

Remembering the past to imagine the future: the prospective brain

Daniel L. Schacter, Donna Rose Addis and Randy L. Buckner

Abstract | A rapidly growing number of recent studies show that imagining the future depends on much of the same neural machinery that is needed for remembering the past. These findings have led to the concept of the prospective brain; an idea that a crucial function of the brain is to use stored information to imagine, simulate and predict possible future events. We suggest that processes such as memory can be productively re-conceptualized in light of this idea.

For more than a century, memory research has focused on the past. Psychologists have analysed the cognitive processes that allow individuals to retain past experiences, and neuroscientists have identified the brain structures, such as the hippocampus, that support this ability. A function of memory that has been largely overlooked until recently is its role in allowing individuals to imagine possible future events. In this article, we consider emerging evidence which indicates that memory — especially episodic memory — is crucially involved in our ability to imagine non-existent events and simulate future happenings. Indeed, brain regions that have traditionally been associated with memory appear to be similarly engaged when people imagine future experiences. We believe that such observations might have far-reaching implications for conceptions of memory and its functions.

Memory for the future: background

In 1985, D. H. Ingvar published a paper with the seemingly paradoxical title “Memory for the future”. According to Ingvar, “concepts about the future, like memories of past events, can be remembered, often in great detail” (REF. 1). Ingvar summarized evidence which indicated that regions within the prefrontal cortex have a crucial role in the planning, foresight and programming of complex action sequences — examples of “memory for the future” (REFS 2–6). At approximately the same time, E. Tulving argued that episodic memory,

which has traditionally been defined as a memory system that supports remembering personal experiences, allows individuals to engage in “mental time travel” into both the past and the future^{7,8}. Tulving also claimed that the capacity for mental time travel is uniquely human⁹.

Perhaps as a result of this claim, much research has focused on whether non-human animals are capable of mental time travel (for reviews, see REFS 10–12), using ingenious demonstrations to question the claim for human uniqueness. For example, there is compelling evidence that food-caching scrub jays can retrieve detailed information about what food they have cached, as well as when and where they cached it^{10,13}. Furthermore, recent work indicates that jays can cache food in a manner that reflects some form of planning for the future¹⁴ that is not simply a reflection of current motivational needs¹⁵.

Debates about mental time travel in non-human animals might never be settled definitively, given that animals lack the linguistic capacity to describe mental contents. At the same time, research in the child-development literature has investigated the development of mental time travel in children, and found that both episodic remembering and future thinking emerge relatively late in development, between approximately three and five years of age. However, similar issues regarding the ability of young children to communicate their mental contents have arisen^{9,16,17}.

These issues have diverted attention away from the relationship between future event simulation and memory processes in humans. During the past year, however, the growing number of papers published on this topic have changed this situation dramatically.

Insights from memory impairments

Early indications of a link between the processing of past and future events were provided by observations of patients with memory impairments. In a seminal description of patients with Korsakoff’s amnesia, marked deficiencies in personal planning were noted¹⁸. The amnesic patient K.C., who showed a total loss of episodic memory after a head injury, reported a ‘blank’ when asked about his personal future or past⁸. (For related observations, see REF. 19.)

Expanding on these observations, the ability of five amnesic patients with bilateral hippocampal damage to imagine novel experiences was examined systematically²⁰. The patients were asked to generate everyday imaginary experiences and were specifically instructed not to provide a memory of a past event, but to construct something new. Participants described their imaginary scenarios, which were scored based on their content, their spatial coherence and their subjective qualities. The imaginary constructions produced by four of the five patients were greatly reduced in richness and content compared with those of controls. The impairment was especially pronounced for the measure of spatial coherence, indicating that the constructions of the amnesic patients tended to consist of isolated fragments of information, rather than connected scenes. It is important to note that this study did not specifically require patients to construct scenes pertaining to future events, suggesting a more general deficit in the patients’ ability to construct novel scenes.

The ability to remember the past and imagine the future is also affected in psychiatric disorders. A decade ago, a link was reported between deficits in accounts of past and future events in patients with suicidal depression²¹. In response to word cues, depressed patients showed less specific retrieval of past events, and less specific imagining of future autobiographical events.

A similar cueing procedure was recently used to study past and future events in schizophrenic patients²². Schizophrenics recalled fewer specific past events and imagined fewer specific future events than did control subjects, but the schizophrenic patients' deficits were even greater for future than for past events. Interestingly, this reduction in past and future specificity was correlated with the extent of the patients' positive symptoms (delusions and hallucinations), but not with their negative symptoms (such as blunted affect). Other evidence correlated positive symptoms in schizophrenics with problems remembering contextual details, suggesting that the patients' impairments on the past and future tasks reflect impairments in accessing contextual details for the purpose of constructing specific simulations of their personal future or past.

A similar pattern was also recently reported in healthy older adults, when they were compared with college students²³. When asked to generate past and future events, the older adults generated fewer episode-specific details relating to the past events than the younger adults, which replicated earlier results²⁴. Importantly, the same

effect occurred for future events: imagined happenings also contained sparse episodic information (TABLE 1).

The ability of older adults to generate episode-specific details of both past and future events was correlated with their ability to integrate information and form relationships between items (relational memory). This suggests that the simulation of future episodes draws on relational processes that flexibly recombine details from past events into novel scenarios. Combined with other recent data that indicate similar temporal distributions for past and future events in older adults²⁵, there is now an empirical basis for proposing that aging has parallel effects on both imagining the future and remembering the past.

Insights from neuroimaging

Several recent neuroimaging studies have directly contrasted situations where young adults either recall from their own personal pasts or imagine future events. These studies have provided insights into three central issues: whether common brain systems are used while remembering the past and imagining the future, which specific brain system(s) are used for imagining the

future, and the differences between the two temporal directions of episodic thought.

In the first study, participants were instructed to talk freely about either the near or distant past or future²⁶ while a positron emission tomography scan was carried out. The scans showed evidence of shared activity during descriptions of past and future events in a set of regions that included the prefrontal cortex and parts of the medial temporal lobe (namely the hippocampus and the parahippocampal gyrus).

More recent studies have taken advantage of the temporal resolution of functional MRI (fMRI) (BOX 1). In one study, participants were instructed to remember specific past events, imagine specific future events or imagine specific events that involved a familiar individual (specifically, Bill Clinton) in response to event cues²⁷. Again, there was striking overlap in the activity associated with past and future events in prefrontal and medial temporal regions, as well as in a posterior midline region at or near the precuneus. These regions were not activated to the same extent when imagining events that involved Bill Clinton, which demonstrates the existence of a neural

Table 1 | **Examples of past and future events generated by older and younger adults**

Age group	Event type	Cue word	Event description	
			Non-episodic information	Episodic information
Young	Past	Tree		"I went hiking in Muir Woods in California ... with my boyfriend then and his room-mates ... we went through all these different ecosystems ... and you would see different kinds of plants, so like we would see orchids ... and I said, "Wow it's so beautiful and it's like wild" ... that part was like a jungle: wet, very lush and green. At the end of that trail, was like the beach ... so we had bread and cheese and it was very fun and good... ...because I love cheese."
Young	Future	Oven	None	"I'm going to bake my first loaf of bread. It's going to be probably Friday afternoon before Yom Kippur ... I'll get the recipe from an old cookbook... The room's going to be hot even though we have the windows open, because we're going to turn on the oven in the middle of the summer. The light, bright kitchen light will be off, and instead, we're going to light a candle. BBC will be on in the living room, it'll be kind of static..."
Older	Past	Toy	" This reminds me of those toys that our grandchildren have. I think they're spoiled... Our son, the teacher, doesn't have a lot of money, and I think his wife is just can't say no to the kids. Every time she goes out, there's a toy coming home... I generally will give my son money for specific things..."	...Like he had a problem with his knee and I, so, to help him with his doctor's bill, I gave him some money, and on the check I wrote, 'Don't spend on toys with this check'."
Older	Future	Engine	" In the next few years I hope we have an engine that doesn't have to use gas to run. I hope we come up with an alternate source of energy to run vehicles. Because they're a polluter, and its getting to be very expensive to drive, and there's a lot of driver irritability over stop and go driving, having the carbon poisoning happening..."	...The scene is I'm just driving along, in the Saab, and... not worrying about high energy costs..."

Excerpts from event descriptions are from REF 23 (only a representative portion of the event description is shown here). Notably, older adults' ability to generate specific details did not correlate with the overall ability to generate information (as measured by verbal fluency).

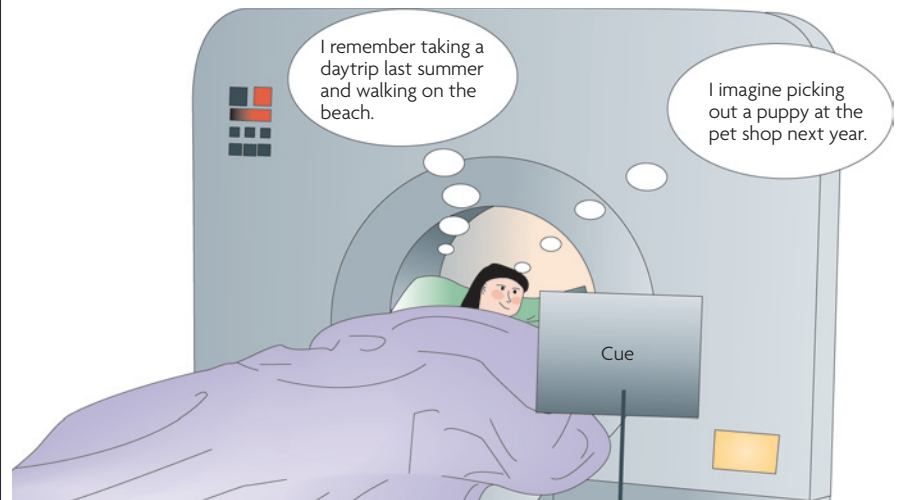
signature that is specific to the construction of events in one's personal past or future.

Another fMRI study²⁸ experimentally equated the level of detail and the related phenomenological features of past and future events. Tasks consisted of a construction phase, during which participants generated a past or future event, and an elaboration phase, during which participants generated as much detail as possible about the event. The construction phase was associated with common past–future activity in posterior visual regions and the left hippocampus, which might reflect the interaction between visually presented cues and hippocampally mediated pointers to memory traces²⁹. During the elaboration phase, there was striking overlap between the activity generated in the past and future tasks in the prefrontal cortex, medial temporal lobe regions including the hippocampus and parahippocampal gyrus, and a posterior midline region near the precuneus. This study again reveals strong evidence of overlap between the brain systems that are used while remembering the past and imagining the future.

Integrating the data from these three studies with related studies of autobiographical memory^{30,31}, it has been suggested that the processes of remembering the past and imagining the future are associated with a highly specific core brain system³² (FIG. 1). This core brain system involves prefrontal and medial temporal lobe regions, as well as posterior regions (including the precuneus and the retrosplenial cortex) that are consistently observed as components of brain networks that are important for memory retrieval³³. Detailed analyses of the interactions that take place among the brain regions within this core system further reveal that all of the component regions are selectively correlated with one another within a large-scale brain system that includes the hippocampal formation^{34,35}. It thus appears that a brain system that involves direct contributions from the medial temporal lobe supports both remembering the past and imagining the future.

In addition to this core brain system, direct comparisons between imagining the future and remembering the past consistently reveal greater activity during episodic thought about the future. Greater activity is observed in frontopolar and medial temporal regions when the future is imagined than when the past is remembered²⁶. A direct comparison of the activity that is associated with thinking about past and future events²⁷ also identified several regions that were significantly more active for thinking about future events. In another study, the

Box 1 | The typical paradigm for probing past and future events



The typical paradigm used in experiments that examine past and future events involves instructing the participant to either remember a personally experienced event in their past or imagine a plausible event in their future. Events are elicited by a cue word which might be a noun²⁸ (in the study illustrated the cues were 'beach' or 'dog'), an emotional word (such as 'argument' or 'enthusiastic')²¹ or an event (such as 'birthday' or 'barbecue')²⁷. Transcriptions of events are then scored according to the episodic specificity of the event produced (that is, whether the event is specific in time and place)²¹ and/or the types of detail that comprise the event (such as episodic details or other factual information²³; see TABLE 1). This general behavioural paradigm has since been adapted for functional neuroimaging studies, in which a past or future event is silently remembered or imagined while lying inside a functional MRI scanner (as depicted in the illustration) over a span of 10–20 seconds^{27,28}. Subjective ratings of event phenomenology (such as vividness and emotionality) can be obtained either during the scan or in the post-scan interview. Detailed descriptions of the events that were generated in response to each cue shown during the scan are also obtained during the post-scan interview, in order to confirm that an episodic event was successfully generated.

early, constructive phase of future thinking revealed greater activity during future conditions in multiple regions, including the prefrontal cortex²⁸.

It has been argued that this pattern might reflect a more active type of imagery processing that is required by thoughts of the future but not of the past²⁷. Others have proposed that it might reflect the more intensive constructive processes that are required in order to imagine future events³⁶. Both past and future event tasks require the retrieval of information from memory, and hence both engage common memory networks. However, only the future task requires that event details gleaned from various past events be flexibly recombined into a novel future event. Thus, additional regions that support these processes might be recruited by the future event tasks.

The prospective brain

The evidence that we have considered converges on the conclusion that the process of imagining or simulating future events depends on many of the same neural processes that are involved in episodic

remembering. At the broadest level, these observations provide an insight into the adaptive functions of memory. The medial temporal lobe system, which has long been considered to be crucial for remembering the past, might actually gain adaptive value through its ability to provide details that serve as the building blocks of future event simulation.

Along these lines, the constructive episodic simulation hypothesis was advanced^{36,37}. In this hypothesis, the simulation of future episodes is thought to require a system that can flexibly recombine details from past events. This idea was put forward in an attempt to understand why memory involves a constructive process of piecing together bits and pieces of information, rather than a literal replay of the past; the suggested answer is that a crucial function of memory is to make information available for the simulation of future events. According to this idea, thoughts of past and future events are proposed to draw on similar information stored in episodic memory and rely on similar underlying processes, and episodic memory is proposed to support the construction of

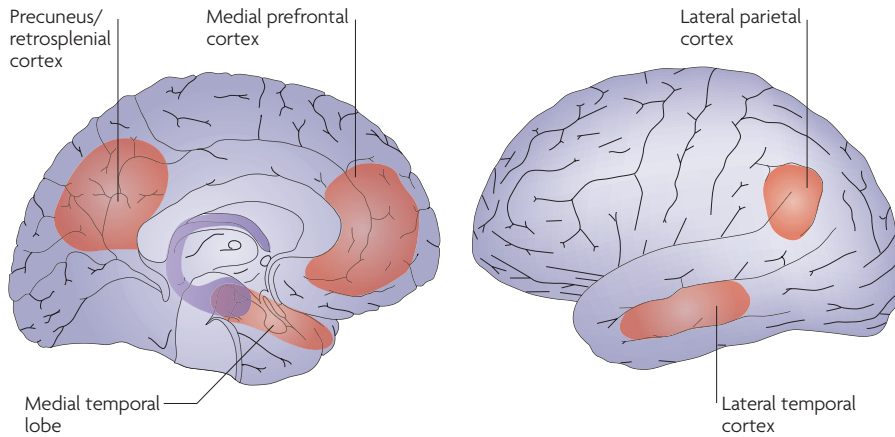


Figure 1 | The core brain system that mediates past and future thinking. The core brain system that is consistently activated while remembering the past^{30,31,33}, envisioning the future^{26–28} and during related forms of mental simulation³² is illustrated schematically. Prominent components of this network include medial prefrontal regions, posterior regions in the medial and lateral parietal cortex (extending into the precuneus and the retrosplenial cortex), the lateral temporal cortex and the medial temporal lobe. Moreover, regions within this core brain system are functionally correlated with each other and, prominently, with the hippocampal formation^{34,35}. We suggest that this core brain system functions adaptively to integrate information about relationships and associations from past experiences, in order to construct mental simulations about possible future events.

future events by extracting and recombining stored information into a simulation of a novel event. The hypothesis receives general support from findings of neural and cognitive overlap between thoughts of past and future events, and receives specific support from recent research³⁸ in which college students reported more vivid and more detailed future event simulations when imagining events that might occur within the next week in a familiar context (their own or a friend's home) than in a novel context (a jungle or the North Pole). Similarly, future events were more vivid and more detailed when imagined in recently experienced contexts (university locations) than when imagined in remotely experienced contexts (school settings). These results support the idea that episodic information is used to construct future event simulations.

The constructive episodic simulation hypothesis also receives specific support from evidence that links hippocampal function and relational processing with future event simulation: the hippocampal region is thought to support relational processes³⁹, which are in turn suggested to be crucial for recombining stored information into future event simulations. One important issue that needs to be addressed by further studies concerns whether future event simulations simply reflect the retrieval of parts or fragments of prior episodes, or whether elements from different episodes must be combined, as proposed by the constructive episodic simulation hypothesis.

Although the constructive episodic simulation hypothesis emphasizes the contribution of episodic memory to future event simulation, it seems likely that semantic memory also plays a part. Semantic memory is the source of knowledge about the general properties of events, and it is presumably used to guide the construction of future scenarios in line with these known event properties. Research that directly compares episodic and semantic contributions to future event simulations is needed.

It has been suggested that the core brain system is also used by many diverse types of task that require mental simulation of alternative perspectives³². The idea is that the core brain system allows one to shift from perceiving the immediate environment to an alternative, imagined perspective that is based largely on memories of the past. Future thinking, by this view, is just one of several forms of such ability. Thinking about the perspectives of others (theory of mind) also appears to use the core brain system⁴⁰, as do certain forms of navigation^{20,32,41}.

An unresolved issue is the nature of the information being processed when one engages in forms of mental simulation that depend on the core brain system. Buckner and Carroll³² suggest that an important processing component is that the simulated perception is of an alternative perspective referenced to oneself — a process they

termed 'self-projection'³². After noting that most of the tasks that activate the core brain system require individuals to mentally construct an alternative visual scene, Hassabis and Maguire⁴² recently suggested that 'scene building' is the common element. Although the details of these ideas require further exploration, both emphasize that shifts along the temporal dimension (past versus future) are probably not the vital element. Adaptive constructive simulations that use the core brain system might extend to alternative perspectives of the present. An important research task will be to assess the contribution of temporal versus non-temporal factors to the kinds of questions highlighted here, and to determine whether the activity of any component of the system is modulated by temporal factors, such as whether an event occurs in the recent versus the remote future or past.

Whatever the outcome of such studies, we believe that functional considerations still mandate assigning a key role to the specifically prospective features of the neural and cognitive processes we have considered. From an adaptive perspective, preparing for the future is a vital task in any domain of cognition or behaviour that is important for survival. The processes of event simulation probably have a key role in helping individuals plan for the future, although they are also important for other tasks that relate to the present and the past.

Given the adaptive priority of future planning, we find it helpful to think of the brain as a fundamentally prospective organ that is designed to use information from the past and the present to generate predictions about the future^{43–45}. Memory can be thought of as a tool used by the prospective brain to generate simulations of possible future events. Such a hypothesis calls for a shift of conceptual emphasis, and even a change in methodology. The time for taking the prospective brain seriously appears to be at hand.

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1. Ingvar, D. H. 'Memory of the future': an essay on the temporal organization of conscious awareness. *Hum. Neurobiol.* **4**, 127–136 (1985).
2. Fuster, J. M. *The Prefrontal Cortex: Anatomy, Physiology, and the Frontal Lobe*. (Raven Press, New York, 1989).
3. Knight, R. T. & Grabowecy, M. in *The New Cognitive Neurosciences* (ed. Gazzaniga, M. S.) 1319–1339 (MIT Press, Cambridge Massachusetts, 2000).
4. Mesulam, M. M. in *Principles of Frontal Lobe Function* (eds Stuss, D. T. & Knight, R. T.) 8–30 (Oxford Univ. Press, New York, 2002).
5. Stuss, D. T. & Benson, D. F. *The Frontal Lobes*. (Raven Press, New York, 1986).
6. Shallice, T. & Burgess, P. The domain of supervisory processes and the temporal organization of behaviour. *Phil. Trans. R. Soc. Lond. B Biol.* **351**, 1405–1411 (1996).
7. Tulving, E. *Elements of Episodic Memory*. (Clarendon Press, Oxford England, 1983).
8. Tulving, E. Memory and consciousness. *Can. Psychol.* **26**, 1–12 (1985).
9. Tulving, E. in *The Missing Link in Cognition* (eds Terrace, H. S. & Metcalfe, J.) 3–56 (Oxford Univ. Press, New York, 2005).
10. Clayton, N. S., Bussey, T. J. & Dickinson, A. Can animals recall the past and plan for the future? *Nature Rev. Neurosci.* **4**, 685–691 (2003).
11. Suddendorf, T. & Corballis, M. C. Mental time travel and the evolution of the human mind. *Genet. Soc. Gen. Psychol. Monogr.* **123**, 133–167 (1997).
12. Suddendorf, T. & Corballis, M. C. The evolution of foresight: what is mental time travel, and is it unique to human? *Behav. Brain Sci.* (in the press).
13. Clayton, N. S. & Dickinson, A. Episodic-like memory during cache recovery by scrub jays. *Nature* **395**, 272–274 (1998).
14. Raby, C. R., Alexis, D. M., Dickinson, A. & Clayton, N. S. Planning for the future by western scrub-jays. *Nature* **445**, 919–921 (2007).
15. Correia, S. P. C., Dickinson, A. & Clayton, N. S. Western scrub-jays anticipate future needs independently of their current motivational state. *Curr. Biol.* **17**, 856–861 (2007).
16. Atance, C. M. & O'Neill, D. K. The emergence of episodic future thinking in humans. *Learn. Motiv.* **36**, 126–144 (2005).
17. Suddendorf, T. & Busby, J. Making decisions with the future in mind: developmental and comparative identification of mental time travel. *Learn. Motiv.* **36**, 110–125 (2005).
18. Talland, G. A. *Deranged Memory: A Psychonomic Study of the Amnesic Syndrome*. (Academic Press, New York, 1965).
19. Klein, S. B. & Loftus, J. Memory and temporal experience: the effects of episodic memory loss on an amnesic patient's ability to remember the past and imagine the future. *Soc. Cogn.* **20**, 353–379 (2002).
20. Hassabis, D., Kumaran, D., Vann, S. D. & Maguire, E. A. Patients with hippocampal amnesia cannot imagine new experiences. *Proc. Natl Acad. Sci. USA* **104**, 1726–1731 (2007).
21. Williams, J. M. et al. The specificity of autobiographical memory and imageability of the future. *Mem. Cognit.* **24**, 116–125 (1996).
22. D'Argembeau, A., Raffard, S. & Van der Linden, M. Remembering the past and imagining the future in schizophrenia. *J. Abnorm. Psychol.* (in the press).
23. Addis, D. R., Wong, A. T. & Schacter, D. L. Age-related changes in the episodic simulation of future events. *Psychol. Sci.* (in the press).
24. Levine, B., Svoboda, E., Hay, J. F., Winocur, G. & Moscovitch, M. Aging and autobiographical memory: dissociating episodic from semantic retrieval. *Psychol. Aging* **17**, 677–689 (2002).
25. Spreng, R. N. & Levine, B. The temporal distribution of past and future autobiographical events across the lifespan. *Mem. Cognit.* **34**, 1644–1651 (2006).
26. Okuda, J., et al. Thinking of the future and the past: the roles of the frontal pole and the medial temporal lobes. *NeuroImage* **19**, 1369–1380 (2003).
27. Szpunar, K. K., Watson, J. M. & McDermott, K. B. Neural substrates of envisioning the future. *Proc. Natl Acad. Sci. USA* **104**, 642–647 (2007).
28. Addis, D. R., Wong, A. T. & Schacter, D. L. Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. *Neuropsychologia* **45**, 1363–1377 (2007).
29. Moscovitch, M. Memory and working-with-memory: a component process model based on modules and central systems. *J. Cogn. Neurosci.* **4**, 257–267 (1992).
30. Cabeza, R. & St. Jacques, P. Functional neuroimaging of autobiographical memory. *Trends Cogn. Sci.* **11**, 219–227 (2007).
31. Maguire, E. A. Neuroimaging studies of autobiographical event memory. *Phil. Trans. R. Soc. Lond. B Biol.* **356**, 1441–1451 (2001).
32. Buckner, R. L. & Carroll, D. C. Self-projection and the brain. *Trends Cogn. Sci.* **11**, 49–57 (2007).
33. Wagner, A. D., Shannon, B. J., Kahn, I. & Buckner, R. L. Parietal lobe contributions to episodic memory retrieval. *Trends Cogn. Sci.* **9**, 445–453 (2005).
34. Greicius, M. D., Srivastava, G., Reiss, A. L. & Menon, V. Default-mode network activity distinguishes Alzheimer's disease from healthy aging: evidence from functional MRI. *Proc. Natl Acad. Sci. USA* **101**, 4637–4642 (2004).
35. Vincent, J. L., et al. Coherent spontaneous activity identifies a hippocampal–parietal memory network. *J. Neurophysiol.* **96**, 3517–3531 (2006).
36. Schacter, D. L. & Addis, D. R. The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Phil. Trans. R. Soc. Lond. B Biol.* **362**, 773–786 (2007).
37. Schacter, D. L. & Addis, D. R. The ghosts of past and future. *Nature* **445**, 27 (2007).
38. Szpunar, K. K. & McDermott, K. B. Episodic future thought and its relation to remembering: evidence from ratings of subjective experience. *Conscious Cogn.* 29 May 2007 (doi:10.1016/j.concog.2007.04.006).
39. Eichenbaum, H. & Cohen, N. J. *From Conditioning to Conscious Recollection: Memory Systems of the Brain* (Oxford Univ. Press, New York, 2001).
40. Saxe, R. & Kanwisher, N. People thinking about thinking people: the role of the temporo–parietal junction in theory of mind. *NeuroImage* **19**, 1835–1842 (2003).
41. Byrne, P., Becker, S. & Burgess, N. Remembering the past and imagining the future: a neural model of spatial memory and imagery. *Psychol. Rev.* **114**, 340–375 (2007).
42. Hassabis, D. & Maguire, E. A. Deconstructing episodic memory with construction. *Trends Cogn. Sci.* **11**, 299–306 (2007).
43. Bar, M. The proactive brain: using analogies and associations to generate predictions. *Trends Cogn. Sci.* **11**, 280–289 (2007).
44. Gilbert, D. T. *Stumbling on Happiness*. (Alfred A. Knopf, New York, 2006).
45. Hawkins, J. & Blakeese, S. *On Intelligence*. (Times Books, New York, 2004).

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Competing interests statement

The authors declare no competing financial interests.

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