

The construction system of the brain

Demis Hassabis and Eleanor A. Maguire

Phil. Trans. R. Soc. B 2009 **364**, 1263-1271
doi: 10.1098/rstb.2008.0296

References

[This article cites 70 articles, 20 of which can be accessed free](#)
<http://rstb.royalsocietypublishing.org/content/364/1521/1263.full.html#ref-list-1>

Rapid response

[Respond to this article](#)
<http://rstb.royalsocietypublishing.org/letters/submit/royptb;364/1521/1263>

Subject collections

Articles on similar topics can be found in the following collections
[neuroscience](#) (276 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

The construction system of the brain

Demis Hassabis* and Eleanor A. Maguire*

*Wellcome Trust Centre for Neuroimaging, Institute of Neurology, University College London,
12 Queen Square, London WC1N 3BG, UK*

The ability to construct a hypothetical situation in one's imagination prior to it actually occurring may afford greater accuracy in predicting its eventual outcome. The recollection of past experiences is also considered to be a reconstructive process with memories recreated from their component parts. Construction, therefore, plays a critical role in allowing us to plan for the future and remember the past. Conceptually, construction can be broken down into a number of constituent processes although little is known about their neural correlates. Moreover, it has been suggested that some of these processes may be shared by a number of other cognitive functions including spatial navigation and imagination. Recently, novel paradigms have been developed that allow for the isolation and characterization of these underlying processes and their associated neuroanatomy. Here, we selectively review this fast-growing literature and consider some implications for remembering the past and predicting the future.

Keywords: episodic memory; imagination; hippocampus; autobiographical;
functional magnetic resonance imaging; episodic future thinking

1. INTRODUCTION

The recollection of episodic memories is widely accepted to be a reconstructive process as opposed to the simple retrieval of a perfect holistic record (Bartlett 1932; Schacter *et al.* 1998, 2008; Conway & Pleydell-Pearce 2000; Rubin *et al.* 2003; Hassabis & Maguire 2007). Recollection relies on a number of component processes. These include a sense of subjective time (Tulving 2002), connection to the self (Conway & Pleydell-Pearce 2000; Gallagher 2000), narrative structure (Rubin *et al.* 2003), retrieval of relevant semantic information (Wheeler *et al.* 1997, 2000; Gottfried *et al.* 2004), feelings of familiarity (Wagner *et al.* 2005) and rich multimodal re-experiencing of the event (Tulving 2002) in a coherent spatial context (Byrne *et al.* 2007; Hassabis & Maguire 2007; Hassabis *et al.* 2007b; Bird & Burgess 2008). From functional magnetic resonance imaging (fMRI) studies, we also know that a distributed and highly consistent network of brain regions supports memory for past experiences. This comprises dorsal and ventromedial prefrontal cortex (PFC), lateral PFC, the hippocampus, parahippocampal gyrus, lateral temporal cortices, temporoparietal junction, thalamus, retrosplenial cortex (RSC), posterior cingulate cortex (PCC), precuneus and cerebellum (Maguire 2001a; Maguire & Frith 2003; Svoboda *et al.* 2006; Cabeza & St Jacques 2007; Hassabis *et al.* 2007a; figure 1). Despite over a decade of activating this network, however, surprisingly little is understood about the contributions individual brain areas make to the overall recollective experience (Hassabis & Maguire 2007).

Taking a different approach, several recent fMRI studies compared recall of autobiographical memories with predicting possible personally relevant future events (known as episodic future thinking (EFT), Atance & O'Neill 2001), and found near complete overlap in the brain networks activated (Okuda *et al.* 2003; Szpunar *et al.* 2007; Botzung *et al.* 2008, but see Addis *et al.* 2007). In terms of characterizing the underlying processes and their mapping to specific brain regions, however, it is clear from these studies that only limited further progress can be made by using EFT as a comparison task because it engages all of the same processes as episodic memory and to a similar degree (Suddendorf & Corballis 1997; Schacter *et al.* 2007). Here, we suggest that in the context of real-world experiences, a productive way to investigate recollection of the past and prediction of the future is, ironically, not to study the past or the future at all. We argue that because the core processes underlying prediction of the future can be co-opted by a range of other atemporal cognitive functions, these processes may be best isolated and understood in the context of paradigms where time is not an explicit factor, such as imagining fictitious experiences. We believe that time does not merit elevation to the level of an independent process with a distinct neural signature. Instead, we view the time-stamp of an event (whether future or past) as simply the result of a content or goal difference rather than a change in the fundamental processes involved (see Hassabis & Maguire 2007). In order to test this idea, it has been necessary to develop novel experimental paradigms.

2. USING IMAGINATION

Recently, one important tool in the development of novel tasks has been imagination (Hassabis & Maguire 2007). In many ways, imagining new experiences can be regarded as the purest expression of construction.

* Authors for correspondence (d.hassabis@fil.ion.ucl.ac.uk, e.maguire@fil.ion.ucl.ac.uk).

One contribution of 18 to a Theme Issue 'Predictions in the brain: using our past to prepare for the future'.

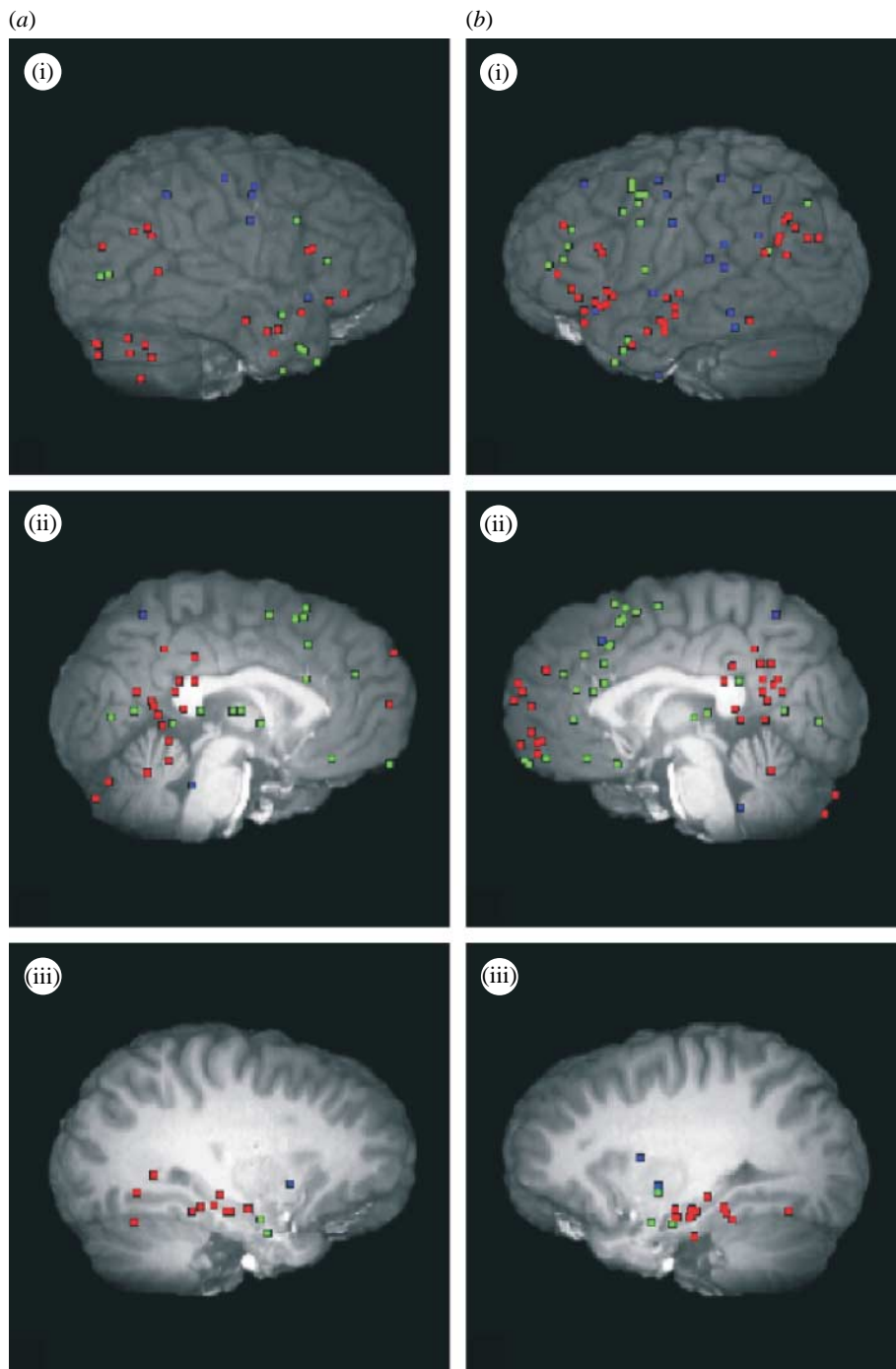


Figure 1. (*a,b(i)–(iii)*) The episodic memory network. Significant peaks of activity from a meta-analysis of 24 neuroimaging studies of autobiographical memory (Svoboda *et al.* 2006). The classic core episodic memory network can be seen in red and includes the hippocampus bilaterally, parahippocampal gyrus, retrosplenial, posterior cingulate and posterior parietal cortices and medial PFC. Activations in core (red), secondary (green) and infrequently reported regions (blue) are depicted across right and left, lateral, medial and subcortical planes. Adapted from Svoboda *et al.* (2006) with permission from Elsevier.

All healthy volunteers can effortlessly use their imagination to a basic degree (indeed humans have told stories and delighted in fiction and narrative for thousands of years), and verbally induced imagination of scenes has been shown to be possible and useful in the neuropsychological context (Bisiach & Luzzatti 1978). Experiences constructed by the imagination, while having much in common with episodic memories, have the advantage of being easier to systematize and experimentally manipulate (Hassabis & Maguire 2007). For example, participants can be asked to construct the same fictitious situations, and their

performances can be compared and contrasted more directly than would be possible in a standard episodic memory recall paradigm (Hassabis *et al.* 2007b).

Crucially, tasks involving imagined scenarios can be designed to de-emphasize key features allowing insights to be gained into the neural substrates of these features when compared with episodic memories (Hassabis *et al.* 2007a). For example, participants can be asked to construct fictitious experiences in their imagination that are atemporal (i.e. not set in the past or in the future) and with a low connection to the self. Figure 2a shows a description of one such imagined

(a)
 Cue: Imagine standing by a small stream somewhere deep in a forest
 'It's a pine forest. What I can see on the ground all around me are patches of pine needles and brown earth with nothing really growing. The tree trunks are quite narrow. Overhead are the spikes of the green pines and you can only just see the sky. There's a pine needle smell but down towards the stream there's a slightly rotting smell. It's quite a narrow stream with stones in it and dark water rushing round them causing little white water eddies. There's not much life around the stream and the banks are quite steep sloping down to the stream. It's peaceful and quiet...'

(b)
 Time scale: 5 years in future; cue: dress
 'My sister will be finishing... her undergraduate education, I imagine some neat place, Ivy League private school... it would be a very nice spring day and my mom and my dad will be there, my dad with the camcorder as usual, and my mom with the camera as usual. My sister will be in the crowd and they'd be calling everyone's name... I can see her having a different hair style by then, maybe instead of straight, very curly with lots of volume. She would be wearing contacts by then and heels of course. And I can see myself sitting in some kind of sundress, like yellow, and under some trees... the reception either before or after and it would be really nice summer food, like salads and fruits, and maybe some sweets, and cold drinks that are chilled but have no ice. And my sister would be sitting off with her friends, you know, talking with them about graduating, and they'd probably get emotional.'

Figure 2. Descriptions of experiences. Representative examples of participant transcripts when cued to describe (a) an imagined fictitious experience (data from Hassabis *et al.* 2007a) and (b) a personally relevant future experience (data from Addis *et al.* 2007). Note the absence of explicit temporal and self-relevant statements in (a) that are commonplace in (b) such as 'I will be' and 'my sister is there'.

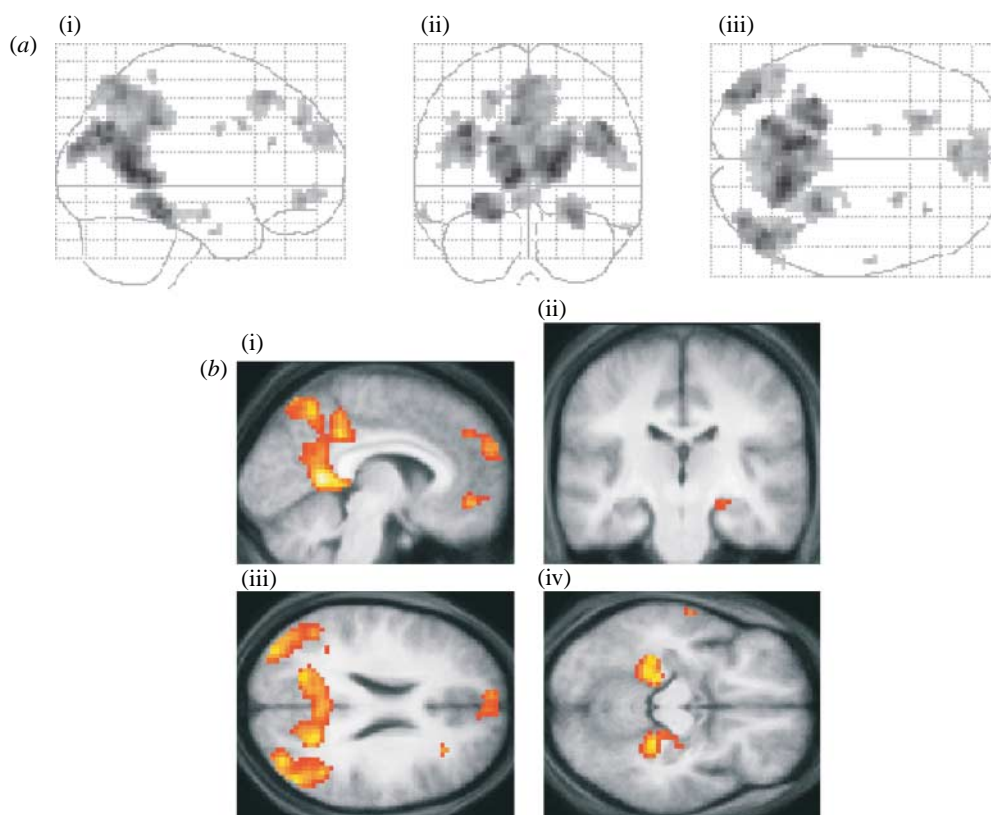


Figure 3. The imagination network. Brain regions active when recalling imagined fictitious experiences that were previously created in a pre-scan interview included the hippocampus, parahippocampal gyrus, retrosplenial and posterior parietal cortices and medial PFC. (a)(i) Sagittal, (ii) coronal and (iii) axial images from a 'glass brain', which enables one to appreciate activations in all locations and levels in the brain simultaneously. (b) Activations on a selection of relevant (i) sagittal, (ii) coronal and ((iii),(iv)) axial sections from the averaged structural MRI scan of the 21 study participants at a threshold of $p < 0.001$ uncorrected (data from Hassabis *et al.* 2007a).

experience (Hassabis *et al.* 2007a). It is interesting to contrast this transcript with one from an fMRI study involving plans for a future personal experience (Addis *et al.* 2007; figure 2b). Clearly the imagined scenario is set in the present and in this case does not have the same involvement with the imaginer's self-schema as the personal future event (Conway & Pleydell-Pearce 2000; Gallagher 2000) although both types of scenario involve the adoption of an egocentric viewpoint on the part of the imaginer (Burgess 2006). Being able to manipulate factors such as the level of self-relevance/involvement and the degree of overlap between memories and imagined experiences has the potential to progress our understanding of the core processes and brain areas involved (Hassabis & Maguire 2007).

To this end, we designed a novel imagination task that involved participants richly imagining new fictitious experiences (Hassabis *et al.* 2007b). We reasoned that if episodic memory recall was truly a reconstructive process (Bartlett 1932; Schacter *et al.* 1998), with a memory reassembled from its stored constituent components, then some of these integrative processes should also be co-opted by a purely constructive task involving imagination (Hassabis *et al.* 2007b). We tested patients with primary damage to the hippocampus bilaterally as this structure is well known to be critical in supporting episodic memory (Scoville & Milner 1957). We found that, as well as being impaired at recalling the past, the patients were not able to richly imagine new experiences. This was the case for EFT scenarios (see also Klein *et al.* 2002; Rosenbaum *et al.* 2005) and, crucially, for constructions that were atemporal and low in self-relevance. Even when all the components necessary to construct a fictitious experience were supplied in the form of visual elements, sounds and smells, patients' performance did not improve (Hassabis *et al.* 2007b). The source of their deficit was an inability to integrate the imagined experience into a coherent whole manifesting itself most obviously in the discontinuity of the spatial context. We concluded that the hippocampus plays a critical role in imagination by binding together the disparate elements of an event or scene (O'Keefe & Nadel 1978; Cohen & Eichenbaum 1993).

If the hippocampus plays a critical integrative role in a constructive process such as imagination, it seems plausible that it might also have a similar role in supporting the rich recollection of episodic memories and in predicting the future (Hassabis *et al.* 2007b). It has long been known that the hippocampus is required to initially encode the memory of an ongoing event (Scoville & Milner 1957). The traditional view of memory posits that over time these memories are consolidated to neocortex, which is then able to support the recall of remote memories independently from the hippocampus (Squire *et al.* 2004). Conversely, other accounts (Sanders & Warrington 1971; Cipolotti *et al.* 2001; Murray & Bussey 2001; Moscovitch *et al.* 2005; Maguire *et al.* 2006a), supported by the results of the majority of fMRI studies on episodic memory (Maguire 2001a; Svoboda *et al.* 2006), have suggested that the hippocampus is always required for rich episodic memory recall irrespective of memory age. Various patient studies have been unable to arbitrate

between these two positions largely due to disparate testing protocols, patient aetiologies and scoring systems (Levine *et al.* 2002; Moscovitch *et al.* 2005; Kirwan *et al.* 2008). It has been suggested that discrepancies between studies of remote episodic memory in hippocampal-damaged patients (Bayley *et al.* 2003) might be accounted for by differences in the quality or richness of the recollective experience (Gilboa *et al.* 2004), a feature that is not always captured by existing scoring systems (Kopelman *et al.* 1989; Hassabis *et al.* 2007b).

Considering the extant literature above and now also the findings from our imagination study (Hassabis *et al.* 2007b), we suggest that the hippocampus may have two distinct functions in episodic memory recall. Furthermore, we propose that such a dual role may help to resolve the long-standing debate about the time scale of hippocampal involvement in episodic memory. First, the hippocampus may be the initial location for the memory index (Marr 1971) which reinstates the active set of contextual details (Wheeler *et al.* 2000; Polyn *et al.* 2005; Polyn & Kahana 2008) and later might be consolidated out of the hippocampus (Squire *et al.* 2004). Second, the hippocampus may have another role as an online integrator supporting the binding of these reactivated components into a coherent whole to facilitate the rich recollection of a past episodic memory, regardless of its age. Such a function would be of great use also for predicting the future, imagination and navigation.

Further empirical evidence hinting at a two-process function of the hippocampus comes from structural MRI studies of expert navigators (London taxi drivers) who show increased grey matter volume in posterior hippocampus seemingly at the expense of reduced grey matter volume in anterior hippocampus (Maguire *et al.* 2006b). Moreover, their increased spatial knowledge appears to come at a cost to the acquisition of new visual associative information (Maguire *et al.* 2006b; Woollett & Maguire 2009). The hippocampus is ideally placed to support these two roles both in terms of the diversity of its multisensory inputs and its specific anatomical properties (Andersen *et al.* 2007), such as the high number of recurrent connections, although clearly more work is required to categorically ascertain if the hippocampus is performing more than one function in episodic memory recall.

3. THE CONSTRUCTION SYSTEM

The (re)constructive process, although critically reliant on the hippocampus, is not supported by it alone. We sought to characterize the entire construction network by using fMRI to compare imagination with episodic memory recall (Hassabis *et al.* 2007a). Healthy participants engaged in three tasks while in the scanner: (i) vivid recall of recent real memories, (ii) vivid recall of previously created imaginary experiences, and (iii) construction of new imaginary experiences for the first time in the scanner. Recall of recent autobiographical memories activated the now classic network shown in figure 1 (Maguire 2001a; Svoboda *et al.* 2006). Interestingly, imagined experiences were associated with increased activity in many of the same

brain areas (figure 3). A conjunction analysis was performed in order to examine the brain regions activated in common by the three conditions. A distributed brain network was implicated involving the hippocampus, parahippocampal gyrus, RSC, posterior parietal cortices, middle temporal cortices and ventromedial PFC (figure 4). This construction network cannot only account for a large part of the episodic memory recall network (figure 1) and EFT (Addis *et al.* 2007; Szpunar *et al.* 2007; Botzung *et al.* 2008), but also bears a striking resemblance to networks activated by navigation (Maguire 2001b; Burgess *et al.* 2002), spatial (Maguire *et al.* 2003; Kumaran & Maguire 2005) and place tasks (Epstein & Kanwisher 1998; Sugiura *et al.* 2005), as well as those associated with mind wandering (Mason *et al.* 2007) and the default network (Raichle *et al.* 2001; Buckner *et al.* 2008). This suggests there may be a set of key component processes underlying all of these cognitive functions (Buckner & Carroll 2007; Hassabis & Maguire 2007; Spreng *et al.* in press).

We have suggested that these common processes can be characterized by the concept of scene construction (Hassabis & Maguire 2007). Scene or event construction involves the mental generation and maintenance of a complex and coherent scene or event. This is achieved by the reactivation, retrieval and integration of relevant semantic, contextual and sensory components, stored in their modality specific cortical areas (Wheeler *et al.* 2000), the product of which has a coherent spatial context (Hassabis *et al.* 2007b), and can then later be manipulated and visualized. In fact, scene construction is a specific example of 'associative construction', which involves visual imagery, binding and also disparate multimodal elements that, when bound together, (re)create an event as a whole. This includes contextual details such as sounds and smells in addition to visual inputs, people, objects, entities and their actions.

Scene construction differs markedly from 'simple' visual imagery such as that for single objects (Kosslyn *et al.* 2001), in that it requires the flexible association and integration of many scene elements. Our fMRI study also included tasks requiring vivid visualization of acontextual single objects as a baseline task (Hassabis *et al.* 2007a). Recalling previously seen or previously imagined objects, or imagining objects for the first time in the scanner resulted in activation of brain areas associated with supporting object representations and manipulations, namely lateral occipital complex and intraparietal sulcus (e.g. Sugiura *et al.* 2005; figure 5). Moreover, there was no overlap between this simple object network (Sugiura *et al.* 2005) and that of complex scene construction (Hassabis *et al.* 2007a), suggesting that they represent dissociable cognitive processes with distinct neural bases. Nevertheless, complex scenes and experiences are clearly constructed out of simpler elements. It has been suggested that past and future experiences draw on information stored in episodic memory (Schacter *et al.* 2007, 2008). However, we argue that the component elements of constructions are not simply fragments of past events, but can comprise elements that are more abstracted and semantic such as the sound of ocean waves

crashing on the shore or the face of your best friend, and potentially learned over and shared across multiple episodic memories.

Alternatives to scene construction have been proposed (Buckner & Carroll 2007; Schacter & Addis 2007; Schacter *et al.* 2008). Similar to scene construction, the process of 'self-projection' (Buckner & Carroll 2007) defined as 'the shifting of the self to alternative perspectives in time or space' has been posited as an underlying process common to a set of disparate cognitive functions including episodic memory recall, EFT and navigation. However, while self-projection is clearly an important concept, it conflates several distinct component processes including scene construction (Hassabis & Maguire 2007) and theory of mind (Amodio & Frith 2006). For the purposes of teasing apart the various component processes underpinning episodic memory we suggest it is advantageous to consider constituent processes in as reduced a form as possible. Thus, we believe the construction network is most accurately characterized as being invoked whenever attention is directed away from the current external situation and instead focused inwards towards a rich internal representation of an event, real or imagined. Processes such as theory of mind are only engaged if required, i.e. in the case of EFT or episodic memory recall but not necessarily in imagination or navigation. This may explain why the construction network has a similar pattern of activity to that associated with the default network (Raichle *et al.* 2001; Buckner *et al.* 2008) and mind wandering (Mason *et al.* 2007), cognitive functions that involve minimal external stimuli combined with introspection and rich internal imagery. These constructed scenes or events, created and maintained by the construction network, can then be manipulated further by other processes, such as theory of mind, to allow shifting of the self to alternative perspectives in space or subjective time (Buckner & Carroll 2007; Arzy *et al.* 2008).

4. ADD-ONS TO THE CONSTRUCTION SYSTEM

We have demonstrated that scene construction is a dissociable set of processes supporting the episodic memory system (Hassabis *et al.* 2007a), both past and future, but what are some of the other processes that together with the construction system underpin the special properties of episodic memory? We addressed this question using our fMRI imagination paradigm by contrasting the recall of real memories to the recall of previously created imaginary memories matched for difficulty, age, detail and vividness, thus partialling out the effects of the common construction network (Hassabis *et al.* 2007a). Three distinct areas were more active for real compared to imaginary memories, the anterior medial PFC, PCC and the precuneus (figure 6).

The precuneus has been implicated in studies of recognition memory with increased activity in response to familiar items (Rugg *et al.* 2002; Wagner *et al.* 2005; Hornberger *et al.* 2006; Vincent *et al.* 2006). Therefore, the increased precuneus activity here probably reflects the relatively greater familiarity of the visualized experience for real memories over more novel

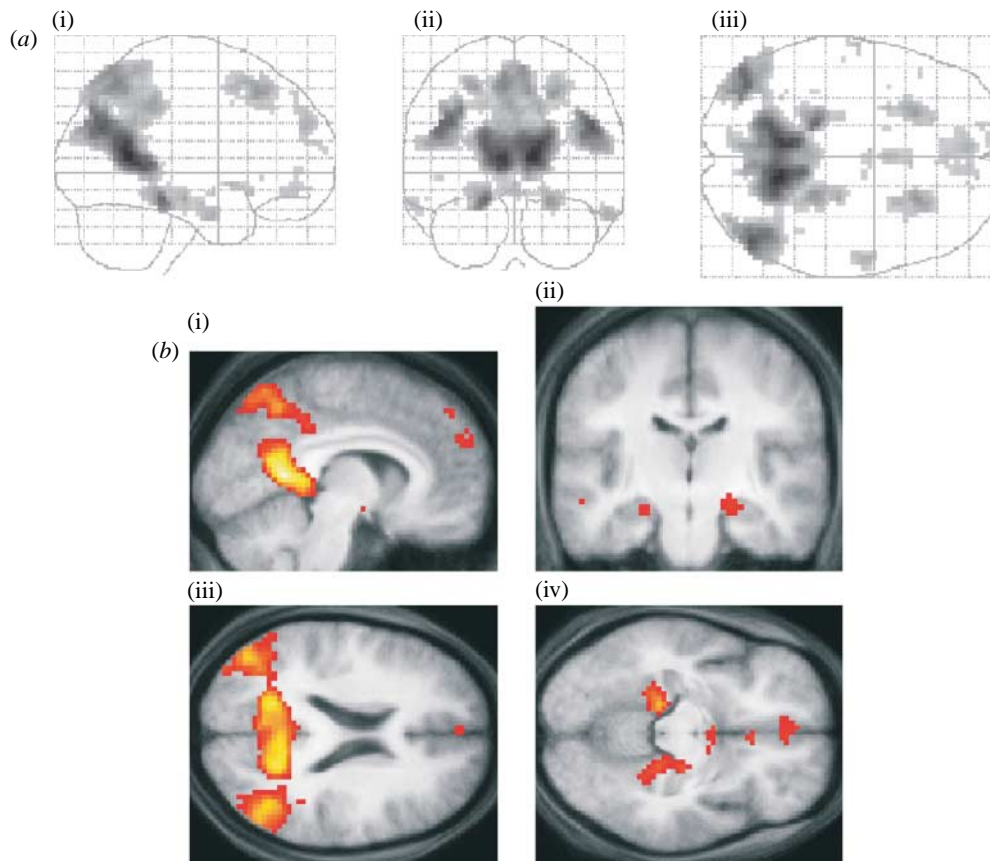


Figure 4. (a(i)–(iii)) The construction system. This conjunction analysis shows the brain regions activated in common by three tasks: recall of recent real memories; recall of previously imagined experiences; and the construction of imaginary scenarios for the first time in the scanner. This network of areas is probably involved in scene or event construction, the primary process these three conditions have in common. This construction network included hippocampus bilaterally, parahippocampal gyrus, retrosplenial and posterior parietal cortices, middle temporal cortices and medial PFC. Views of this distributed brain network are also shown in (b) on a selection of relevant (i) sagittal, (ii) coronal and (iii, iv) axial sections from the averaged structural MRI scan of the 21 study participants at a threshold of $p < 0.001$ uncorrected (data from Hassabis *et al.* 2007a).

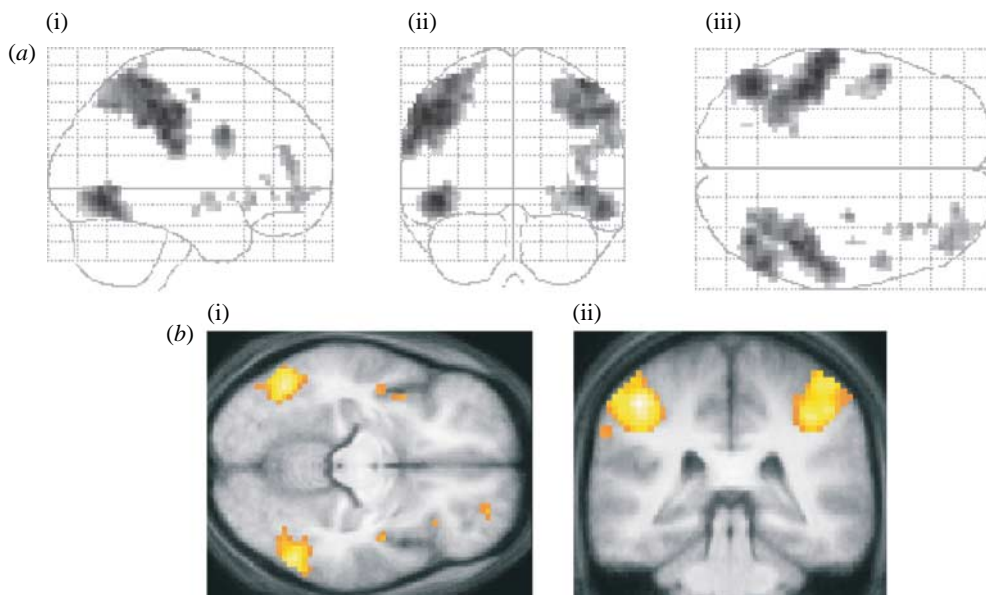


Figure 5. (a(i)–(iii)) Neural correlates of recalling single objects. These are the brain areas activated more for recalling (real or imagined) single objects than for complex experiences, and include the lateral occipital complex bilaterally, intraparietal sulcus bilaterally and right lateral PFC. Views of these brain regions are also shown in (b) on an (i) axial and (ii) coronal sections from the averaged structural MRI scan of the 21 subjects, at a threshold of $p < 0.001$ uncorrected (data from Hassabis *et al.* 2007a).

imaginary memories, given that we controlled for vividness. Activation in anterior medial PFC and PCC is consistent with studies of self-reflection

(Johnson *et al.* 2002) and theory of mind (Kumaran & Maguire 2005; Amodio & Frith 2006) suggesting that these two regions support processes related to the self.

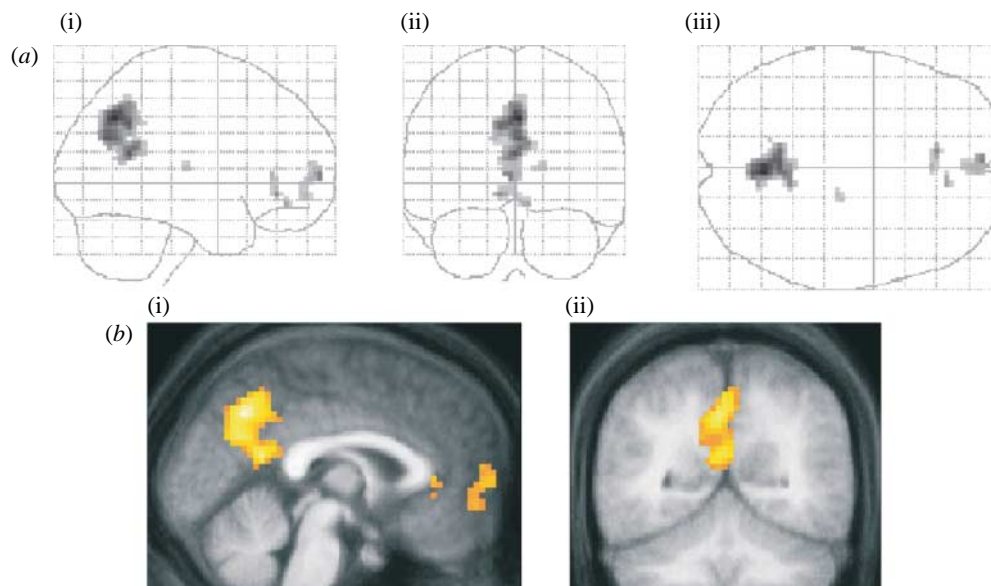


Figure 6. (a)(i)–(iii)) Comparison of real and imagined memories. Contrast showing brain regions more active for the recall of real memories compared to the recall of imaginary memories matched for difficulty, age, vividness and detail. This revealed three well-defined regions preferentially engaged for real memories: precuneus; PCC; and anterior medial PFC (BA10). Views of these brain regions are also shown in (b) on (i) sagittal and (ii) coronal sections from the averaged structural MRI scan of the 21 study participants at a threshold of $p < 0.001$ uncorrected (data from Hassabis *et al.* 2007a).

Together, then, we suggest that during episodic memory retrieval, the interaction or cooperation between the self-processing and familiarity functions performed by the anterior medial PFC/PCC and precuneus, respectively, may be sufficient to distinguish between real and fictitious memories. Further work examining these brain areas and their roles in supporting the ‘selfness’ and ‘realness’ of memories and constructions are clearly required and are beginning to emerge (Abraham *et al.* 2008; Summerfield *et al.* 2009). It should be noted that while we have proposed that intact self-reflection and theory of mind processes are also recruited in addition to scene construction to support episodic memory, this does not imply that the episodic memory system as a whole is required for the operation of any individual component process. This erroneous logic was applied recently in a study showing, not surprisingly, that a patient with amnesia retained intact theory of mind abilities (Rosenbaum *et al.* 2007).

In summary, as a first approximation at the process level, episodic memory and prediction of self-relevant future events rely on scene construction, self-connection and familiarity processes, supported by at least two sets of distinct and dissociable brain networks, in addition to general attentional and control/monitoring processes performed by parietal and frontal regions, respectively.

5. CONCLUSION

The scene construction network highlighted here supports the construction system of the brain allowing for the internal rehearsal of events or scenes. Scene construction underpins the process of creating a setting in which a simulated event can unfold whether past, present, future, atemporal or hypothetical. Undoubtedly, we still have a long way to go to understand exactly how scenes and events are

constructed, and the precise role of each brain area in the system. Nevertheless, it is clear that the ability to pre-experience hypothetical events confers an evolutionary advantage in planning for the future. 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 enact possible future states before making a decision would help to evaluate the desirability of different outcomes and also the planning processes needed to make them happen.

In humans, the use of this constructive process goes far beyond simply predicting the future, to the general evaluation of fitness for purpose. For example, a scriptwriter or novelist who is writing a passage in a film or book may play out the whole scene using their construction system, not with the idea of predicting the future, but instead for the purpose of evaluating its aesthetic suitability. Similarly, an engineer might approach the problem of designing the features of a new household product by envisaging how it would be used by someone in the home. Again, the use of construction is not for future prediction *per se* but to facilitate evaluation judgements of general fitness for purpose of a tool. The construction process, the ability to flexibly recombine stored information in novel ways, in conjunction with evaluation functions attuned to assess fitness and possibly mediated in some instances by the emotional system (Gilbert & Wilson 2007; Sharot *et al.* 2007; D’Argembeau *et al.* 2008), arguably sits near the apex of human intellectual abilities. This allows humans to be limitlessly creative and inventive even though constrained by a basic set of raw component elements gleaned over a lifetime of experiences.

This work was supported by the Wellcome Trust and the Brain Research Trust.

REFERENCES

- Abraham, A., von Cramon, D. Y. & Schubotz, R. I. 2008 Meeting George Bush versus meeting Cinderella: the neural response when telling apart what is real from what is fictional in the context of our reality. *J. Cogn. Neurosci.* **20**, 965–976. (doi:10.1162/jocn.2008.20059)
- Addis, D. R., Wong, A. T. & Schacter, D. L. 2007 Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. *Neuropsychologia* **45**, 1363–1377. (doi:10.1016/j.neuropsychologia.2006.10.016)
- Amodio, D. M. & Frith, C. D. 2006 Meeting of minds: the medial frontal cortex and social cognition. *Nat. Rev. Neurosci.* **7**, 268–277. (doi:10.1038/nrn1884)
- Andersen, P., Morris, R., Amaral, D. G., Bliss, T. & O'Keefe, J. 2007 *The hippocampus book*. New York, NY: Oxford University Press.
- Arzy, S., Molnar-Szakacs, I. & Blanke, O. 2008 Self in time: imagined self-location influences neural activity related to mental time travel. *J. Neurosci.* **28**, 6502–6507. (doi:10.1523/JNEUROSCI.5712-07.2008)
- Atance, C. M. & O'Neill, D. K. 2001 Episodic future thinking. *Trends Cogn. Sci.* **5**, 533–539. (doi:10.1016/S1364-6613(00)01804-0)
- Bartlett, F. C. 1932 *Remembering*. Cambridge, UK: Cambridge University Press.
- Bayley, P. J., Hopkins, R. O. & Squire, L. R. 2003 Successful recollection of remote autobiographical memories by amnesic patients with medial temporal lobe lesions. *Neuron* **38**, 135–144. (doi:10.1016/S0896-6273(03)00156-9)
- Bird, C. M. & Burgess, N. 2008 The hippocampus and memory: insights from spatial processing. *Nat. Rev. Neurosci.* **9**, 182–194. (doi:10.1038/nrn2335)
- Bisiach, E. & Luzzatti, C. 1978 Unilateral neglect of representational space. *Cortex* **14**, 129–133.
- Botzung, A., Denkova, E. & Manning, L. 2008 Experiencing past and future personal events: functional neuroimaging evidence on the neural bases of mental time travel. *Brain Cogn.* **66**, 202–212. (doi:10.1016/j.bandc.2007.07.011)
- Buckner, R. L. & Carroll, D. C. 2007 Self-projection and the brain. *Trends Cogn. Sci.* **11**, 49–57. (doi:10.1016/j.tics.2006.11.004)
- Buckner, R. L., Andrews-Hanna, J. R. & Schacter, D. L. 2008 The brain's default network: anatomy, function, and relevance to disease. *Ann. NY Acad. Sci.* **1124**, 1–38. (doi:10.1196/annals.1440.011)
- Burgess, N. 2006 Spatial memory: how egocentric and allocentric combine. *Trends Cogn. Sci.* **10**, 551–557. (doi:10.1016/j.tics.2006.10.005)
- Burgess, N., Maguire, E. A. & O'Keefe, J. 2002 The human hippocampus and spatial and episodic memory. *Neuron* **35**, 625–641. (doi:10.1016/S0896-6273(02)00830-9)
- Byrne, P., Becker, S. & Burgess, N. 2007 Remembering the past and imagining the future: a neural model of spatial memory and imagery. *Psychol. Rev.* **114**, 340–375. (doi:10.1037/0033-295X.114.2.340)
- Cabeza, R. & St Jacques, P. 2007 Functional neuroimaging of autobiographical memory. *Trends Cogn. Sci.* **11**, 219–227. (doi:10.1016/j.tics.2007.02.005)
- Cipolotti, L., Shallice, T., Chan, D., Fox, N., Scahill, R., Harrison, G., Stevens, J. & Rudge, P. 2001 Long-term retrograde amnesia: the crucial role of the hippocampus. *Neuropsychologia* **39**, 151–172. (doi:10.1016/S0028-3932(00)00103-2)
- Cohen, N. J. & Eichenbaum, H. 1993 *Memory, amnesia and the hippocampal system*. Cambridge, MA: MIT Press.
- Conway, M. A. & Pleydell-Pearce, C. W. 2000 The construction of autobiographical memories in the self-memory system. *Psychol. Rev.* **107**, 261–288. (doi:10.1037/0033-295X.107.2.261)
- D'Argembeau, A., Xue, G., Lu, Z. L., Van der Linden, M. & Bechara, A. 2008 Neural correlates of envisioning emotional events in the near and far future. *Neuroimage* **40**, 398–407. (doi:10.1016/j.neuroimage.2007.11.025)
- Epstein, R. & Kanwisher, N. 1998 A cortical representation of the local visual environment. *Nature* **392**, 598–601. (doi:10.1038/33402)
- Gallagher, S. 2000 Philosophical conceptions of the self: implications for cognitive science. *Trends Cogn. Sci.* **4**, 14–21. (doi:10.1016/S1364-6613(99)01417-5)
- Gilbert, D. T. & Wilson, T. D. 2007 Propection: experiencing the future. *Science* **317**, 1351–1354. (doi:10.1126/science.1144161)
- Gilboa, A., Winocur, G., Grady, C. L., Hevenor, S. J. & Moscovitch, M. 2004 Remembering our past: functional neuroanatomy of recollection of recent and very remote personal events. *Cereb. Cortex* **14**, 1214–1225. (doi:10.1093/cercor/bhh082)
- Gottfried, J. A., Smith, A. P., Rugg, M. D. & Dolan, R. J. 2004 Remembrance of odors past: human olfactory cortex in cross-modal recognition memory. *Neuron* **42**, 687–695. (doi:10.1016/S0896-6273(04)00270-3)
- Hassabis, D. & Maguire, E. A. 2007 Deconstructing episodic memory with construction. *Trends Cogn. Sci.* **11**, 299–306. (doi:10.1016/j.tics.2007.05.001)
- Hassabis, D., Kumaran, D. & Maguire, E. A. 2007a Using imagination to understand the neural basis of episodic memory. *J. Neurosci.* **27**, 14 365–14 374. (doi:10.1523/JNEUROSCI.4549-07.2007)
- Hassabis, D., Kumaran, D., Vann, S. D. & Maguire, E. A. 2007b Patients with hippocampal amnesia cannot imagine new experiences. *Proc. Natl Acad. Sci. USA* **104**, 1726–1731. (doi:10.1073/pnas.0610561104)
- Hornberger, M., Rugg, M. D. & Henson, R. N. 2006 fMRI correlates of retrieval orientation. *Neuropsychologia* **44**, 1425–1436. (doi:10.1016/j.neuropsychologia.2005.12.009)
- Johnson, S. C., Baxter, L. C., Wilder, L. S., Pipe, J. G., Heiserman, J. E. & Prigatano, G. P. 2002 Neural correlates of self-reflection. *Brain* **125**, 1808–1814. (doi:10.1093/brain/awf181)
- Kirwan, C. B., Bayley, P. J., Galvan, V. V. & Squire, L. R. 2008 Detailed recollection of remote autobiographical memory after damage to the medial temporal lobe. *Proc. Natl Acad. Sci. USA* **105**, 2676–2680. (doi:10.1073/pnas.0712155105)
- Klein, S. B., Loftus, J. & Kihlstrom, J. F. 2002 Memory and temporal experience: the effects of episodic memory loss on an amnesic patient's ability to remember the past and imagine the future. *Social Cogn.* **20**, 353–379. (doi:10.1521/soco.20.5.353.21125)
- Kopelman, M. D., Wilson, B. A. & Baddeley, A. D. 1989 The autobiographical memory interview: a new assessment of autobiographical and personal semantic memory in amnesic patients. *J. Clin. Exp. Neuropsychol.* **11**, 724–744. (doi:10.1080/01688638908400928)
- Kosslyn, S. M., Ganis, G. & Thompson, W. L. 2001 Neural foundations of imagery. *Nat. Rev. Neurosci.* **2**, 635–642. (doi:10.1038/35090055)
- Kumaran, D. & Maguire, E. A. 2005 The human hippocampus: cognitive maps or relational memory? *J. Neurosci.* **25**, 7254–7259. (doi:10.1523/JNEUROSCI.1103-05.2005)
- Levine, B., Svoboda, E., Hay, J. F., Winocur, G. & Moscovitch, M. 2002 Aging and autobiographical memory: dissociating episodic from semantic retrieval. *Psychol. Aging* **17**, 677–689. (doi:10.1037/0882-7974.17.4.677)
- Maguire, E. A. 2001a Neuroimaging studies of autobiographical event memory. *Phil. Trans. R. Soc. B* **356**, 1441–1451. (doi:10.1098/rstb.2001.0944)

- Maguire, E. A. 2001*b* The retrosplenial contribution to human navigation: a review of lesion and neuroimaging findings. *Scand. J. Psychol.* **42**, 225–238. (doi:10.1111/1467-9450.00233)
- Maguire, E. A. & Frith, C. D. 2003 Aging affects the engagement of the hippocampus during autobiographical memory retrieval. *Brain* **126**, 1511–1523. (doi:10.1093/brain/awg157)
- Maguire, E. A., Valentine, E. R., Wilding, J. M. & Kapur, N. 2003 Routes to remembering: the brains behind superior memory. *Nat. Neurosci.* **6**, 90–95. (doi:10.1038/nn988)
- Maguire, E. A., Nannery, R. & Spiers, H. J. 2006*a* Navigation around London by a taxi driver with bilateral hippocampal lesions. *Brain* **129**, 2894–2907. (doi:10.1093/brain/awl286)
- Maguire, E. A., Woollett, K. & Spiers, H. J. 2006*b* London taxi drivers and bus drivers: a structural MRI and neuropsychological analysis. *Hippocampus* **16**, 1091–1101. (doi:10.1002/hipo.20233)
- Marr, D. 1971 Simple memory: a theory for archicortex. *Phil. Trans. R. Soc. B* **262**, 23–81. (doi:10.1098/rstb.1971.0078)
- Mason, M. F., Norton, M. I., Van Horn, J. D., Wegner, D. M., Grafton, S. T. & Macrae, C. N. 2007 Wandering minds: the default network and stimulus-independent thought. *Science* **315**, 393–395. (doi:10.1126/science.1131295)
- Moscovitch, M. *et al.* 2005 Functional neuroanatomy of remote episodic, semantic and spatial memory: a unified account based on multiple trace theory. *J. Anat.* **207**, 35–66. (doi:10.1111/j.1469-7580.2005.00421.x)
- Murray, E. A. & Bussey, T. J. 2001 Consolidation and the medial temporal lobe revisited: methodological considerations. *Hippocampus* **11**, 1–7. (doi:10.1002/1098-1063(2001)11:1<1::AID-HIPO1014>3.0.CO;2-V)
- O'Keefe, J. & Nadel, L. 1978 *The hippocampus as a cognitive map*. Oxford, UK: Oxford University Press.
- Okuda, J. *et al.* 2003 Thinking of the future and past: the roles of the frontal pole and the medial temporal lobes. *Neuroimage* **19**, 1369–1380. (doi:10.1016/S1053-8119(03)00179-4)
- Polyn, S. M. & Kahana, M. J. 2008 Memory search and the neural representation of context. *Trends Cogn. Sci.* **12**, 24–30. (doi:10.1016/j.tics.2007.10.010)
- Polyn, S. M., Natu, V. S., Cohen, J. D. & Norman, K. A. 2005 Category-specific cortical activity precedes retrieval during memory search. *Science* **310**, 1963–1966. (doi:10.1126/science.1117645)
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A. & Shulman, G. L. 2001 A default mode of brain function. *Proc. Natl Acad. Sci. USA* **98**, 676–682. (doi:10.1073/pnas.98.2.676)
- Rosenbaum, R. S., Kohler, S., Schacter, D. L., Moscovitch, M., Westmacott, R., Black, S. E., Gao, F. & Tulving, E. 2005 The case of K.C.: contributions of a memory-impaired person to memory theory. *Neuropsychologia* **43**, 989–1021. (doi:10.1016/j.neuropsychologia.2004.10.007)
- Rosenbaum, R. S., Stuss, D. T., Levine, B. & Tulving, E. 2007 Theory of mind is independent of episodic memory. *Science* **318**, 1257. (doi:10.1126/science.1148763)
- Rubin, D. C., Schrauf, R. W. & Greenberg, D. L. 2003 Belief and recollection of autobiographical memories. *Mem. Cognit.* **31**, 887–901.
- Rugg, M. D., Otten, L. J. & Henson, R. N. 2002 The neural basis of episodic memory: evidence from functional neuroimaging. *Phil. Trans. R. Soc. B* **357**, 1097–1110. (doi:10.1098/rstb.2002.1102)
- Sanders, H. I. & Warrington, E. K. 1971 Memory for remote events in amnesic patients. *Brain* **94**, 661–668. (doi:10.1093/brain/94.4.661)
- Schacter, D. L. & Addis, D. R. 2007 The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Phil. Trans. R. Soc. B* **362**, 773–786. (doi:10.1098/rstb.2007.2087)
- Schacter, D. L., Norman, K. A. & Koutstaal, W. 1998 The cognitive neuroscience of constructive memory. *Annu. Rev. Psychol.* **49**, 289–318. (doi:10.1146/annurev.psych.49.1.289)
- Schacter, D. L., Addis, D. R. & Buckner, R. L. 2007 Remembering the past to imagine the future: the prospective brain. *Nat. Rev. Neurosci.* **8**, 657–661. (doi:10.1038/nrn2213)
- Schacter, D. L., Addis, D. R. & Buckner, R. L. 2008 Episodic simulation of future events: concepts, data, and applications. *Ann. NY Acad. Sci.* **1124**, 39–60. (doi:10.1196/annals.1440.001)
- Scoville, W. B. & Milner, B. 1957 Loss of recent memory after bilateral hippocampal lesions. *J. Neurol. Neurosurg. Psychiatry* **20**, 11–21. (doi:10.1136/jnnp.20.1.11)
- Sharot, T., Riccardi, A. M., Raio, C. M. & Phelps, E. A. 2007 Neural mechanisms mediating optimism bias. *Nature* **450**, 102–105. (doi:10.1038/nature06280)
- Spreng, R. N., Mar, R. A. & Kim, A. S. N. In press. The common neural basis of autobiographical memory, prospection, navigation, theory of Mind and the default mode: a quantitative meta-analysis. *J. Cogn. Neurosci.* (doi:10.1162/jocn.2008.21029)
- Squire, L. R., Stark, C. E. & Clark, R. E. 2004 The medial temporal lobe. *Annu. Rev. Neurosci.* **27**, 279–306. (doi:10.1146/annurev.neuro.27.070203.144130)
- Suddendorf, T. & Corballis, M. C. 1997 Mental time travel and the evolution of the human mind. *Genet. Soc. Gen. Psychol. Monogr.* **123**, 133–167.
- Sugiura, M., Shah, N. J., Zilles, K. & Fink, G. R. 2005 Cortical representations of personally familiar objects and places: functional organization of the human posterior cingulate cortex. *J. Cogn. Neurosci.* **17**, 183–198. (doi:10.1162/0898929053124956)
- Summerfield, J. J., Hassabis, D. & Maguire, E. A. 2009 Cortical midline involvement in autobiographical memory. *NeuroImage* **44**, 1188–1200. (doi:10.1016/j.neuroimage.2008.09.033)
- Svoboda, E., McKinnon, M. C. & Levine, B. 2006 The functional neuroanatomy of autobiographical memory: a meta-analysis. *Neuropsychologia* **44**, 2189–2208. (doi:10.1016/j.neuropsychologia.2006.05.023)
- Szpunar, K. K., Watson, J. M. & McDermott, K. B. 2007 Neural substrates of envisioning the future. *Proc. Natl Acad. Sci. USA* **104**, 642–647. (doi:10.1073/pnas.0610082104)
- Tulving, E. 2002 Episodic memory: from mind to brain. *Annu. Rev. Psychol.* **53**, 1–25. (doi:10.1146/annurev.psych.53.100901.135114)
- Vincent, J. L., Snyder, A. Z., Fox, M. D., Shannon, B. J., Andrews, J. R., Raichle, M. E. & Buckner, R. L. 2006 Coherent spontaneous activity identifies a hippocampal–parietal memory network. *J. Neurophysiol.* **96**, 3517–3531. (doi:10.1152/jn.00048.2006)
- Wagner, A. D., Shannon, B. J., Kahn, I. & Buckner, R. L. 2005 Parietal lobe contributions to episodic memory retrieval. *Trends Cogn. Sci.* **9**, 445–453. (doi:10.1016/j.tics.2005.07.001)
- Wheeler, M. A., Stuss, D. T. & Tulving, E. 1997 Toward a theory of episodic memory: the frontal lobes and autonoetic consciousness. *Psychol. Bull.* **121**, 331–354. (doi:10.1037/0033-2909.121.3.331)
- Wheeler, M. E., Petersen, S. E. & Buckner, R. L. 2000 Memory's echo: vivid remembering reactivates sensory-specific cortex. *Proc. Natl Acad. Sci. USA* **97**, 11 125–11 129. (doi:10.1073/pnas.97.20.11125)
- Woollett, K. & Maguire, E. A. 2009 Navigational expertise may compromise anterograde associative memory. *Neuropsychologia* **47**, 1088–1095. (doi:10.1016/j.neuropsychologia.2008.12.036)