Deconstructing episodic memory with construction

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It has recently been observed that the brain network supporting recall of episodic memories shares much in common with other cognitive functions such as episodic future thinking, navigation and theory of mind. It has been speculated that 'self-projection' is the key common process. However, in this Opinion article, we note that other functions (e.g. imagining fictitious experiences) not explicitly connected to either the self or a subjective sense of time, activate a similar brain network. Hence, we argue that the process of 'scene construction' is better able to account for the commonalities in the brain areas engaged by an extended range of disparate functions. In light of this, we re-evaluate our understanding of episodic memory, the processes underpinning it and other related cognitive functions.

Introduction

Episodic memory [1,2], the memory for our everyday personal experiences, is an essential ingredient in shaping how we perceive ourselves [3]. Tulving [2,4] seminally defined three key properties of episodic memory recall: a subjective sense of time (mental time travel), connection to the self, and autonoetic consciousness – a special kind of consciousness that accompanies the act of remembering, enabling one to be aware of the self in subjective time [2]. Others have since identified visual imagery [5], narrative structure [5], retrieval of semantic information [6], and feelings of familiarity [7] as also being important aspects of recollection. Episodic memory recall is, therefore, a highly complex cognitive function that can be conceptually divided into several distinct component processes [3,6,8,9] and is accompanied by a rich recollective experience (Box 1) [2,4]. Although numerous functional magnetic resonance imaging (fMRI) studies investigating the neural basis of episodic memory recall [10–12] have revealed a consistent and distributed network of associated brain regions, surprisingly little is understood about the contributions individual areas make to the overall recollective experience [10–12].

In a stimulating Opinion article published in the February 2007 issue of *Trends in Cognitive Sciences*, Buckner and Carroll [13] make the astute observation that there is extensive overlap in the brain network activated during fMRI studies of remembering the past [10–12], and that engaged during other activities as diverse as thinking

about the future [14–16], navigation [17], theory of mind (perspective taking) [18], and the 'default network' [19] (and related to the 'default network', perhaps also 'mind wandering' [20]). This presents the intriguing possibility that these disparate cognitive functions, hitherto treated as distinct, might share common underlying processes. Buckner and Carroll [13] suggest that self-projection might be a crucial common process. They define self-projection as 'the ability to shift perspective from the immediate present to alternative perspectives…requiring a shift in perception from the immediate environment to the alternative, imagined future environment…referenced to oneself'. Thus, their proposal closely connects to Tulving's original ideas of mental time travel of the self [4]. Self-projection is undoubtedly important, perhaps even uniquely so for episodic memory recall and thinking about the future [2]. However, recent convergent neuropsychological [21], electroencephalographic (EEG) [22] and fMRI (D. Hassabis, D. Kumaran and E.A. Maguire, unpublished) findings suggest that at least one further important cognitive function, namely that of richly imagining fictitious experiences [21], is also reliant on the same brain network, but is not explicitly connected to either the self or a subjective sense of time.

Our Opinion article differs from that of Buckner and Carroll [13] in several ways. First we put forward the case for mental scene construction as a well-defined and key component process in supporting recollective experiences. Second, we argue that rather than self-projection [13], the process of scene construction is better able to account for the commonalities in the brain networks activated by all the disparate cognitive functions noted above (and possibly others in addition – see Box 2). Third, we link the process of scene construction with existing theories that view the recollection of complex episodic memories as a (re)constructive process [3–5,8,23–25].

Scene construction

We define scene construction as the process of mentally generating and maintaining a complex and coherent scene or event. This is achieved by the retrieval and integration of relevant informational components, stored in their modality-specific cortical areas [26], the product of which has a coherent spatial context [21], and can then later be manipulated and visualized. The full recollective experience of richly recalling an episodic memory [2], for example, remembering what you did last Saturday evening, is nearly always accompanied by complex mental imagery [5] of that event played out within a spatial context [27,28] – likewise if you

Box 1. What, where, when – are they equally important?

In the classic taxonomy of episodic memory [1,2], what, where and when, have been traditionally regarded as equally important properties of an episodic memory [2,4]. Indeed, a memory of an event is only defined as truly episodic if one remembers when and where it happened in addition to what happened [2]. The rich recollective experience that accompanies the recall of an episodic memory [2,4] has content and a spatial context, the what and the where – the central contribution of the scene construction process to the provision of this coherent spatial context has been highlighted in the main text. But what role does time have, and is it really as important to the recollective experience as the other two aspects of an episodic memory? Much has been written about time [2,75–78] and there are at least two types of time that have relevance to the recollective experience of episodic memory. There is the moment by moment order in which an event or sequence unfolds [72] or 'micro-time'. Then there is subjective time [2], the timeline against which the events in our lives play out, the conscious awareness of which has been dubbed chronesthesia [76], and which we view as 'macro-time'. Micro-time, then, is an intrinsic property of an episodic memory that when recalled ensures it is played back in the same (or reverse [79]) temporal sequence in which it was recorded [43]. It is related to the physical laws of nature, for example, one must open a door before going through it, and it might be reliant on the special anatomical properties of the hippocampus [43,44].

By contrast, macro-time is a concept that, unlike micro-time [72], perhaps only humans possess [2,73]. But should it be elevated to the status of a special sense or process as some have suggested [13,76], and is it necessary for the full recollective experience of an episodic memory? Recent empirical evidence does not support the idea that chronesthesia is an independent process with a distinct neural signature. Near total overlap has been found in brain regions supporting past episodic memory recall and episodic future thinking [15,16]. Besides the subjective sense of past/future as described by Tulving [4], macro-time has also been commonly interpreted to mean that there are specific time-tags associated with each episodic memory. Interestingly, studies testing memories from distinct time periods have also failed to show consistent neural correlations in response to macro-time modulation [15,41,51,80,81], and time is also a poor retrieval cue for episodic memory [82]. Finally, if the age of a memory has some intrinsic neural basis then it seems plausible it might be related to the age of its memory trace [41,83]. However, in light of current ideas regarding reconsolidation [84], it is not clear whether one can meaningfully talk about the age of a memory because the act of recalling it refreshes the trace anew [84].

Thus, although macro or subjective time is frequently part of a true episodic memory it is not clear whether it can be meaningfully separated from ideas of the self and autonoetic consciousness [2]. This is in contrast to micro-time, which appears to be an intrinsic property of an episodic memory [43,79]. By this view then, the timestamp of an event simply becomes another piece of semantic knowledge that might or might not be retrieved or logically deduced at the point the event is recalled, perhaps not too dissimilar to the name of the place it occurred in or the names of any people involved.

cast your mind forwards to what you might be doing next Saturday evening [14]. However, we believe that scene construction is not just limited to remembering the past [2] or thinking about the future [14]. For example, nowhere is it more necessary than for navigation [29]. Think about how you would get to your favourite restaurant and chances are you will construct a mental representation of the street, the surrounding vicinity, and perhaps where you might park. Alternatively, imagine taking a pleasant walk through a forest that you have never been to, seen, or recognize but is instead purely a product of your imagination. Again, construction of a coherent scene would appear to be integral to the process of vividly imagining such a fictitious experience

[21]. Thus, we argue that the cognitive functions outlined in Box 2 are related because they all crucially rely on scene construction as a common core process, and that this can account for a large proportion of the overlapping network found in neuroimaging studies of these functions [13]. If scene construction is a key underlying component process of episodic memory, this would accord well with theories of memory that propose the recollection of complex episodic memories is actually a (re)constructive process [3–5,8,23–25] as opposed to the all-or-nothing retrieval of a perfect 'holistic' record often implicitly assumed (e.g. Ref. [30]; also see discussions in Refs [31,32]). Indeed, well-known memory errors and inconsistencies [33,34], such as misattribution [33], provide further tacit evidence for constructivist views of episodic memory [3–5,8,23–25].

Neuropsychological evidence

So which brain regions might support scene construction and what are their roles? Neuropsychological studies of patients with hippocampal damage confirm that the hippocampus is crucial for episodic memory [35,36] and navigation [37]. It has also been demonstrated that hippocampal damage [21,38–40] is associated with an impairment in thinking about one's personal future [14]. However, a recent study [21] showed that the deficit might not be limited to just past and future personal experiences as some have suggested [13,15,40], but possibly to any task that requires a rich 'recollection-like' experience [21]. Hassabis *et al.* [21] devised a novel paradigm where participants, rather than recollecting the past, had to construct new imagined experiences in response to short verbal cues that outlined a range of simple commonplace scenarios. In all previous studies and discussions [13], it is assumed that imagination necessarily involves mental time travel involving the self into the future, and is a form of episodic future thinking [14]. By contrast, Hassabis *et al.* do not make such an assumption, and maintain that it is possible to richly imagine and visualize a new fictitious experience that is not explicitly temporal in nature, and that is not necessarily self-relevant, plausible or even possible (Box 2). They found that amnesic patients with bilateral hippocampal damage were markedly impaired relative to matched control subjects at imagining new fictitious experiences (Figure 1). Moreover, Hassabis *et al.* [21] identified a possible source for this deficit. Although patients were able to produce considerable detail when asked to imagine fictitious new experiences, their descriptions lacked spatial coherence and were instead fragmented and considerably less rich [21].

We believe these findings provide empirical evidence that the hippocampus supports scene construction, crucial for imagining new experiences (and we would argue for recollecting the past, imagining the future and navigation; Box 2), either through its ability to process spatial information [27,28,41,42] or bind together disparate elements of the imagined scene [43–46]. These findings could also have implications for the ongoing debate [47] concerning whether the hippocampus is necessary [41] or not [48] for supporting remote episodic memories. It has been suggested that discrepancies between studies of remote episodic memory in hippocampal patients [47] might be accounted for by differences in the quality or richness of the recollective

Box 2. Component processes

The intention here (Table I) is to summarize the mapping of the component processes discussed in the main text onto a set of related cognitive functions. It is not intended to be an exhaustive list of all possible processes involved in these cognitive functions, nor are we suggesting these are the only cognitive functions these processes are involved in. Nonetheless we believe this provides a useful overview of our argument.

Definitions of cognitive functions
- Episodic memory recall – vivid recollection of a personal past event [2].
- Episodic future thinking – envisaging a plausible personal future event [14].
- Navigation – route planning and wayfinding [17].
- Imagination – richly imagining and visualizing a new fictitious experience [21] that is not explicitly temporal in nature and is not necessarily self-relevant, plausible or even possible. Although it might involve the adoption of an egocentric viewpoint [59] on the part of the imaginer, a purely created imagined experience would not have the same reliance or effect on the imaginer's self-concept [3] compared with a real episodic memory.
- Default network – so-called default network activated when no overt task is assigned [19], also suggested to be related to mind wandering or daydreaming [20].
- Viewer replay – the vivid replay of an episodic-like memory even though the specific temporal time tag cannot be remembered, it has only an internal spatial context and, as with imagination (see above), does not explicitly involve the self or affect the viewer's self-concept. For example, the recollection of one's favourite episode from an old TV series can be vivid and detailed, even though often one can no longer remember when or where it was seen. This type of memory is of ambiguous theoretical status (because it only has

the 'what' [2]) and does not fit easily into definitions of episodic or semantic memory [2].
- Vivid dreaming – vivid visual dreaming usually takes place during the rapid eye movement (REM) phase of sleep [85]. Interestingly, global cessation of dreaming has been associated with damage to either frontal or parietal cortex [85].
- Theory of mind – modelling the mental states and intentions of others [18].

Definitions of processes
- Scene construction – includes the retrieval of relevant semantic and sensory information [9,26], its integration into a coherent spatial context [21] and online maintenance for later manipulation and visualization [5] including possible viewpoint transformation [59].
- Subjective time – sense of the self in the context of the timeline against which the events in our lives play out [2] or chronesthesia [76].
- Self – processes reliant on or affecting the concept of oneself [3] and thereby having a direct connection to or influence over our self-perception [2].
- Autonoetic consciousness – a special kind of consciousness that accompanies the act of remembering, allowing one to be aware of the self in subjective time [2].
- Narrative – a story structure formed by the unfolding of a sequence of events [5].
- Familiarity – a subjective feeling or judgement of oldness [7].
- Visual imagery – complex visual imagery, involving the composition of simple imagery such as single objects [5].
- Prospective planning – making plans about how to achieve future goals [61].
- Task monitoring – executive processes overseeing successful constructive task performance [61].

Table I. Mapping of component processes to cognitive functions[a]

	Scene construction	Subjective time	Self	Autonoetic consciousness	Narrative	Familiarity	Visual imagery	Prospective planning	Task monitoring
Episodic memory recall	Y	Y	Y	Y	Y	Y	Y	N	Y
Episodic future thinking	Y	Y	Y	Y	Y	Y	Y	Y	Y
Navigation	Y	N	D	N	N	D	Y	Y	Y
Imagination	Y	N	N	N	D	D	Y	N	Y
Default network	Y	N	Y	D	D	D	D	N	U
Viewer replay	Y	N	N	N	Y	Y	Y	N	Y
Vivid dreaming	Y	N	D	N	Y	D	Y	N	U
Theory of mind	D	N	Y	N	N	D	D	D	D

Abbreviations: Y, yes – process is involved in that cognitive function; N, no – process is not involved in that cognitive function; D, depends – process involvement depends on the precise nature of the task and the content operated on; U, unknown – unclear if process is involved in that cognitive function.
[a]Processes are labelled along the top and cognitive functions down the left hand side.

experience, a feature that is not always captured by existing scoring systems [41,49,50]. Indeed, recent evidence suggests that the hippocampus might be crucial for recollecting vivid, detailed episodic memories, regardless of their age [41,51, 52]. Hassabis *et al.*'s results [21] are consistent with this perspective and moreover suggest that the crucial attribute determining whether internally generated experiences, either real or imaginary, are hippocampal-dependent might be the extent to which they are vividly (re-)experienced.

Neuroimaging evidence
The hippocampus, although apparently vital, does not support scene construction on its own. In contrast to

neuropsychological studies, fMRI permits examination of distributed networks of brain regions engaged during tasks. In addition, by using what is known as a conjunction analysis, it is possible to ascertain the brain areas that are engaged in common during the performance of different tasks. Imagining fictitious experiences and reliving past memories share many of the same psychological processes [3,6,8,9] primarily related to scene construction [21]. We recently investigated whether they had neural substrates in common using fMRI (D. Hassabis, D. Kumaran and E.A. Maguire, unpublished). During scanning, subjects were asked to recall recent episodic memories. They also retrieved fictitious experiences previously constructed one
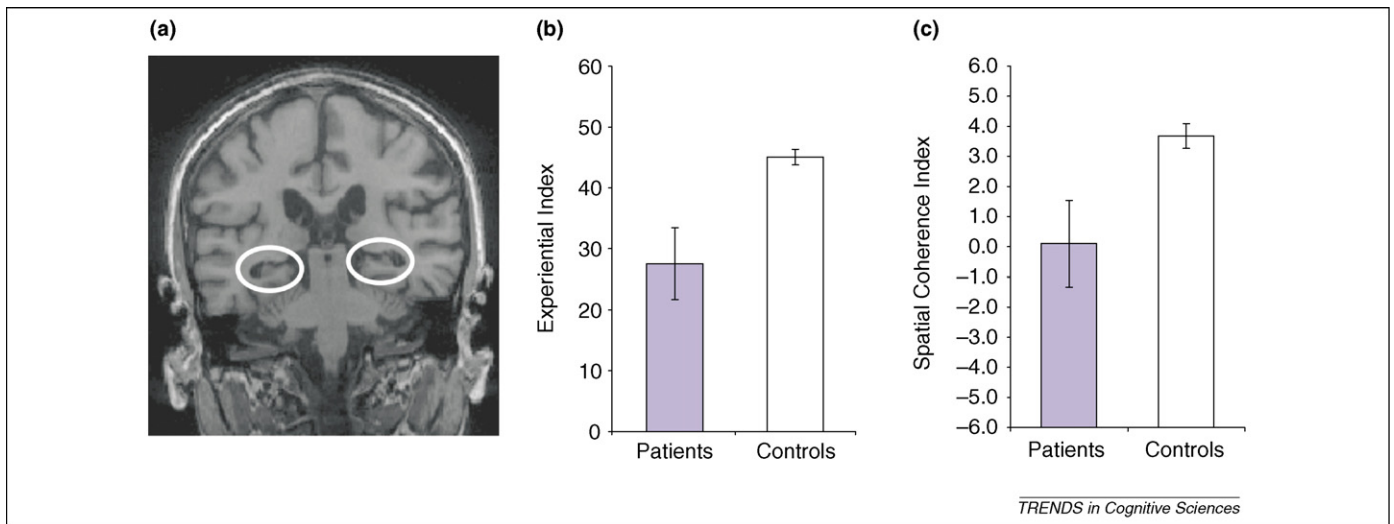
Figure 1. The hippocampus and scene construction. Hassabis *et al.* [21] devised a novel paradigm where patients with bilateral hippocampal damage (see example patient MRI scan in **(a)**, with atrophied hippocampi circled) and matched control subjects, rather than recollecting the past, had to imagine fictitious experiences. Patients were significantly impaired on this task. The mean scores (and standard errors) on the overall composite measure, the Experiential Index, are shown in **(b)**. The findings also offer some insight into a mechanism whose absence could underpin the deficit. Patients' imagined experiences were strikingly deficient in spatial coherence **(c)**, resulting in their constructions being fragmented and lacking in richness.

week before, and in addition constructed new fictitious experiences for the first time while in the scanner. A conjunction analysis of the three conditions, which have scene construction as their primary process in common, revealed activation of a network of regions including, not surprisingly, (compare with Ref. [21]) the hippocampus, but also parahippocampal gyrus, retrosplenial cortex, and posterior parietal cortex, as well as the ventromedial prefrontal cortex (vmPFC, BA 12) and middle temporal cortices (Figure 2). Previous fMRI studies have consistently observed activation of a similar network during navigation [17,53], spatial [54,55], place [56,57] and episodic memory [10,11] tasks lending further credence to the notion of scene construction as a common core process.
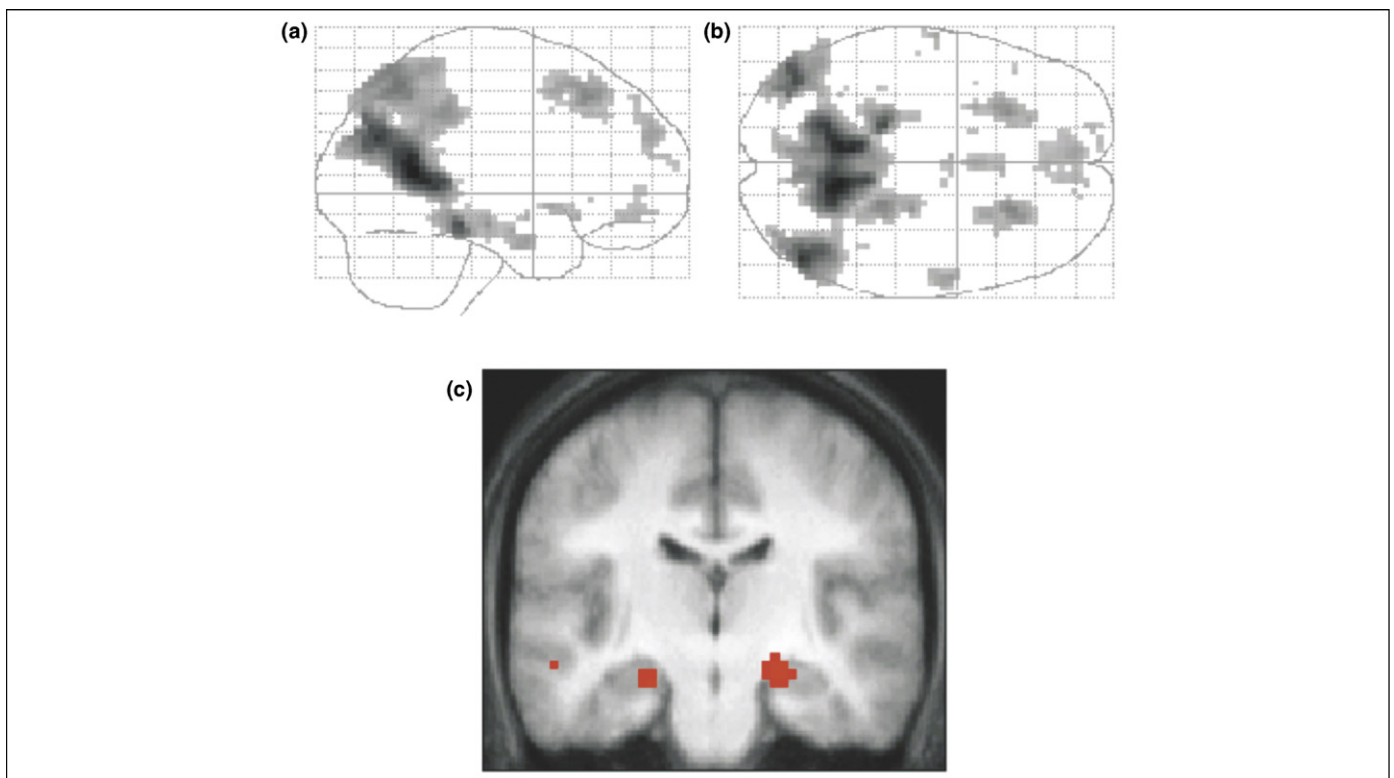

Figure 2. The extended brain network involved in scene construction. The common brain network that underlies the recall of episodic memories, recall of previously imagined experiences, and the creation of new imagined experiences (D. Hassabis, D. Kumaran and E.A. Maguire, unpublished; also see main text). Sagittal **(a)** and axial **(b)** images from a 'glass brain' – this enables one to appreciate activations in all locations and levels in the brain simultaneously. The glass brain reveals an extensive temporo-parietal-frontal network including bilateral hippocampus, parahippocampal gyrus, retrosplenial and posterior parietal cortices, and ventromedial prefrontal cortex. **(c)** Bilateral hippocampus activation on a coronal section of an averaged structural MRI scan.

Although relatively understudied, the retrosplenial cortex [58] plays a major role in memory and navigation [53]. Perhaps through facilitating viewpoint transformation from an allocentric to egocentric framework [29,59] or by acting as an output buffer to represent dynamically episodic information [7,60] that has been retrieved and bound by the hippocampus [21,43]. Moreover, retrosplenial cortex is known to have major anatomical connections to vmPFC [58], also activated in the conjunction analysis (Figure 2). The vmPFC has been implicated in performance monitoring [61] and semantic detail generation [15], both of which would be required in scene construction, with the middle temporal cortex activations probably reflecting the retrieval of semantic information [62]. The vmPFC might therefore work in concert with medial temporal lobe structures and retrosplenial cortex to monitor successfully the scene construction process [61].

Other key properties of episodic memory

Scene construction can, therefore, account for a good deal of the brain network consistently activated by episodic memory. In our recent fMRI study (D. Hassabis, D. Kumaran and E.A. Maguire, unpublished), not only could we examine the commonalities across different types of tasks using a conjunction analysis, but we could directly compare the recall of recent real episodic memories with the recall of previously constructed fictitious experiences that were well-matched for difficulty, age, detail and vividness. This allowed us to partial out the effects of scene construction, and ask which brain regions might be responsible for other key aspects of the recollective experience, namely subjective sense of time,

connection to self, and autonoetic awareness [2,6]. The anterior medial prefrontal cortex (amPFC, BA 10) and regions of the posterior medial parietal cortex, including posterior cingulate cortex and precuneus, were the only regions found to be preferentially engaged during the recall of real episodic memories as opposed to imaginary memories (Figure 3). This pattern of activation bears a striking resemblance to networks found to support self-reflection [63], theory of mind [54,64] and episodic future thinking [15]. The amPFC in particular has been heavily implicated in mentalizing [18,64] and self-perception processes [3,63], and has long been predicted by Tulving [2,6] as an area important for autonoetic consciousness and mental time travel on the basis of findings from patients with frontal lesions [6]. By contrast, activation of posterior parietal regions has previously been observed in studies of recognition memory, responding preferentially to old or familiar items [7,65], suggesting that real memories are in some sense more familiar than imagined fictitious memories, which is perhaps not surprising given their often highly familiar content. We therefore suggest that during recall of real episodic memories the interaction or cooperation between these self-relevant and familiarity functions might be sufficient to give rise to the phenomenological feeling of whether a re-experienced event actually happened to one in the past or not [2], or indeed whether it could plausibly happen to one in the future [14,15]. It is interesting to speculate whether this process might have malfunctioned in patients with schizophrenia [66] and in confabulators [67].

These findings connect with those from a recent fMRI study [15] that explored episodic future thinking [14].
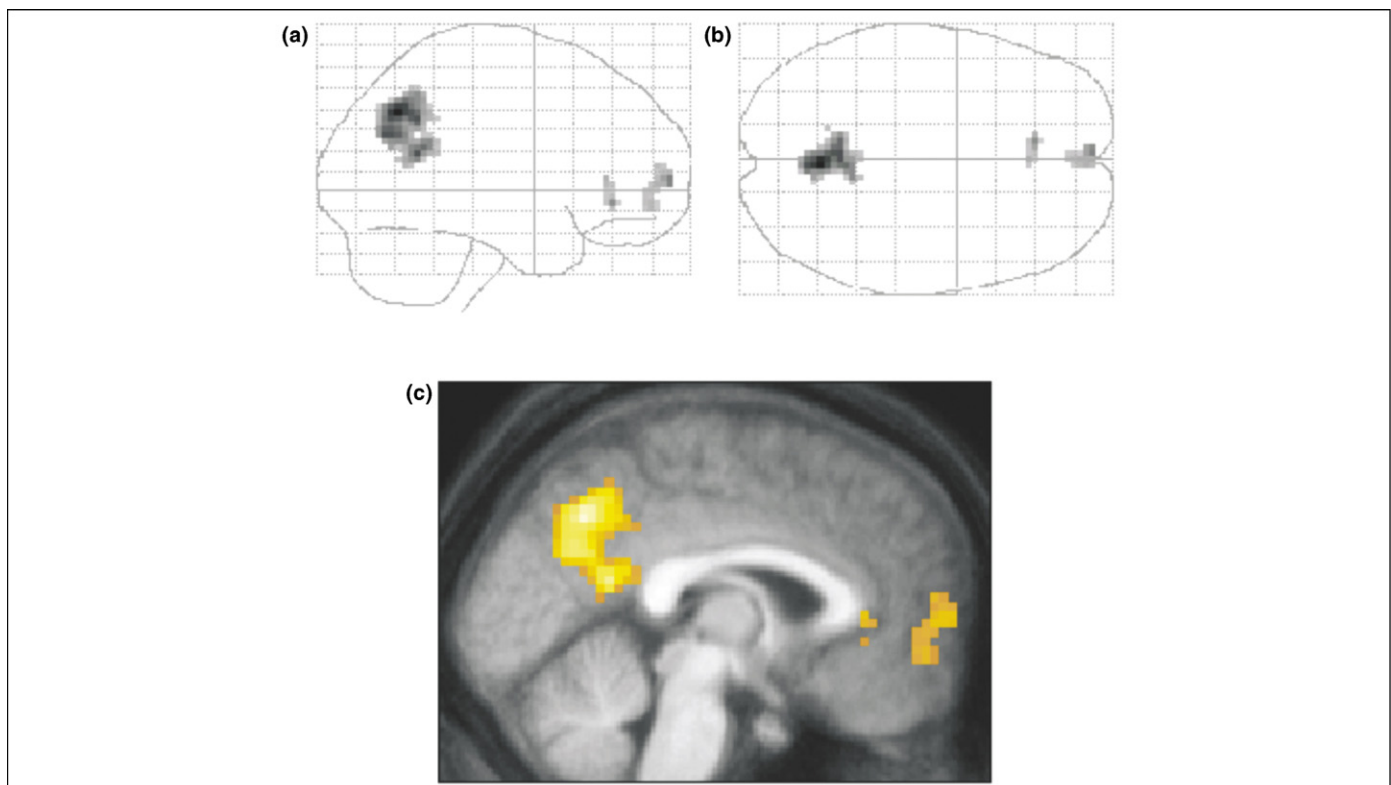

Figure 3. Recall of real versus imaginary memories. Sagittal **(a)** and axial **(b)** images from a 'glass brain', showing that anterior medial prefrontal cortex (BA 10) and posterior parietal cortex, including the precuneus and posterior cingulate cortex, are preferentially engaged by the recall of real memories (D. Hassabis, D. Kumaran and E.A. Maguire, unpublished). **(c)** These activations can be seen on a sagittal section of an averaged structural MRI scan.

Addis *et al.* [15] found comprehensive overlap between the brain networks supporting recall of past memories and thinking about plausible personal future events. Indeed, if considered from a process point of view, then all the processes highlighted so far (see Table I in Box 2), including scene construction and the self, are present in both episodic memory recall and episodic future thinking. Therefore, one would predict the more or less complete overlap in brain networks that was indeed found by Addis *et al.* [15]. We suspect that the reason a study by Szpunar *et al.* [16], which also examined episodic future thinking, did not observe some of the brain regions involved in scene construction that we highlight here is because their baseline task (imagining Bill Clinton in various situations) would also have activated regions involved in scene construction, making it difficult for this factor to be examined. This is also true of other studies where, although scene construction might have been involved, the process was not formally considered, controlled or manipulated (e.g. Ref. [68]).

Conclusions and future directions

A rich recollective experience is a key feature of episodic memory recall [2,4]. Here, we have put forward the case for scene construction as a well-defined and key component process in supporting that recollective experience. Scene construction provides the stage on which the remembered event is played or the 'where' for the 'what' to occur in, using Tulving's 'what, where, when' taxonomy of episodic memory [2] (Box 1). Moreover, we argue that scene construction is an excellent candidate for a common core process that underpins a host of related cognitive functions [13] (Box 2) including navigation and imagination. A swathe of temporal and parietal regions, as well as ventromedial prefrontal cortex, support the construction, maintenance and visualization of a scene, including prominent roles for the hippocampus and retrosplenial cortex and, thus, potentially accounting for a large part of the network consistently activated in episodic memory recall tasks [10,11].

From a systems standpoint, therefore, it could prove fruitful to consider episodic memory within the context of a set of related cognitive functions, some non-mnemonic, that share common component processes including scene construction, the self, autonoetic consciousness and familiarity. This accords well with views of memory [69] that posit that one-to-one mapping does not exist between tasks and systems but that instead all tasks are 'multiply determined' [2]. Different cognitive functions call on combinations of different component processes depending on the precise nature of the content and the goal to be achieved, with episodic memory, arguably the most complex of these functions, recruiting all these processes and, thus, sitting at the apex of this group. It follows then that damaging any of these operating components will, in turn, impair any cognitive functions relying on that process [69]. This would explain why episodic memory appears to be more vulnerable than other memory systems [2] because it relies on so many wide-ranging underlying component processes across an extensive network of brain regions [10,11].

In the future, new paradigms will be needed to make progress in further disambiguating the myriad of

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Box 3. Evolutionary function of construction

If constructive processes (i.e. the ability to put informational components together in novel ways in the service of a goal) underlie episodic memory and many other related high-level cognitive functions (see Box 2), what, if any, evolutionary advantages does this confer? [2,76]. From a computational perspective, reconstructing a memory from its components is more efficient in terms of storage capacity than the alternative of storing each memory separately as an intact record [25,33]. Furthermore, this kind of storage structure lends itself conveniently to making abstraction and generalization inferences across distinct experiences [44].

One can speculate as to whether episodic memory evolved as the ultimate expression of the combination of these underlying processes [2,76] or whether these processes developed to support episodic memory and were then later co-opted for use by other functions. Either way it seems clear that the resultant flexible system is useful for survival [13,25]. Consider an organism that, in their present situation, is confronted by several choices of what to do next. Being able to accurately and richly mentally simulate [13] or construct what those possible future states might be like, before making the decision, would aid both the evaluation of the desirability of those outcomes and the planning processes needed to make them happen. The applications of construction go beyond just planning for and anticipating possible future events [13,14,25,71] based on past experience. It forms the basis of imagination and possibly creativity, where constructions are envisaged that are not directly related to a temporal future or past, or to prediction *per se*, but for general problem-solving and invention purposes such as tool manufacture or art.

It has been suggested that the episodic memory system is unique to humans [2,73]. This might be true for properties such as autonoetic consciousness and self-awareness that are difficult to categorically test for in animals given the absence of language [71]. However, there is considerable evidence that certain animals do possess at least some of these constructive episodic capabilities [13,71,75]. This has been demonstrated most persuasively in scrub-jays, a member of the corvid family of birds [71]. They intelligently and flexibly cache food for future consumption [74,75] and display impressive 'causal reasoning, imagination and prospection abilities' [71]. The complexity of the constructive episodic memory system and its underlying processes might be the key to its flexibility [2]. It could also explain its vulnerability (see main text) and why it is relatively late developing, only becoming fully operational in humans at the age of about four years [2].

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component processes that underlie episodic memory. We have demonstrated the novel task of richly imagining fictitious experiences as an example of a valuable tool in the service of this aim. Further work will also be required to ascertain the precise contribution of regions such as the amPFC and retrosplenial cortex, how the machinery that supports scene construction might be related to that which supports scene perception [46,70], and how the role of emotion should be included [5]. In light of recent ideas [13,71,72] (Box 1), it might also be worth reconsidering to what extent animals have some or all the abilities that characterize episodic memory [13,71–73], particularly given the intriguing findings from scrub-jays in a series of elegant experiments by Clayton and colleagues [74,75] (Box 3). In summary, we believe that by focussing on the constructive nature of episodic memory recall [3–5,8,23–25], with processes such as scene construction at their core, we can begin to understand what makes episodic memory the distinct kind of memory Tulving so presciently argued for more than three decades ago [1,2].

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