

9. Compare this to perceptual processes where it is a common trope to point out that high-level beliefs do not and should not have any influence on what we perceive (Firestone & Scholl 2016).

10. Event memory can be considered to be past-directed only in a minimal, non-conceptual sense (see Russell 2014).

11. Note that we thus take the primary relevant contrast to be the one to event memory and not to semantic memory. To be sure, there is much to be said about the function of event memory (e.g., Nagy & Orban 2016), but this will not be our focus here.

12. Michaelian (2016a) has offered a more extensive discussion of the issues addressed in this section than we can cover here. Here we simply point out what we perceive to be the most central of our disagreements with his account.

13. To be sure, we frequently rely on epistemic authority in argumentation. Nonetheless, the mechanisms (by which claims to authority and arguments we try to change others' minds) differ.

14. In fact, from our perspective, the term *source monitoring* is slightly misleading because what these mechanisms monitor is not the source of our memories but their believability. Although the outcome of this process might be the ascription of a source, it does not monitor sources.

15. This is not to say that there are no other reasons why *event memory* requires veridicality. Because we are not concerned with event memory here, however, we do not discuss this issue.

be organized so that some temporally adjacent events are associated with one another, I might just as well have strong associations between stories about Anatolia, or facts related to the military.

Mahr & Csibra (M&C) provide a list of the distinctive features of episodic memory that form the basis for their argument that episodic memory serves a communicative function. These features delineate the general content of episodic memory and the manner in which the content is presented—but not how the content is retrieved or which contents are more likely to be retrieved. Although it would be unfair to expect the authors to discuss all of the distinctive features, I argue that the omission of temporally ordered retrieval, and of retrieval effects more generally, raises serious issues for their account.

I propose the following methodological principle for functional theories in an evolutionary context: If a distinctive feature of a system explains a significant number of the system's failures and successes, then this feature is likely relevant for understanding the function of the system. I'll now present a success of the episodic memory system that is best explained by appealing to temporally ordered retrieval. Then I'll discuss common memory failures that reflect problems with retrieval.

One way to get a handle on memory successes is to study memory experts. A technique of memory experts that has been documented as early as Roman times is the *method of loci* (MoL) (Cicero, 55 BCE/1948). This technique is used by mnemonists such as Shereshevsky in Luria's famous case study (Luria 1987), but is also effective as an intervention in normal and clinical contexts (Dalgleish et al. 2013; Gross et al. 2014). The therapeutic use of the MoL by Dalgleish et al. indicates that it is not only a neat party trick, but also an intervention that can increase fitness. In the MoL, a list or other kind of minimally structured set of items is learned by visualizing a well-known environment. Then the subject imagines herself walking through the environment and storing each item on the list in a different location. In short, the MoL takes semantic information and transposes it onto an episodic structure. Insofar as we are in a position to identify any memory successes, the MoL is an excellent candidate—and it relies on temporally ordered retrieval.

Now for failures. It's close to a consensus in research on all kinds of long-term memory that retrieval tends to be a functional bottleneck (Sweatt 2010). One way of seeing this intuitively is to think of all the times you couldn't remember some fact that later came to you easily. That you can be cued into remembering in a different context indicates that the memory trace was there the whole time. Your failure was not a failure to encode or a failure to store the encoded trace for long enough, but a failure to retrieve the stored information. A clinical example is the selective retrieval of traumatic episodic memories in posttraumatic stress disorder (PTSD). Patients with PTSD experience retrieval of memories related to the traumatic event in an uncontrolled fashion in contexts in which these memories are not useful or relevant. PTSD is manifestly unhealthy for the patient and, therefore, a memory failure in the fitness sense.

In summary, temporally ordered retrieval is a feature of the episodic memory system that is critical for some significant memory successes and is implicated in other memory failures. Combined with the aforementioned methodological principle, we can conclude that a satisfactory theory of the function of episodic memory should involve an explanation of how the distinctive features of episodic retrieval contribute to that function, including but not limited to temporal ordering.

Can M&C accommodate temporally ordered retrieval into their framework? To do so, they would need to argue that it serves a communicative function. I'd be very interested to see how this could be accomplished, but I'll end by noting a possible obstacle. The example of the MoL suggests that episodic temporal ordering works closely with semantic retrieval—recall that the MoL records semantic information using the episodic system. To explain this relationship between the two memory systems and their respective content, M&C might have to extend their account to semantic

## Open Peer Commentary

### Retrieval is central to the distinctive function of episodic memory

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**Abstract:** Episodic retrieval is heavily and asymmetrically dependent on the temporal order of the remembered events. This effect, or rather the underlying structure which it reflects, is a distinctive feature missing from the account in the target article. This structure explains significant successes and failures of episodic retrieval, and it has clear consequences for the fitness of the organism extending beyond communication.

*"I can't find my keys!"*

*"When did you last see them?"*

When having trouble retrieving an episodic event, such as where I put my keys, a common strategy is to run through the preceding events in order. For example, once I remember going out to get the mail, I'm more likely to remember hanging up my coat, and so on. This strategy works only because of a feature of episodic memory, which I'll refer to as *temporally ordered retrieval*. That is, the memory traces underlying episodic recall are organized such that the likelihood of retrieving information about an event at time *t* is significantly higher if someone is cued to retrieve information about an event at time *t*−1. Effects of this phenomenon have been well documented at the behavioral level, the most obvious being the asymmetrical contiguity effect in free recall (Healey & Kahana 2014), and the underlying temporal structure of memory representations is the subject of several computational hypotheses (Buzsáki 2005; Gallistel & King 2009). Temporally ordered retrieval is a distinctive feature of episodic memory; semantic memory, by contrast, seems to be far more permissive about the types and directions of associations. For instance, although my semantic memories of the history of Turkey might

memory function. In particular, I suspect that because the distinctively episodic mode of retrieval follows a standardized, inflexible rule for forming associations, it's more faithful than the mode used in semantic memory. In tasks where we're required to report unstructured information, especially in a fixed order, a faithful, standardized retrieval system is ideal. However, the more flexible semantic system for associations is more effective for other tasks. This suggests a function for the cooperation and division of labor between the two memory systems, which is unlikely to be only adaptive for communication.

## An adaptive function of mental time travel: Motivating farsighted decisions

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**Abstract:** The episodic memory system allows us to experience the emotions of past, counterfactual, and prospective events. We outline how this phenomenological experience can convey motivational incentives for farsighted decisions. In this way, we challenge important arguments for Mahr & Csibra's (M&C's) conclusion that future-oriented mental time travel is unlikely to be a central function of episodic memory.

Mahr & Csibra (M&C) dismiss future-oriented mental time travel as a central function of episodic memory (sect. 2.1.). In this commentary, we seek to challenge two central arguments to their conclusion: (1) their argument that deficient episodic memory does not impair future-oriented decisions and (2) their argument that a functional account of episodic memory based on future-directed mental time travel struggles to explain why it is possible to veridically recall past events.

There has been tremendous interest in mental time travel over the past decade, with a growing number of studies examining our capacity to imagine hypothetical episodes that either may take place in the future or that – counterfactually – could have happened in the past (Schacter et al. 2015). These studies have revealed striking similarities between such episodic simulation and episodic memory. For example, as mentioned by M&C, the two capacities are supported by the same core network of brain regions (Addis et al. 2007; Benoit & Schacter 2015; Hassabis et al. 2007a; Szpunar et al. 2007), are similarly deficient in amnesic patients (Hassabis et al. 2007b; Klein et al. 2002b; Race et al. 2011, but see also Squire et al. 2010), and also seem to exhibit parallel life span developmental trajectories (Addis et al. 2008; Busby & Suddendorf 2005). These observations have been taken to suggest that episodic simulation is based on an episodic memory system that provides stored details and constructive processes to recombine such details into novel events (Schacter et al. 2007).

Central to our commentary is a common feature of episodic memory and episodic simulation that is grounded in their auto-noetic format: The two capacities allow for the experience of “what it felt like” in past events, “what it could have felt like” in counterfactual events, and “what it would feel like” in prospective events. In the following, we describe how these mental experiences can facilitate farsighted decisions. We thereby seek to challenge the aforementioned two arguments.

First, as M&C rightly point out, despite their inability to imagine coherent future episodes, amnesic patients are not generally blind to the future (Craver et al. 2014b). A paradigmatic

example for future-oriented decisions consists of situations in which we have to choose between a smaller reward that we can receive immediately and a larger reward that we would receive only at a later time. People often make myopic decisions for the smaller reward in such situations, because they tend to discount the value of delayed rewards as a function of the time they would have to wait. M&C cite important evidence that amnesic patients don't discount future rewards more strongly than healthy people, despite their deficiency in simulating future episodes (Kwan et al. 2012; see also Kwan et al. 2013). These data thus seem to indicate that mental time travel does not contribute to future-oriented decisions. However, although amnesic patients typically don't show exaggerated discounting, we suggest, as detailed in the following, that they lack a particular mechanism that can adaptively *attenuate* such impulsive tendencies.

A possible reason for temporal discounting is that we generally don't experience the anticipated emotional impact of a future reward when making a decision (e.g., Rick & Loewenstein 2008). However, by simulating the future moment of consuming the reward, we can mentally create this experience. This simulated experience, in turn, has been hypothesized to increase the valuation of the delayed reward and, consequently, to attenuate discounting (Benoit et al. 2011; Boyer 2008). A growing number of studies have provided support for this hypothesis (e.g., Benoit et al. 2011; Liu et al. 2013; O'Donnell et al. 2017; Palombo et al. 2015; Peters & Büchel 2010). Critically, there is evidence that patients with hippocampal damage or atrophy following Alzheimer's disease, who are impaired at imagining future events, do not show reduced discounting in situations nominally fostering episodic simulation (Lebreton et al. 2013; Palombo et al. 2015; but see Kwan et al. 2015, where participants may have benefited from semantic, rather than episodic, future simulation; for further discussion, see Schacter et al. 2017). Although episodic memory is not necessary for all future-oriented decisions, we thus argue that – due to its auto-noetic format – it conveys prospective emotions that can render such decisions more farsighted, thereby supporting a fitness-relevant mechanism that maximizes future benefits.

Second, M&C argue that a future-directed account of episodic memory struggles to explain why memories can be veridically recalled. Specifically, they suggest that re-experiencing a past episode does not contribute to future planning beyond what can be provided by semantic memory. In their example, one can infer that there is going to be a long line at the swimming pool without re-experiencing the extended wait during one's last visit. By contrast, we suggest that the emotions elicited by episodically remembering a past event (D'Argembeau et al. 2003) can further serve to motivate future plans (e.g., avoiding the pool to prevent repeated boredom). Critically, this is only the case to the degree that our memories are veridical (e.g., if the line was indeed that long).

Moreover, memories of actual experiences can be contrasted with simulations of counterfactual events (e.g., “If instead we had taken a trip to the lake ...”). These counterfactuals induce emotional responses, such as regret, that further intensify with repeated simulations (Stanley et al. 2017) and that have been shown to influence prospective choices (Camille et al. 2004). Counterfactual simulations of reliably remembered events can thus motivate future-oriented decisions, which we argue constitutes an adaptive role for the veridical recall of the past (see also Schacter et al. 2015).

To conclude, we propose that episodic simulation – due to its auto-noetic format – allows for the experience of prospective and counterfactual emotions that convey motivational incentives for farsighted decisions. We don't assume that there is necessarily only one central function to episodic memory, nor do we challenge a possible contribution to human communication. However, we suggest that future-oriented mental time travel – with its outlined adaptive value – remains a candidate that should not readily be dismissed.