by looking for behavioural, neural, and computational markers.<sup>15</sup> In addition to this direct evidence, we might invert the argument above, accepting P1 but therefore treating any evidence of any feature of episodic memory as evidence for the presence of recollective phenomenology (Eichenbaum et al. 2005). So, if demonstrating that animals



have recollective phenomenology simply means finding strong evidence that they do, this is possible.

One might interpret P2 differently, as claiming that we cannot rule out the possibility that animals are ‘zombies’, merely behaving *as if* they are conscious. But establishing scientific claims does not require ruling out such sceptical possibilities. After all, the zombie possibility arises for other humans too, yet we do not take it to be impossible to establish scientific claims about human minds (Hoerl and McCormack 2017).

## 4.2 | Kind Scepticism

Some have argued that whilst the evidence suggests animals have something *similar* to episodic memory, this differs in kind from human episodic memory. Boyle (2022) labels this ‘Kind Scepticism’.

For example, Keven (2016), (2022) proposes that human episodic memories have narrative structure, representing causal and temporal relations, and that animals cannot represent such relations. So, whilst they may form simpler ‘event memories’, they cannot have episodic memories proper. Similarly, Mahr and Csibra (2018) propose that animals only have ‘event memory’, lacking metacognitive ‘feelings of remembering’.

One might dispute whether animals’ memory capacities differ from human episodic memory in these ways. Some of the evidence surveyed above, for example, seems to suggest that animals represent events’ temporal structure. Alternatively, one might dispute whether human episodic memory requires these features. For example, vivid, snapshot-like memories lacking narrative structure and metacognitive feelings would likely be classified as episodic in humans.

More importantly, Kind Scepticism highlights a challenging theoretical problem arising whenever we try to identify traits in different species: traits exhibit interspecific variation. For example, fish hearts have two chambers, amphibian and reptile hearts have three, mammalian and avian hearts four. Similarly, if different species share a *cognitive* trait, it may have species-specific manifestations. The differences highlighted by Kind Scepticism might indicate that animals have species-specific manifestations of episodic memory, rather than a different kind of memory (Boyle 2022). The problem is determining whether that’s so:

*The Problem of Interspecific Variation.* Which differences between human and animal memory simply mean that an animal has a variant of episodic memory, and which mean that it has a different kind of memory altogether?

Answering this problem requires addressing several difficult questions: Is there a principled way of individuating episodic and other kinds of memory? For example, are intuitions relevant? Given episodic memory’s ethical significance, might values play a role? Is episodic memory—or, indeed, *memory*—a natural kind (Michaelian 2011; Cheng and Werning 2016; Andonovski et al. 2024)? Should we expect a pluralist account

(Boyle 2022, 2024), where episodic memory is individuated differently in different contexts?<sup>16</sup>

## 4.3 | Functional Scepticism

A third sceptical response rests on functional considerations. The reasoning is that we should expect to find episodic memory’s function being performed in all animals with episodic memory—yet in many animals, we do not. There are two versions of this thought, corresponding to two senses of ‘function’: evolutionary function, the contribution to fitness episodic memory was selected for; and causal role function, episodic memory’s contributions to broader phenomena (Neander 2016). Call this family of views ‘Functional Scepticism’.

For example, some propose that episodic memory’s function, in both senses of function, is to support future-planning.<sup>17</sup> This suggests that any animal with episodic memory should be able to plan (Section 3). Some who are sceptical about animal planning consequently doubt that animals have episodic memory (e.g., Suddendorf et al. 2022; Suddendorf and Busby 2003).

Functional Scepticism is only as persuasive as the underlying account of episodic memory’s function, itself the subject of a lively ongoing debate.<sup>18</sup> Some functional accounts stress episodic memory’s role in processes that are unarguably present in animals, such as learning (Boyle 2021b). Others link it to forms of learning which may not be present in animals, suggesting that these kinds of learning matter more than planning (Boyle 2019; Brown 2024).

The evolutionary variant of Functional Scepticism faces further obstacles. Episodic memory could be a functionless by-product of another trait (Schulz and Robins 2022). Episodic memory is often said to be a costly capacity,<sup>19</sup> so one might think that it must confer significant advantages to have been retained. But it is unclear what costs are associated with episodic memory, and which alternatives these should be weighed against (see Section 5). Episodic memory might also have more than one function (Schwartz 2020), or could be an *exaptation*, a trait with different functions in different species, having acquired new functions during evolution—much as electric eels’ ability to zap prey was exapted from other fish’s abilities to generate electric fields for sensing and communicating (Futuyma 1986, 432–434; cited in Godfrey-Smith 1994, 358).

Moreover, establishing any functions of episodic memory requires identifying selection-relevant problems faced by the relevant ancestral populations, which would have been solved more economically by episodic memory than by available alternatives. But this raises several further questions we are poorly-placed to answer (Boyle 2019). Among other things, identifying the relevant ancestral populations requires knowing which animals have episodic memory now. So, judgements about episodic memory in animals should arguably not be held hostage to accounts of its evolutionary functions: episodic memory’s phylogenetic distribution should inform evolutionary accounts, rather than vice versa (Boyle and Brown 2024).

Despite this cluster of issues, one core idea underlying Functional Scepticism is highly plausible: finding episodic memory in animals is importantly related to understanding its function (s). This motivates a second philosophical problem:

*The Problem of Functional Variation.* How should we conceptualise the functions of episodic memory and other capacities across species and across evolutionary time?

#### 4.4 | Simplicity-Based Scepticism

Finally, one might worry that the evidence described in §III fails to rule out simpler explanations. For example, Hoerl and McCormack (2019) argue that behaviour in what-where-when studies might be explained by a ‘temporal updating system’, which is ‘less sophisticated’ than a temporal reasoning system incorporating episodic memory. Similarly, Brea et al. (2023) take their models to suggest that ‘higher cognitive processes like mental time-travel’ are not required to explain jays’ caching behaviour.

However, it is unclear what ‘simplicity’ involves, leaving it unclear which explanations simplicity favours in the episodic memory debate. To say that episodic memory is a ‘sophisticated’ or ‘higher’ capacity is unhelpful without knowing what sophistication consists in. One idea is that ‘simpler’ explanations are those with fewer postulates. Hoerl and McCormack (2019), for instance, suggest that *any* explanation of jays’ caching behaviour must postulate a mechanism enabling jays to track elapsed time, but that this would be sufficient to explain their behaviour without episodic memory. But since their ‘temporal updating system’ contains other components besides a mechanism for tracking elapsed time, it is not clearly simpler in this sense. Another way of elucidating simplicity favours evolutionary age: we should prefer explanations that appeal to evolutionarily older or more widespread traits (Currie 2021). But it is a live possibility that episodic memory is evolutionarily old and widespread (Allen and Fortin 2013), which might make it ‘simpler’ than many rivals.

Whatever ‘simplicity’ means, the idea that simpler explanations should enjoy ‘default’ status in comparative cognition has been the target of much recent criticism.<sup>20</sup> In many cases, which of two competing explanations is correct seems like a matter to be determined empirically rather than through parsimony considerations. For example, whilst Brea et al. (2023) show that their plastic caching model fits existing scrub jay data as well the mental time travel model, and take the former to be simpler, which of these models is to be preferred should be determined through further empirical tests. Indeed, they propose a novel behavioural experiment which they suggest would discriminate the two models. In other cases, ‘simpler’ capacities seem less likely explanations than ‘complex’ ones on theoretical grounds. Even sophisticated patterns of human behaviour can in principle be explained through Hoerl and McCormack’s (2019) ‘less sophisticated’ ‘temporal updating system’; yet Brown (2023) casts doubt on whether such mechanisms are genuine alternatives to mechanisms involving representation.

Perhaps a bigger obstacle to evaluating ‘simpler’ alternatives is that they are often underspecified. For example, Suddendorf and Corballis (2007) suggest that information in what-where-when studies ‘may be known rather than remembered’, but this is somewhat vague. Similarly, characterising animals’ memories as ‘episodic-like’ does not tell us what they actually are.

This gives us our third major problem:

*The Problem of Alternatives.* What, besides episodic memory, might explain the evidence—and how should we evaluate competing explanations?

#### 5 | If Not Episodic Memory, What?

The Problem of Alternatives is central to the difficulties of determining which animals have episodic memory. Individuating episodic memory, weighing accounts of its function, and evaluating evidence concerning its distribution all require an account of both what episodic memory is and what the relevant alternatives are.

It is crucial to focus on *relevant* alternatives here—that is, other capacities that might explain the body of evidence outlined in Section 3. To illustrate this, consider the following idea, which might occur to a reader familiar with the philosophy of memory. It seems that addressing the Problem of Alternatives, and indeed all of the problems described in Section 4, requires giving an account of what episodic memory is. This is what philosophers of memory aim to do. So, why not turn to prominent philosophical accounts of memory to make progress with these problems? The answer is that recent work in philosophy of memory has primarily been concerned with the distinction between episodic memory and *imagination*. For example, given evidence that the mechanisms of episodic memory and imagination overlap, could there be episodic memories not involving a memory trace? Is there any fundamental difference between episodic memory and imagination (Michaelian and Robins 2018)? This work offers little help with respect to the Problem of Alternatives, because imagination does not provide a plausible alternative explanation for the evidence—behaviour in what-where-when studies, for example, must be explained by *some form of memory*, not by scrub jays fortuitously imagining the locations of their caches. For related reasons, this work sheds little light on the Problems of Interspecific Variation and Functional Variation: because its focus is the nature of *human* episodic memory, it does not purport to offer guidance on how episodic memory might vary across species or evolutionary time.

We can more directly address the Problem of Alternatives by discussing three important families of alternatives: *associative learning*, *semantic memory*, and *previously unrecognised kinds of memory*.

A long tradition takes learned associations to provide default explanations of animal behaviour. States like ‘episodic-like memory’ are typically ascribed only once associative explanations have been ruled out. But it is a difficult philosophical

question how associative explanations relate to cognitive processes like episodic memory. One possibility is that these are genuine competitors. Another is that associative models show how operations like episodic memory retrieval are implemented: indeed, this is another interpretation of Brea et al. (2023)'s 'associative' model.<sup>21</sup>

You likely know what, where, and when information about many events without 're-experiencing' them: instead you *semantically remember* these facts. Perhaps birds' cache-memories are similar. This proposal raises intriguing, somewhat neglected, questions. What precisely is semantic memory? Do animals *have* semantic memory—or, at any rate, is that any simpler or more likely than their having episodic memory? Influential accounts of semantic memory look just as demanding as episodic memory, appealing to 'noetic consciousness' (a counterpart to autonoesis [Tulving 1983]) and to apparently language-related capacities (e.g., Tulving 1972, 386). Furthermore, semantic memory seems to raise its own version of the Problem of Interspecific Variation.

These considerations might prompt us to revise the traditional typology of memory. Older philosophical discussions make related distinctions (e.g., Broad 1925, 221) and there are intuitive differences between remembering events and remembering facts. Yet the terms 'episodic memory' and 'semantic memory' were only introduced by Tulving (1972), and were always supposed to be terms of art within scientific psychology. So this traditional typology is not set in stone, and could be expanded. Keven (2016) and Mahr and Csibra (2018) aim to do this with their 'event memory' proposals—but given the Problem of Interspecific Variation, we might question whether event memory is really distinct from episodic memory. Conversely, Rubin and Umanath (2015) use 'event memory' for a type of memory humans and animals share, of which episodic memory is just one kind—but Boyle (2021a) argues that this just *is* episodic memory. Alternatively, we might postulate kinds of memory specific to food caching or navigation. Any such proposal would need to clarify whether humans have this novel kind of memory, and how it relates to other kinds of memory. For example, is it homologous to episodic or semantic memory, part of their mechanistic bases, or completely independent?

More radical proposals introduce *multiple* new categories of memory. Perhaps there are dedicated kinds of memory for food caching, navigation, individual conspecifics, social relations, event scripts, and more, some of which are unique to humans and some to other species. Murray et al. (2017) develop a view along these lines. For them, at least seven long-term memory systems have evolved for different functions, but semantic and episodic memory are unique to humans, requiring interactions between these memory systems and human-specific mechanisms.

Murray et al.'s proposal raises a further issue: should we think of episodic and semantic memory as kinds of *system*, *state*, *event*, *process*, or something else?<sup>22</sup> If mental events, states or processes result from multiple systems interacting, perhaps the episodic-semantic distinction only applies at one of these levels. There could be dedicated episodic and semantic memory *systems*, both contributing to most events of remembering, such that the latter cannot be meaningfully divided into episodic and

semantic. Or perhaps episodic and semantic remembering are two kinds of *event*, with no single system dedicated to either. Either way, the issues discussed in Section 4 arise. For example, Pan (2022) argues that animals probably have the same memory systems as humans, but that episodic remembering is a distinctive state animal's lack—but this turns on his assumption that episodic remembering essentially involves autonoesis, which might be disputed (Section 4.1). Meanwhile, if one holds there is a distinctive episodic memory system, and that the crucial question is which species have this system, one must determine how to individuate that system across species (Section 4.3).

Still more radical proposals challenge the episodic-semantic distinction itself. Semantic memories may form through a process of semanticisation, gradually abstracting details away from episodic memories. If so, many memories may not belong neatly to either category.<sup>23</sup> There are also pervasive interactions between episodic and semantic memory, such that deficits in one are accompanied by deficits in the other.<sup>24</sup> Perhaps episodic memory is one pole in a continuum rather than a kind, or there are cross-cutting categories of memory.

## 6 | Conclusion

Whether animals have episodic memory is an important question in its own right. But it also serves as a case study illustrating the difficulties involved in understanding animals' minds, even when faced with a substantial body of empirical evidence. We are arguably not yet in a position to settle the question empirically: the theoretical foundations of research in this area are too unstable, reflecting unresolved metaphysical and epistemological questions about both memory and animal minds.

Rather than focusing on narrow questions about whether animals' memory capacities resemble humans' in particular respects, we propose that future research should focus on these deeper philosophical issues: the Problem of Interspecific Variation, the Problem of Functional Variation and the Problem of Alternatives. Since these problems arise quite generally when we try to understand nonhuman, addressing them in the context of episodic memory would not only transform our understanding of nonhuman memory; it would serve as a case study with far wider significance for the philosophy and the science of thinking things.

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## Data Availability Statement

There are no data associated with this article.

## Endnotes

- <sup>1</sup> Hereafter, simply ‘animals’.
- <sup>2</sup> for example Clayton and Dickinson (1998); Davies et al. (2022); Easton et al. (2012); Martin-Ordas et al. (2010); Sato (2021); Schnell et al. (2021).
- <sup>3</sup> Individuals with episodic memory are capable of surprisingly many such tasks (Craver et al. 2014). This shows that episodic memory is not strictly necessary for them. However, this is compatible with its being central to the way these tasks are performed in neurotypical individuals: there may be multiple ways of achieving the same ends, some involving episodic memory and others not.
- <sup>4</sup> *Might*: for more on these disputed issues, see for example Korsgaard (2018, 32–33); Mahr and Fischer (2023); McMahan (2002, 189–209); Mendl and Paul (2008); read and Birch (2023); Regan (2004, 94–103); Selter (2020); Velleman (1991, 68–71).
- <sup>5</sup> Findings in C. Liu et al. (2023) preliminarily suggest they do.
- <sup>6</sup> for example see Feeney et al. (2009); Ferkin et al. (2008); Jozet-Alves et al. (2013); Kaminski et al. (2008); Pahl et al. (2007); Sherry (1984); Zhou and Crystal (2009); Zinkivskay et al. (2009).
- <sup>7</sup> Davies et al. (2022); Fugazza et al. (2016); Sato (2021); Zentall et al. (2008); Zhou et al. (2012).
- <sup>8</sup> Reviewed in Musgrave et al. (2023); Redshaw and Bulley (2018); Scarf et al. (2014); for philosophical discussion, see Kaufmann (2015); Selter (2020).
- <sup>9</sup> For an overview, see Murray et al. (2017, 61–78). It should be noted that in birds and fish, other areas including the hippocampal homologue may serve prefrontal-like functions—Allen and Fortin (2013); Zacks and Jablonka (2023)
- <sup>10</sup> Barker et al. (2017); Fortin et al. (2002); Kesner et al. (2002); Krebs et al. (1989); Panoz-Brown et al. (2018); Sato (2021); Sherry (2011); Sherry et al. (1989); Sherry and Vaccarino (1989); Zhou et al. (2012).
- <sup>11</sup> For reviews, see A. A. Liu et al. (2022); Ólafsdóttir et al. (2018).
- <sup>12</sup> Gelbard-Sagiv et al. (2008); Kurth-Nelson et al. (2016); Y. Liu et al. (2019); Norman et al. (2019, 2021).
- <sup>13</sup> See Suddendorf (2013) for a critical reply, and Cheng et al. (2016); Mahr and Fischer (2023) for more complex views.
- <sup>14</sup> Work approaching episodic memory from a computational perspective raises intriguing questions about whether any AI systems have episodic memory. We set this aside (but see Boyle and Blomkvist (2024) for discussion).
- <sup>15</sup> See, for example Browning and Birch (2022); Hampton et al. (2020); Irvine (2020); Shea and Heyes (2010).
- <sup>16</sup> Note that this problem does not depend on assuming that there are strict necessary and sufficient conditions for episodic memory. One might hope that we can dissolve the Problem of Interspecific Variation by classifying animal memory as a borderline or peripheral case of episodic memory, or calling it ‘episodic-like’. However, this will not resolve important disputes without a defence of why they are peripheral cases: there is such deep disagreement about which features are core to episodic memory that plausible views will insist either that they are clearly core cases of episodic memory, or that they are clearly not.
- <sup>17</sup> See, for example De Brigard (2014); Schacter et al. (2007); Schulz and Robins (2022); Suddendorf and Busby (2003); Suddendorf and Corballis (1997, 2007).
- <sup>18</sup> See, for example, Aronowitz (2018); Boyer (2008); Boyle (2019), (2021b); Brown (2024); De Brigard (2014); Hoerl and McCormack (2016); Mahr and Csibra (2018); Mok et al. (2020); Schwartz (2020).
- <sup>19</sup> See, for example, Bar (2007); Brown (2024); Dessalles (2007); Dukas (1999); Mar and Spreng (2018); Suddendorf and Corballis (2007).

- <sup>20</sup> For discussion, see (Bausman and Halina 2018; Dacey 2016b; Fitzpatrick 2008; Meketa 2014; Sober 2009).
- <sup>21</sup> For related discussions about the interpretation of reinforcement learning and associations, see Brown (2023); Buckner (2011), (2023); Dacey (2016a); Haas (2022).
- <sup>22</sup> Andonovski (2023); De Brigard et al. (2022); Pan (2022); Robins (2020).
- <sup>23</sup> Andonovski (2020); Aronowitz (2022); De Brigard et al. (2022).
- <sup>24</sup> Boyle (2021b); Greenberg and Verfaellie (2010); Renoult et al. (2019).

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