Title: Dissociating Memory Traces and Scenario Construction in Mental Time Travel

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Abstract

There has been a persistent debate about how to define episodic memory and whether it is a uniquely human capacity. On the one hand, many animal cognition studies employ content-based criteria, such as the what-where-when criterion, and argue that nonhuman animals possess episodic memory. On the other hand, many human cognition studies emphasize the subjective experience during retrieval as an essential property of episodic memory and the distinctly human foresight it purportedly enables. We propose that both perspectives may examine distinct but complementary aspects of episodic memory by drawing a conceptual distinction between episodic memory traces and mental time travel. Episodic memory traces are sequential mnemonic representations of particular, personally experienced episodes. Mental time travel draws on these traces, but requires
other components to construct scenarios and embed them into larger narratives. Various nonhuman animals may store episodic memory traces, and yet it is possible that only humans are able to construct and reflect on narratives of their lives – and flexibly compare alternative scenarios of the remote future.

Keywords: mental time travel; episodic memory; scenario; episodic memory trace; animal cognition; episodic-like memory

1 Introduction

When Tulving (1972) first conceptualized episodic memory as memory of personally-experienced events, he hypothesized that episodic memories could be distinguished on the basis of the information that they contain (Fig. 1). He suggested that “[e]pisodic memory receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events.” (Tulving, 1972, p. 385) This criterion later came to be known as the what-where-when (Griffiths et al., 1999) or WWW criterion (Suddendorf and Busby, 2003). Tulving (1972) thought that, on this basis, episodic memories could be distinguished from other memory systems such as semantic or procedural memory. However, Tulving (1985) later realized that the WWW criterion was neither necessary nor sufficient to define episodic memory. It is possible, for instance, to know what happened where and when (e.g., such as details about the battle of Hastings) without the events having been personally experienced and recalled. He therefore changed his definition to one that emphasized the distinct subjective experience during the retrieval of episodic memories. Tulving (1985) suggested that the recall of the three different types of memory: procedural, semantic and episodic is characterized by varying levels of conscious awareness: anoetic, noetic, and autonoetic, respectively. Roughly speaking, anoetic consciousness lacks awareness of the content of
the memory, noetic consciousness includes awareness of the content, and auto-noetic consciousness includes the awareness that one self has been part of the recalled event. The experience during retrieval of episodic memories was likened to mental time travel (MTT) into the past (Suddendorf and Corballis, 1997; Tulving, 1985), a virtual reliving of the past (Fig. 1).

Although it took some time to develop behavioral paradigms to test whether nonhuman animals store memories of combined WWW information (Clayton and Dickinson, 1998), once published, the what, where, when approach to studying episodic memory became very popular in animal cognition studies. The WWW criterion has been tested in a variety of species and purportedly passed by scrub jays (Clayton and Dickinson, 1998; Dally et al., 2006); pigeons (Zentall et al., 2001); black-capped chickadee (Feeney et al., 2009); magpies (Zinkivskay et al., 2009); mice (Dere et al., 2005); rats (Babb and Crystal, 2005; Eacott et al., 2005); meadow voles (Ferkin et al., 2008); Yucatan minipigs (Kouwenberg et al., 2009); dogs (Kaminski et al., 2008); rhesus monkey (Hoffman et al., 2009, but see Hampton et al., 2005); and chimpanzees and bonobos (Martin-Ordas et al. 2010, but see Dekleva et al. 2011).

Clayton and Dickinson (1998) introduced the term episodic-like memory to acknowledge that memory of what, where, when might not be the same as human episodic memory and, at the same time, to suggest that there might be a close link between the two. While a number of authors maintain this cautious middle ground, others swing more towards the extremes. On the one hand, some students of human episodic memory insist that, no matter what information a nonhuman animal might be able to retrieve about its past, without evidence for autonoetic consciousness we should not attribute episodic memory to them (Klein, 2013; Tulving, 2001). On the other hand, some researchers of memory in nonhuman animals argue that if a memory in nonhuman
animals can be operationalized in a way similar to episodic memory in humans, then the subjective experience is immaterial and nonhuman animals should be considered to have episodic memory (Eichenbaum et al., 2005).

Suddendorf and colleagues suggest a third perspective. The subjective experience, in itself, is nothing that evolution can directly select for (Suddendorf and Busby, 2003; Suddendorf and Corballis, 2010, 2008, 2007, 1997). It is consequences for fitness that matter, and these can only be found in how certain characteristics effect survival and reproduction in the present and the future. Given that mental time travel into the past and into the future appear to draw on many of the same neurocognitive mechanisms, they may be regarded as two sides of the same coin (Dudai and Carruthers 2005; Byrne et al. 2007; Schacter et al. 2007; Suddendorf & Corballis, 1997). Rather than being a system designed to capture the past, Suddendorf and Corballis (e.g., 2007) suggest that MTT evolved primarily to enable foresight. By considering potential future events, one can plan and prepare in ways that convey distinct fitness benefits. Species that are capable of episodic memory should hence be able to demonstrate flexible foresight in their behavior, yet there is little indication that nonhuman animals do (Suddendorf and Corballis 2010, see also Raby and Clayton 2009).

What complicates the debate further is that the neural mechanisms of episodic memory are still not well understood. The hippocampus is the brain region most closely associated with episodic memory in humans (Harande et al., 2012; Nadel et al., 2000; Scoville and Milner, 1957; Zola-Morgan et al., 1986). In rodents (O’Keefe and Dostrovsky, 1971) and bats (Ulanovsky and Moss, 2007), numerous studies have found neurons in the hippocampus that are selectively active in certain spatial locations. A study reported so-called place cells even in humans (Ekstrom et al., 2003). Based on the early physiological results, O’Keefe and Nadel (1978) suggested that the hippocampus
forms a mental representation of space and that space plays such a central role in episodic memory that the hippocampus is essential for episodic memory. However, this view does not easily account for observations that the hippocampus is required for temporal learning that does not involve learning spatial locations (Fortin et al., 2002; McEchron et al., 1998). Recently, Michael Corballis (2013), once one of the most ardent supporters of the “uniquely human” hypothesis, suggested that neural sequences of place cells that are generated in the rat hippocampus while the animal is resting (Diba and Buzsáki, 2007; Foster and Wilson, 2006; Lee and Wilson, 2002; Pfeiffer and Foster, 2013; for a review, see Buhry et al., 2011) might be evidence of MTT. His collaborator Thomas Suddendorf disagrees and maintains their original position (Suddendorf, 2013a). This controversy exemplifies the difficulty of relating neurophysiological data directly to cognitive processes (Balter, 2013).

To move beyond the current impasse, we suggest that the three perspectives (focussing on WWW information, autonoetic consciousness, or foresight) may examine distinct but complementary aspects of episodic memory and mental time travel. We propose a conceptual model in which episodic memory traces are separate from the capacity to travel mentally in time. This simple distinction creates a new perspective that is different from each of the three previous perspective, but, at the same time, integrates key aspects of each of them. Based on our model we postulate that some nonhuman animals have the capacity to encode, store and retrieve episodic memory traces, while potentially lacking other critical components of mental time travel. Tulving (2001) suggested that nonhuman animals may have memories of specific past events, but that this was not the same as episodic memory since they lacked autonoetic consciousness. By contrast, we suggest that humans and nonhuman animals share the same type of episodic memory traces, as many researchers in nonhuman animal memory would have it. At the same time, we suggest that mental time travel involves a range of additional
components and thus, that it remains possible that there is something distinctly human about the capacity. In particular, there is no compelling evidence to suggest that other species have the ability to flexibly construct and reflect on alternative scenarios of the remote future. The first-person feel associated with episodic memory (i.e., autonoetic consciousness) is not essential for our distinction but can be accommodated in the model.

2 Components of Mental Time Travel

It has been argued that mental time travel is not an encapsulated module but the product of the workings of a number of components (Suddendorf and Busby, 2003). Suddendorf and Corballis (2007) suggested that a theater production metaphor could help identify the components involved in successful MTT. They pointed out that there must be mental analogs to a stage to hold the scenario, a playwright to construct the narrative, actors that behave according to our notions of folk psychology, the set that is constructed according to folk physics, a director to orchestrate rehearsals, an executive producer to put the play into action, and a broadcaster to communicate these scenarios. These components of the theater metaphor can be associated with the development of distinct cognitive capacities, such as working memory, recursive embedding, theory of mind, executive functions and language (Suddendorf and Redshaw, 2013). However, for these components to come together and allow us to construct events displaced in time, one has to have some memory traces to work with. To these we therefore turn first.

2.1 Episodic Memory Traces

Mental time travel into past and future draws on memories of past experiences (e.g., Szpunar and McDermott, 2008). In order to provide us with some useful information about how to act in the world that we live in and thereby increase our chances of
survival and reproduction, MTT must be grounded in our general knowledge of the world and in our personally experienced episodes. We refer to these two sources as semantic information\(^1\) and episodic memory traces, respectively.

Semantic information are general facts that were extracted from multiple experiences. It is mostly categorical and refers to prototypical properties of objects and relationships between them (Collins and Quillian, 1969; Quillian, 1966; Tulving, 1972). It can also include idiosyncratic properties of and relationships between particular objects, as long as they are consistent across different episodes, such as the name of a particular person (Quiñonero Quiroga et al., 2005) or information of the kind “The Eiffel Tower is in Paris.”

Semantic information can be highly detailed and essential for mental scenario construction. To use the theater metaphor, semantic information, for instance, provides the folk physics necessary to build the set: the objects of a scenario typically behave in accordance with folk physical laws. Or it supplies the folk psychology to direct the actors: psychological knowledge constrains how participants of a scenario typically act.

Episodic memory traces are fairly faithful representations of personally experienced episodes (Tulving, 1972). They are highly specific in that each trace represents one particular experienced episode. They are stored incidentally without a special trigger (Tulving, 1972). In the vast majority of cases, the potential importance of a particular episodic memory trace is not discernable at the time of storage and the usefulness of the

\(^1\) It is commonly assumed that semantic information is stored in semantic memory and that semantic memory is a distinct memory system (Squire and Zola-Morgan, 1988). Even though semantic information is an important ingredient for mental time travel, as we conceive it here, our model remains agnostic about the source of semantic information as well as how and where it is stored in the brain.
stored information might only become apparent in the future. To make it more explicit, we use the term *episodic memory trace* to refer to the information that is stored in the brain about a particular episode and *episodic memory* to refer to the outcome of scenario construction when the information about the episode is retrieved.

A distinction between episodic memory and episodic memory traces has also been suggested by Klein (2013), albeit for a very different reason. Klein does not regard the memory trace as special to episodic memory. In fact, he suggests that the same memory trace could be retrieved as semantic memory if the trace was associated with noetic consciousness during retrieval, implying that autonoetic consciousness is an add-on to the memory trace rather than a property of it. By contrast, Cheng and Werning (2015) recently suggested that episodic memory traces can be distinguished from other memory traces based on their sequential nature and their link to a specific, experienced episode. We acknowledge that there might be no clear line that divides episodic memory traces from semantic information (Klein, 2013; McKoon and Ratcliff, 1986; Toth and Hunt, 1999), since some cases cannot be easily categorized as either one or the other, leaving the possibility that the two are different by degree rather than by kind. Nevertheless, this controversy is orthogonal to our objective here since our model does not rely on a strict distinction between episodic memory traces and semantic information. What our model requires is that some information is linked to one specific experienced episode (episodic memory trace), whereas other information more generally applies to multiple, personally experienced or not, episodes (semantic information).

A common view of memory traces is that they store most, if not all, aspect of the experienced episode for later retrieval (Bernecker, 2010; Martin and Deutscher, 1966; Patiﬁs et al., 2014). This storage view contrasts with the constructive or generative view of memory (Michaelian, 2011a, 2011b), according to which information is
constructed during remembering and this information may bear little resemblance to the information in the original experience. These two views do not necessarily have to be mutually exclusive. Experimental evidence suggests that episodic memory traces store only the gist of an episode (Bartlett, 1932; Deese, 1959; Gernsbacher, 1985; Koutstaal and Schacter, 1997; Roediger and McDermott, 1995; Sachs, 1967). For instance, subjects who saw a cat crossing the road in front of their car are unlikely to remember later the exact coloration of the cat’s fur, what music was playing in the radio, whether there were pedestrians in the distance, or other peripheral features of the episode. We suggest that the gist reflects the information content from the most abstract level that is relevant in that one episode (Koutstaal and Schacter, 1997; Oliva, 2005). The relevant level is established dynamically for each episode depending on the context and attention. For instance, most subjects are unlikely to remember the color of a cat’s nose, after briefly seeing the cat, but they probably would if asked to pay attention to this feature beforehand. In some cases, such as the preceding example, the most abstract level could in fact be quite detailed, but in most cases it is quite coarse. Frequently, the gist includes only highly abstract information and details, if required, are constructed from semantic information during retrieval. For instance, subjects might report that the cat ran onto the sidewalk after crossing the road, because in their experience most roads have sidewalks, even if in that particular episode the road had none. Our model thus incorporates aspects of both the storage and constructive views.

The proposed distinction between episodic memory traces and episodic memory allows us to separate the content of episodic memory from other components necessary for mental scenario construction. There is now considerable evidence that various species store episodic memory traces, as they are conceptualized here. We discuss some of this evidence in section 3.1. Their mental time travel capacities may, however, be limited because of shortcomings in other components involved in scenario construction.
2.2 Scenario Construction

The construction of mental scenarios, as illustrated by Suddendorf and Corballis’ (2007) theater metaphor, depends on a range of sophisticated component capacities that enable dynamic representations of situations. This scenario construction, or what Cheng and Werning call mnemonic simulation when applied to the retrieval of episodic memories (Cheng and Werning, 2015; Werning and Cheng, 2014), is different from the concept of “scene construction”, which Hassabis and Maguire (2007) introduced. The latter refers to scenes that are static spatial arrangements while we view scenarios as extending in time as well as space. Another difference is that scenes are isolated entities, whereas scenarios can be embedded to allow constructions of larger narratives and reflection (Suddendorf, 2013b). Scenarios can contain information about participants, settings, interactions and sequences of events. We are able to explore a scenario by, for instance, focusing on different participants, taking different perspectives, and examining the spatial layout and the sequence of events. For instance, when we put down our keys, we frequently do not make a conscious effort to remember where we placed them. Later when we are looking for our keys, we might be able to reconstruct our actions around that time to infer where the keys are. Thus, the construction of mental scenarios allows us to make new inferences that we did not make at the time when the episode occurred.

MTT into the future and the past use largely overlapping neural mechanisms (Byrne et al., 2007; Dudai and Carruthers, 2005; Schacter et al., 2007; Suddendorf and Corballis, 2007) but differ in the objective. During MTT into the past, scenarios are constructed that more or less accurately represent a past episode. However, since episodic memory traces only contain the gist of the episode, we hypothesize that semantic information is typically used to aid scenario construction. This process occurs even if subjects are explicitly instructed only to retrieve a past experience and might account for the
unreliable nature of human episodic memory (Loftus and Pickrell, 1995; Loftus et al., 1978; Roediger and McDermott, 1995; Schacter, 2002; Zaragoza and Lane, 1994).

During MTT into the future, the motivation is to construct and compare scenarios about potential future episodes that can guide behavior. One way to imagine future episodes is simply to think that past events will reoccur. But humans can do much more. Humans can mentally construct scenarios they have never experienced before by combining and recombining basic elements into novel constellations and comparing them in terms of likelihood, desirability and so forth (e.g. Gilbert, 2007; Suddendorf and Corballis, 2007).

After all, the future is uncertain and often involves entirely new situations for an individual. Nonetheless, scenarios of future events are often based in part on episodic memory traces. For instance, episodic memory of having packed too much luggage for the last vacation, might lead us to try to avoid that error during preparation for our upcoming vacation. Through repetition of this process, we form semantic information about what to pack for vacations, such that we may no longer need to construct specific scenarios when packing for future vacations. The relative contributions of episodic memory traces and semantic information during scenario construction may vary depending on availability, the task demand, and other factors (c.f. Szpunar et al., 2014).

It is important to note that the mechanisms involved in mental scenario construction enable more than just access to what happened and what might happen. For instance, they allow us to consider counterfactuals that could have occurred in the past but did not (De Brigard et al., 2013). They also allow us to imagine the perspectives of other people (Suddendorf and Corballis, 1997), and even to entertain entirely fictional scenarios that do not relate to actual past, present nor future situations (Hassabis et al., 2007; Suddendorf et al., 2009).

Given the complexity of the MTT system, it may not be a fruitful approach to ask
whether a species does or does not have episodic memory (Beran, 2014; c.f., Templer and Hampton, 2013). Rather, we propose to focus on studying the extent of their scenario building capacities and on how these abilities correlate with the extent to which the components underlying MTT are developed. This kind of analyses has been conducted in some detail on the development of mental time travel in children (Suddendorf and Redshaw, 2013). Different limits have different consequences.

For instance, to construct and explore mental scenarios, one needs a sufficient working memory capacity (Baddeley, 2000; Baddeley and Hitch, 1974). One’s working memory capacity limits the number of information chunks that can be used while constructing scenarios and therefore the detailedness and spatio-temporal extent of the scenario. It has been estimated that adult human working memory capacity is as small as 4 chunks (Cowan, 2001), and lower in other great apes (Balter, 2010; Read, 2008), although the measurement of the capacity remains contentious. To combine offline representations of objects, actions and actors requires generativity, i.e., recursive capacity, which is limited by the embedding depth. The embedding depth in turn depends on the working memory capacity. Constructing a realistic scenario depends on considerable understanding of how objects and actors behave, i.e., sufficient folk physics and folk psychology, or in other words, on the complexity and extent of relevant semantic information. Evaluation, comparison and selection of scenarios requires significant metacognitive and executive capacities. Here, too, the embedding depth might be a limiting factor. Furthermore, the properties of the episodic memory traces that are available as bases for scenario construction may play a role in the outcome. Future research may examine the influence of the temporal span (i.e., the time interval between the first and last event in an episode) or of the overall number of traces stored on the range of scenarios individuals construct.

An individual’s capacity for mental time travel may be determined by the combination
of all of the parameters discussed above, and likely by additional factors that we have not considered here.

2.3 How autonoetic consciousness might fit into the model

Our current model does not require *a priori* that episodic memory retrieval is accompanied by autonoetic consciousness. However, it can accommodate conscious awareness during retrieval in humans in a number of potential ways. Consider a simple example. An eye witness who is recounting the details of a crime that she experienced first-hand and a judge who is recounting the same crime after reading the eyewitness account. According to Tulving, the eye witness’ remembering the crime is accompanied by autonoetic consciousness, whereas the judge’s remembering the crime is accompanied by noetic consciousness (even though the judge’s remembering *reading* about the crime is associated with autonoetic consciousness). Klein (2014) suggested that autonoetic consciousness in humans has the function to indicate the presence of retrieved episodic memory as opposed to imaginations and predictions. However, where might the difference in conscious awareness come from?

*Meta-representation account:* One possibility is that noetic and autonoetic consciousness are related to the different informational contents of meta-representations (Redshaw, 2014; Suddendorf, 1999). When a person constructs a scenario during memory retrieval, they also have information about the nature and source of the memory. This information is represented in the meta-representation. Autonoetic consciousness might simply consist in the presence of a meta-representation that one recalls the information about an episode as a result of one’s own experience of that episode. In our example above, the eyewitness meta-represents that her memory is grounded in having witnessed the crime, while the judge meta-represents that her memory is based on having read the written account of another person.
**Viewpoint-dependence account:** Autonoetic consciousness might arise through the point of view a person assumes in the constructed scenario that includes the episode (Russell and Hanna, 2012; Russell et al., 2011). The scenario of an eyewitness has a first-person perspective: The person is at the center of the scenario, what happens in the scenario is related to the person, and the scenario includes her own reactions. The involvement may be minimal, as in the case of a witness who is merely present in the episode but does not influence its course. By contrast, the judge in our example might be able to construct a scenario of the crime, but that scenario does not have a first-person perspective, her body is not at the center of the scenario, and the events in the scenario are not related to herself nor does it involve her reactions.

**Transparent simulation account:** Several authors have suggested that conscious experience is characteristically linked to what is called phenomenal transparency (Harman, 1990; Metzinger, 2003; Moore, 1903; Werning, 2010). An occurring mental state is phenomenally transparent if only its content-properties are accessible to the subject at that moment. In other words: A subject’s experience of a scenario is phenomenally transparent if, and only if, her having that experience is for her just as if the scenario were present (Werning, 2010). Having the experience is in particular not for her as if, in addition to the scenario, a representation of the scenario were present. When the judge reads about the crime, she has access to the crime and its properties, i.e. the properties of the content of the court record. However, there is something else she has access to while reading: namely the words of the court record, which is the representation: the bearer of content. The situation is very different for the eye-witness: Unless one wants to appeal to a sense-datum theory of perception, she has direct, unmediated access to the crime. Proponents of the phenomenal-transparency view, hold that most perceptions, but also certain hallucinations (as in the phenomenon of “hearing voices”, in which subjects take these voices for real), are phenomenally transparent,
whereas many other mental states, e.g., imaginations are typically not (Werning, 2004).\(^2\) When you imagine a gun, you not only access the properties of the gun, but also have access to the mental image, i.e., the representation or content bearer. Even though experiencing a scenario during remembering is not as transparent as a perception of the scenario would be, characterizations of remembering as “re-experiencing or reliving the past” suggest that autonoetic consciousness in certain respects resembles phenomenally transparent mental states. Viewing remembering as a quasi phenomenally transparent simulation of a scenario might, therefore, account for autonoetic consciousness.

In conclusion, our model suggests that autonoetic consciousness is not an essential property of episodic memory, but it nonetheless is or can be associated with human episodic memory.

### 3 Experimental support for our theoretical ideas

Our central hypothesis that the process underlying MTT can be dissociated into episodic memory traces and scenario building makes a number of testable predictions, which we compare to experimental results in the following. The proposed dissociation is consistent with evidence suggesting that episodic memory emerges gradually during human development (Suddendorf and Redshaw, 2013). Even though children appear to

\(^2\) In an fMRI study with schizophrenic patients, Dierks et al. (1999) compared auditory hallucinations to auditory imaginations. In the case of auditory hallucination differential activity in Heschl’s gyrus, a part of the primary auditory cortex, was measured. The location of activity was similar, however, only unilaterally so, to the actual perception of auditory stimuli.
possess adult-like episodic memory only by the age of about four (Hayne and Imuta, 2011; Nelson, 1993; Perner and Ruffman, 1995; Scarf et al., 2013), children as young as 2½ years old show evidence for storing and retrieving episodic memory traces (Bauer et al., 1998; Wenner and Bauer, 1999). In these latter studies, the children were able to re-enact a complex sequence of actions after observing it only once. Importantly, the sequence was arbitrary, and therefore the children could not use semantic information about the natural sequential order of events to reproduce it. If, however, there are so-called enabling relations between the elements of the sequence, even younger toddlers (in these studies, 16 months olds) could remember the sequence. Our interpretation of these results is that children are first able reproduce a sequence based on semantic information, then develop the ability to store and retrieve arbitrary sequences as episodic memory traces, and later develop the capacity to construct nested scenarios and to destill more complex semantic information. The final stages of the development of episodic memory continue well after age 4, when increases in working memory capacity, among others factors, lead to the construction of more complex episodic memories and larger narratives (Suddendorf and Redshaw, 2013).

The distinction between episodic memory and episodic memory traces also allows us to relate findings from nonhuman animal studies to those in humans, which we turn to next.

3.1 Episodic memory traces in the brain

While several brain regions are certainly involved in storing and retrieving episodic memory traces, current evidence suggests that, in mammals, the associative binding of the items involved in the episode and the temporal sequence of events in the episode critically depends on the hippocampus (Cheng and Werning, 2015; Cheng, 2013; Fortin et al., 2002; Levy, 1996; Wood et al., 1999). Binding has been suggested before to be a
central property of episodic memory (Clayton et al., 2003; Crystal, 2010). Our model leads to, at least, three major implications about hippocampal function that are well supported by observations in humans and other mammals, in particular rodents.

First, the responses of hippocampal neurons are invariant with respect to the details of the presented stimuli. In rodents (O’Keefe and Dostrovsky, 1971) and bats (Ulanovsky and Moss, 2007), place cell activity is independent of the view that the subject sees at that location and specific details of the environment (Muller et al., 1994). Furthermore, Quian Quiroga et al. (2005) found that hippocampal neurons in humans are activated when subjects see photos of certain people, irrespective of their hair style, clothes, and pose; and even when only their written name was presented. These results suggest that hippocampal neurons respond to the gist in the stimuli, rather than to their visual details (Cheng and Werning, 2013; Werning and Maye, 2007).

Second, hippocampal neurons respond to different types of information and form arbitrary associations between different pieces of information. Cells in human hippocampus integrate information across different sensory modalities, responding to the auditory presentation of a person’s name as well as visual cues related to that person (Quian Quiroga et al., 2009; Quiroga, 2012). In rodents, studies have found that hippocampal cells respond to complex conjunctions of different types of stimuli. For instance, in a classical conditioning paradigm, hippocampal cells responded to the conditioned stimulus, a tone, but not to the same tone if it was not paired with an unconditioned stimulus (Moita et al., 2003). In addition, the cells’ responses were modulated by the location of the animal. Their conjunctive and multimodal responses make it plausible that hippocampal neurons are involved in storing episodic memory traces that represent unique and highly diverse episodes.

Third, the hippocampus is important for learning temporal sequences and bridging
temporal gaps. Experimental studies suggest that the hippocampus is required for sequence learning (Fortin et al., 2002), trace eye blink conditioning in humans (McGlinchey-Berroth et al., 1997) and in rodents (Weiss et al., 1999), and trace fear conditioning in humans (Clark and Squire, 1998) and in rodents (McEchron et al., 1998). In addition, functional magnetic resonance imaging revealed increased hippocampal activation during trace as compared to delay conditioning (Cheng et al., 2008). For a more detailed discussion of experimental evidence linking the hippocampus to the representation of temporal sequences, see Cheng and Werning (2015).

We conclude that there is strong evidence that the hippocampus plays an important role in the storage of episodic memory traces in both human and nonhuman animals.

### 3.2 Scenario construction in episodic memory

Scenario construction of past episodes during the retrieval of episodic memories has two important implications for human episodic memory.

First, as described above during episodic memory retrieval many details are reconstructed based on semantic information rather than solely on the basis of episodic memory traces. Early evidence for this effect was reported by Bartlett (1932) who observed that English subjects over time did not remember details of the Canadian Indian Folklore "War of the Ghosts" as they were in the original story, but adjusted them to their own cultural expectations. Better controlled laboratory studies into the reconstructive nature of memories are provided by the Deese–Roediger–McDermott (DRM) paradigm (Roediger and McDermott, 1995). After studying a list of semantically related words, subjects will name other semantically related words that were not on the study list when trying recalling the study words.

Second, information from different episodic memory traces are pooled together during
episodic memory retrieval. Confabulations often do result, but need not, when distinct episodic memory traces are combined fallaciously. Imaging experiments suggest that episodes indeed form units of human cognition in that brain activity patterns are more similar within an episode than patterns from distinct episodes (Ezzyat and Davachi, 2011). It is noteworthy that this occurs even when subjects are not consciously aware of the fact that episodes were defined by hidden statistical rules (Schapiro et al., 2013). Nevertheless, as time passes it becomes difficult for subjects to keep separate information that they were exposed to during two distinct episodes. This was mostly studied using the misattribution paradigm, where information that was provided in post-session questions was fallaciously attributed to the original session (Loftus et al., 1978; Marsh et al., 2008; Zaragoza and Lane, 1994).

The results of psychological experiments thus support our model, in which, during episodic memory retrieval, scenarios are constructed based on episodic memory traces enriched with semantic information. The ultimate reason why episodic memory may be vulnerable to integration errors and biases may be that scenario construction evolved primarily to enable flexible simulation of future situations, rather than the faithful recreation of the past (Schacter and Addis 2007; Suddendorf and Corballis 2007).

We acknowledge that it is far simpler to obtain evidence for scenario construction in humans since they can use language to communicate the scenarios they produce. Indeed human’s capacity for flexible communication may have evolved for that very purpose (Suddendorf et al., 2009). However, behavioral evidence for scenario construction could be obtained by other means in principle. It is just that previous attempts at obtaining such evidence have not been compelling (Suddendorf and Corballis, 2010). Recent electrophysiological findings in rodents are also inconclusive. While hippocampal place cells are activated in sequences that were never experienced before (Dragoi and
Tonegawa, 2011; Gupta et al., 2010), there is no indication that these serve a function. It remains possible that these neural sequences are generated randomly by a neural network (Azizi et al., 2013). More relevant, perhaps, is the observation that, in familiar environments, place cell sequences predict upcoming movement trajectories (Pfeiffer and Foster, 2013). However, these sequences appear to correlate with planning a trajectory to a current goal rather than reflect the flexible construction of scenarios. In summary, there is no compelling evidence for scenario construction in non-human animals.

4 Conclusion

We have suggested that disparate findings from human and nonhuman animal studies in episodic-like and episodic memory can be integrated into a fruitful model. We propose that it may be useful to conceive of episodic memory traces as one of several components that are important for MTT, but that episodic memory traces can exist without these other components and may be present early in human development as well as in nonhuman animals. It might therefore be possible to directly apply insights into the neural mechanisms of episodic-like memory in nonhuman animals to understanding human episodic memory traces. At the same time, we are skeptical that nonhuman animals have developed all the other components of MTT and suggest that it remains quite possible that only humans are able to construct nested scenarios and reflect on them with a view to flexibly secure their future needs.

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7 Figure Captions

Figure 1: Schematic of three different models of episodic memory. See the main text for a more detailed description. The dashed box indicates the components most closely associated with Mental Time Travel (MTT). S&C 1997: Suddendorf and Corballis, 1997
Highlights

- Mental time travel (MTT) involves the construction of scenarios
- Scenarios contain information about participants, settings, interactions and events
- Scenarios are constructed based on episodic memory traces and semantic information
- Some nonhuman animals appear to encode, store and retrieve episodic memory traces
- Only humans seem to construct, reflect and flexibly compare alternative scenarios