

The Brain Must Go Back to the Future: an Exploration of Mental Time Travel

*By Luke Kennedy Burke
Physiology, University of Edinburgh
Associate Editor, Biological and Biomedical Sciences*

Quality Standard
Approved
for Membership and the Journal

1. Introduction

Memory research has been ‘stuck in the past’ for more than two decades. In recent years, however, it has been realised that backward travel to relive past events (episodic memory) underlies forward travel to simulate future events (episodic future thinking). This advancement can be attributed to a number of neuroimaging and patient studies that have allowed mental time travel (MTT), the ability to recall the past and simulate the future, to be unpacked. This article will introduce the intriguing concept of MTT and present the recent developments in this field of neural research. Given that the human brain assembles episodic fragments to form a predictive mosaic, researchers have been asking whether animals also possess the capacity to recall or imagine events. The answer to this question is of tremendous importance to animal welfare and may also provide clues about the evolution of the human mind. Since the concept of MTT was first conceived it has been argued that only humans possess this cognitive ability, an assertion referred to as the Bischof-Kohler hypothesis. However, recent studies have challenged this hypothesis by demonstrating that nonhuman animals exhibit behavioural elements expected of MTT. This article will thus also weigh the evidence for the existence of MTT in nonhumans against the null hypothesis.

2. Unpacking the cognitive time machine

2.1. First clues from patient studies

In recent years it has been realised that the brain must go back to the future. Consequently much of the discussion surrounding the neural basis of MTT has centred on the role of brain regions identified with episodic memory in formulating future events. The first indication of this sharing of neural substrates came from studies in amnesic patients K.C (Tulving, 1985) and D.B. (Klein *et al.*, 2002), who demonstrated a significant deficit in both episodic memory and the generation of future episodes. More recent patient studies have provided further insight into the debate. Hassabis *et al.* (2007) reported that when asked to imagine novel experiences, the accounts of patients with bilateral hippocampal amnesia were particularly lacking in spatial coherence. This indicates that the hippocampus may provide the spatial scaffold into which past and future details are placed. Furthermore, Addis *et al.* (2008) demonstrated that the ability of aging adults to generate future episodic details correlated with their relational memory abilities. This emphasises the flexible recombination of past details that occurs during the simulation of future events.

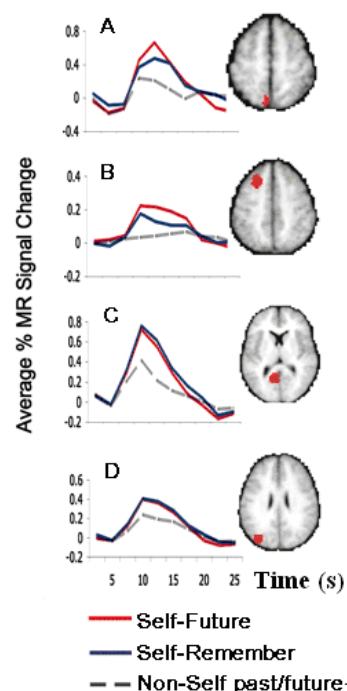
2.2. Neuroimaging culminates in the constructive episodic simulation hypothesis

A number of studies have addressed the limitations of patient work, namely their subjective nature and lack of precise anatomical analysis, and focused instead on neuroimaging. Converging evidence has culminated in the derivation of the constructive episodic simulation hypothesis by Daniel Schacter and Donna Rose Addis at Harvard University in 2007. Firstly, noting that recollecting personal memories and

envisaging future events engage identical neural substrates, the authors proposed that episodic future thinking must therefore draw upon episodic memory. The second part of the hypothesis sought to explain the additional substrates recruited during future episodic thinking. In their 2007 *Nature* paper, Schacter and Addis reasoned that episodic future thinking is a more intensive process because it requires the additional component of flexibly integrating past details to allow the coherent construction of a possible scenario. The role of episodic memory in supplying future mental outlook has been applied with success to personality traits, in particular depressive illnesses where this new insight may find a therapeutic application (Quoidbach, 2008).

The importance of additional neural processes in future time travel has been demonstrated by Szpunar *et al.* (2007) who dissected one set of regions that are more active during future simulation (fig. 1 a-b), from another set of regions that exhibit similar activity during future and past tasks (fig. 1 c-d). The areas of most notable increased activity are involved in the imagination of body movements in mental space. Thus when asked to imagine everyday activities, the simulation of a novel sequence of stored action representations requires additional activation in comparison to the recollection of actions that have already taken place. Another point of note is that regions are activated more strongly when imagining personal past or future as opposed to that of a non-self familiar individual, in this instance Bill Clinton (fig. 1 a-d). This is because episodic memory contains more details of familiar personal events, thus providing richer fragments that will form a more vivid future ‘mosaic’.

Figure 1. Cortical region activity during past and future thought as identified by a two-way ANOVA analysis. The non-self, familiar individual used was Bill Clinton because, as public figure, subjects were better able to relate to his life. A. Lateral premotor cortex B. medial posterior parietal cortex C. Left posterior cingulate cortex D. Left superior occipital gyrus. Adapted from Szpunar *et al.* (2007).



2. 3. A new appreciation of memory

But why is episodic memory a constructive process that pieces together separate fragments of experience? Surely a memory bank storing a literal reproduction of the past would avoid any of the confusion and conflict that characterises memory? Traditionally, the reconstructive nature of episodic memory has been explained as an economical measure that allows the essential essence of an event to be stored without overloading the system with extraneous details. The recent appreciation that memory is important for the future, as well as the past, has provided an additional avenue of explanation. Because a future event is not an exact replica of past events, a memory

system that operates via complete reproduction would not be proficient in simulating the future. It is the constructive nature of episodic memory that permits flexible extraction and recombination of episodic fragments to allow the simulation of a variable future.

2. 4. *Dissecting the cognitive time machine*

In order to better understand the neural basis of MTT, Addis *et al.* (2007) divided past and future mental time travel into two phases – construction and elaboration. The authors reported that neural substrates are most evidently shared during elaboration but are most distinct during construction, allowing the role of further substrates to be inferred (table 1). In their most recent study Addis and Schacter (2008) reported that substrates of the core network vary in their response to particular event characteristics (detail and temporal distance) depending on whether the imagined event is in the past or future (table 1).

Region	Response during testing	Role in mental time travel	Source
Medial temporal lobes (MTL)	engaged in construction of both past and future tasks	common retrieval from episodic memory	Okuda <i>et al.</i> (2003)
Bilateral frontopolar cortex	engaged in construction of both past and future tasks	self-referential nature of both tasks	Okuda <i>et al.</i> (2003); Botzung <i>et al.</i> , 2008
Left parahippocampal gyrus	increasingly with recency of past events	due to increasing detail of recent events	Addis and Schacter (2008)
Bilateral hippocampus	increasingly with remoteness of future events	combination of diverse past facts for future simulation	Addis and Schacter (2008)
Left hippocampus	engaged in construction of both past and future tasks	retrieval and integration of autobiographical memory	Addis <i>et al.</i> (2007)
Left anterior hippocampus	differentially depending on the detail of future event	recombination of details into novel future event	Addis and Schacter (2008)
Left anterior temporal cortex	engaged during construction	stores semantic details	Addis <i>et al.</i> (2007)
Right frontopolar cortex	significantly more by the generation of future details	specifically involved in prospective thinking	Addis <i>et al.</i> (2007); Addis and Schacter (2008)
Left inferior frontal gyrus	engaged during elaboration	generative processes	Addis <i>et al.</i> (2007)
Right hippocampus	engaged during elaboration	novelty of future event tasks	Addis <i>et al.</i> (2007)

Table 1. Summary of the neural substrates involved in MTT.

3. Are nonhuman animals capable of mental time travel?

3.1. *The behavioural hallmarks of MTT*

Before the evidence is examined, the definition of MTT will be further unpacked in order to establish the behavioural criteria required to demonstrate its existence in nonhuman animals. As aforementioned, MTT is a bidirectional process comprised of episodic memory and episodic future thinking. Episodic memory is defined by its content: what happened, where and when ('www'), and how it is experienced: a

conscious awareness of recollection (Mendl and Paul, 2008). The access of phenomenological experience is presently limited to linguistic communication, and is therefore impossible to study in nonhumans. As a result, investigation has focused on whether animals possess the ‘www’ elements that make up ‘episodic-like’ memory. In order to establish the nonhuman existence of the second component of MTT, episodic future thinking, investigators must establish that behaviours are not in response to the present but instead influenced by an anticipated motivational state (Clayton and Emery, 2009).

3.2. *The Western scrub jay demonstrates episodic memory*

Perhaps you have seen the video of crows using passing cars to crack-open their dinner of nuts? Arguably the bird appears even smarter than some humans in that it always obeys the traffic lights. The Western scrub jay (*Aphelocoma californica*), another member of the corvid family, has been used to great effect by University of Cambridge experimental psychologist Nicola Clayton to make strong claims regarding the cognitive abilities of nonhumans. Clayton and Dickinson (1998) demonstrated that jays are capable of encoding information about where a particular food is located and how long it has been stored. When trained to learn that waxworms (preferred food) degrade after four hours but peanuts (less-preferred) do not, jays recovered from appropriate locations depending on the time interval between caching and retrieval. It has also been established that ‘www’ memory can be used in a flexible, declarative manner. After novel information about the rate of food decay was introduced at recovery, jays were able to adapt their retrieval preferences accordingly (Clayton *et al.*, 2003). Jays also engaged in tactics to reduce theft by conspecifics. This protective behaviour has been used to demonstrate that jays store information about whether another individual observed their cache (Emery and Clayton, 2001), and which bird was watching them (Dally *et al.*, 2006).

3.3. *Dissociating episodic from recognition memory*

But how can scientists prove that animals are not simply recognising an event as familiar, a far cry from the recollection of a unique ‘www’ memory that would be required to demonstrate episodic memory? This criticism has been addressed by Eichenbaum *et al.* (2005) who established that rats have the ability to distinguish between memories that share overlapping elements (fig. 2). After being trained to learn two sequences (ABXYEF and LMWZPQ), rats were capable of selecting the fifth element (E or P) according to which elements the sequence started with (AB or LM), despite the common middle elements (XY).

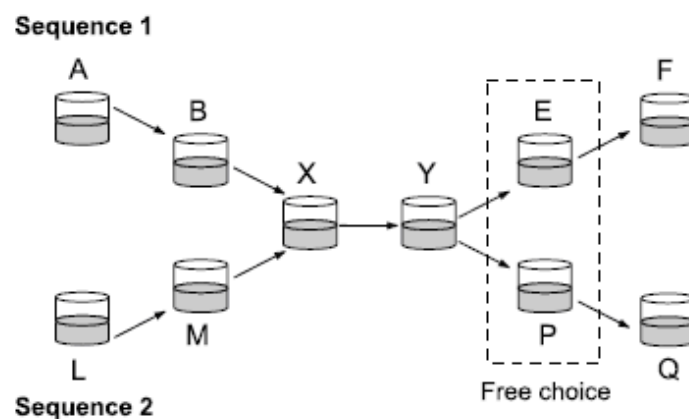


Figure 2. Experimental design used by Eichenbaum *et al.* (2005)

3.4. Scrub-Jays provision for future motivational state

The fact that jays are sensitive to the presence of another bird during caching demonstrates the anticipation of a future cache state. Notably, Emery and Clayton (2001) only observed this behaviour in birds that had previously acted as thieves. This suggests that jays utilise past experience as thieves to predict the future prospect of cache theft. Once again the birds display a strikingly human quality in that they obey the famous proverb “it takes a thief to know a thief”.

Two recent studies have demonstrated that jays unquestionably plan for a future motivational state and may use episodic future thinking to do so. Based on compensatory food storage (fig. 3), Raby *et al* (2007) established that jays plan the next morning’s breakfast menu. Nevertheless, the authors failed to dissociate between present and future motivational states, a criticism used by Suddendorf and Corballis (2008) to dismiss the evidence as conclusive proof of future planning.

When jays are prefed a food they become specifically satiated for that particular food and will preferentially cache a different food type if later given the choice. Correia *et al.* (2007) use this phenomenon, known as specific satiety, to dissociate between present and future motivational state (table 2). If the birds’ decisions are controlled only by their present motivational state then they should cache food B because it is different from food A, which they have been prefed. If, however, the birds can dissociate their present and future motivational states they will behave against the rule of specific satiety and cache the same food type as they were prefed on at stage 1. This is because they will predict the intervening stage 3 prefeeding with a different food type (B) and operate on the basis of their future motivation to eat food A at future recovery (Correia *et al.*, 2007).

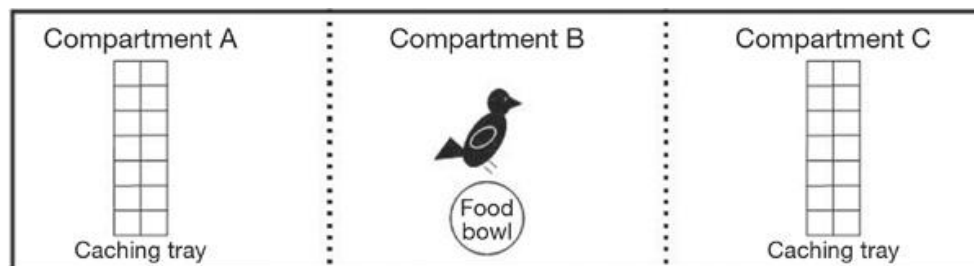


Figure 3. Birds were trained that food would be lacking in one of two compartments (experiment 1) or that one of two foods would be lacking (experiment 2). After unexpectedly being provided with food to cache in the evening, jays preferentially stored in the location where it would be unavailable and differentially cached the food-type that would be unavailable the next morning (Raby *et al.*, 2007).

Group	Stage 1	Stage 2	Stage 3	Stage 4	Trials 1-3
Different	Prefed A	Caching	Prefed B	Recovery	Increase in caching prefed food A because predicted satiation for food B at recovery
Same	Prefed A	Caching	Prefed A	Recovery	Continue caching food B because satiated for food A at recovery

Table 2. Schematic outline of the methodology used by Correia *et al.*, (2007).

However, this interpretation of the data has been subsequently challenged by Suddendorf and Corballis (2008) who contend that although a greater proportion of pre-fed food was cached by the ‘different’ group, the absolute number of pre-fed items stored did not significantly change. Instead, it is the termination in storage of the pre-fed items by the ‘same’ group that causes the shift in proportion. Thus the authors argue that the data does not show that the birds acted to secure a future need, but that they stopped caching items that were plentiful at recovery. In response, Clayton *et al.* (2008) argue that in light of the complex motivational processes (general hunger states and incentive learning) a relative measure is an appropriate analysis.

3.5 Primates pre-experience tool use

While scrub jays have proved to be an instrumental model organism, and have even been referred to as “the feathered primate” (Izawa, 2008), the interpretation of this crucial experiment remains a case for debate. A recent study on real primates by Osvath and Osvath (2008), however, has demonstrated that nonhuman animals are capable of pre-experiencing functional tool use. After learning how to obtain fruit-soup from a bottle using a plastic hose, primates were presented with four novel tools (one functional and three non-functional) and challenged to judge which tool was (a) long enough and (b) open-ended to allow the soup to be accessed (fig. 4). The selection of the appropriate tool and lack of hesitation in tool use suggested that the primates envisioned how the tool would be used (fig. 4). More recently, Osvath (2009) reported that a male chimpanzee exhibits stone-caching behaviour for use during dominance displays. The clear dissociation between current calm state and future aggressive state provides further evidence that MTT may exist in nonhuman animals.

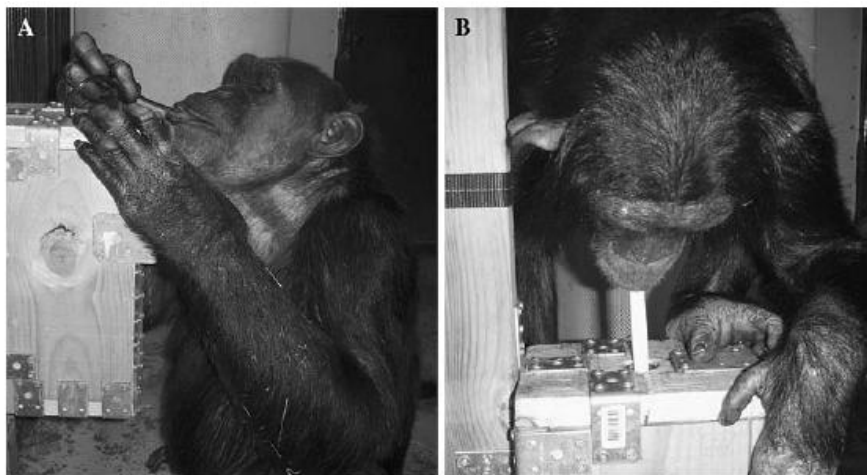


Figure 4. The primates were capable of accessing the fruit-soup using a variety of techniques in response to the dimensions of the tube. The appropriate tool was selected on eight and nine occasions by two chimpanzees, and eleven occasions by an orang-utan over the course of 12 trials.

Species	Where	What	When	Who	Future MTT	Reference
Scrub jays	✓	✓	✓	✓	✓	Clayton <i>et al.</i> 2001; Dally 2006
Rats	✓	✓	✓			Babb and Crystal; Eacott 2005
Mice	✓	✓	✓			Dere <i>et al.</i> 2005
Chimpanzees	✓	✓		✓	✓	Menzel 2005; Osvath and Osvath, 2008
Gorillas	✓	✓		✓		Schwartz <i>et al.</i> 2005
Orangutans	✓	✓		✓	✓	Scheumann and Call 2006; Osvath and Osvath, 2008
Crested Gibbons	✓	✓				Scheumann and Call 2006
Hummingbirds		✓	✓			Henderson <i>et al.</i> 2006
Rhesus monkey	✓	✓	X			Hampton
Pigeon	X	X	X	X		Skov-Rakette 2006

Table 3. The current state of knowledge on the ability of nonhuman animals to display ‘MTT-like’ behaviour. This is not to say that the volume of evidence proves the existence of MTT in nonhumans, nor should future research attempt to add additional species to the list. MTT-like behaviour is highly specific to particular species and stimuli and should be explored accordingly. Instead the table has been included to demonstrate the large body of knowledge that has not been discussed.

3.6. Neurophysiological access to mental content

Studies in rodents have begun to reveal the neural mechanism for simulating future choices. By monitoring the activity of hippocampal place cells, Diba and Buzsáki (2007) revealed ‘forward route preplay’ in anticipation of an upcoming maze run and ‘reverse route replay’ afterward (Diba and Buzsáki, 2007). Incredibly, the electrical preplay activity of these cells mimicked their activity during the actual trial and replayed the behavioural sequence afterward. These findings were complemented by Johnson and Redish (2007) who demonstrated that place cells sweep ahead of the rat at choice points to simulate future consequences. This work demonstrates how the neurophysiological access to mental content may provide an avenue for confirming MTT in nonhuman animals.

4. Conclusion and future directions

Cleverly designed experiments are also beginning to cast doubt on the strong contention for human uniqueness in MTT (Schacter *et al.*, 2008). Nonetheless, the evidence is merely in agreement with behavioural elements expected of MTT and can be viably explained by other cognitive processes. For example, it is possible to remember where a car is parked without cognitively revisiting the ‘www’ event of parking. Crucially, it has not been demonstrated that animals mentally construct the past or future in order to make decisions. In light of recent publications, it appears that primates may have true MTT capabilities whereas nonprimates may possess a ‘prototypic’ neural basis. For the moment, however, the data does not provide sufficient grounds to abandon the Bischof-Kohler hypothesis, nor can it be concluded that nonhuman animals do not possess the capacity for MTT. The answer to this question is not merely of scientific interest, but would radically affect animal welfare because it may show that animals can suffer as a consequence of anticipation and

subsequent reliving of cruelty. At present, converging lines of evidence have allowed the formulation of the “constructive episodic hypothesis” and a crude elucidation of the core network underlying the phenomenon. Understanding the intricacies of this network and the inter-relations of its components represents the next step in understanding the neural basis of MTT. Thus, in both cases further research is required and, thankfully as humans, we can ‘look forward’ to important advances being made in this promising field of study.

References

- Addis, DR; Schacter, DL. (2008). Constructive episodic simulation: Temporal distance and detail of past and future events modulate hippocampal engagement. *Hippocampus* 18, 227-237.
- Addis, DR; Wong, AT; Schacter, DL. (2007) Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia* 45, 1363-1377.
- Addis, DR; Wong, AT; Schacter, DL. (2008). Age-related changes in the episodic simulation of future events. *Psychological Science* 19, 33-41.
- Babb, SJ; Crystal, JD (2006). Episodic-like memory in the rat. *Current Biology* 16, 1317-1321.
- Buckner, RL; Andrews-Hanna, JR; Schacter, DL. (2008). The brain's default network - Anatomy, function, and relevance to disease. *Year in Cognitive Neuroscience* 1124, 1-38.
- Buckner, RL; Carroll, DC. (2007). Self-projection and the brain. *Trends in Cognitive Neuroscience* 11, 49-57.
- 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 and Cognition* 66, 202-212.
- Correia, SPC; Dickinson, A; Clayton, NS. (2007). Western scrub-jays anticipate future needs independently of their current motivational state. *Current Biology* 17, 856-861.
- Clayton, NS; Correia, SPC; Raby, CR, et al. (2008). Response to Suddendorf & Corballis (2008): in defence of animal foresight. *Animal Behaviour* 76, E9-E11.
- Clayton, N. S. & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature* 395, 272-278.
- Clayton, NS; Emery, NJ. (2008). What Do Jays Know About Other Minds and Other Times? *Research and Perspective in Neuroscience* 82, 109-123.

Clayton, N. S. Yu, K. S & Dickinson, A. (2003). Interacting cache memories: evidence of flexible memory use by scrub jays. *Journal of Experimental Psychology: Animal Behavior Processes* 29, 14-22.

Dally, JM; Emery, NJ; Clayton, NS. (2006). Food-caching western scrub-jays keep track of who was watching when. *Science* 312 (1662-1665).

Emery, N. J. & Clayton, N. S. (2001). Effects of experience and social context on prospective caching strategies in scrub jays. *Nature* 414, 443–446. See also *Nature*, 447, 349.

Hassabis, D; Kumaran, D; Vann, SD, et al. (2007). Patients with hippocampal amnesia cannot imagine new experiences. *Proceedings of the National Academy of Sciences of the United States* 104, 1726-1731.

Mendl, M; Paul, ES. (2008). Do animals live in the present? Current evidence and implications for welfare. *Applied Animal Behaviour Science* 113, 357-382.

Osvath, M. (2009). Spontaneous planning for future stone throwing by a male chimpanzee. *Current Biology* 19, 190-191.

Osvath, M; Osvath, H. (2008). Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Animal Cognition* 11, 661-674.

Raby, CR; Alexis, DM; Dickinson, A, et al. (2007). Planning for the future by western scrub-jays. *Nature* 7130, 919-921.

Roberts, WA. (2007). Mental time travel: Animals anticipate the future. *Current Biology* 17, 418-420.

Schacter, DL; Addis, DR. (2007) On the constructive episodic simulation of past and future events. *Behavioural and Brain Sciences* 30 (331-45)

Schacter, DL; Addis, DR. (2007). The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Philosophical Transactions of the Royal Biological Sciences* 362, 773-786.

Schacter, DL; Addis, DR. (2007). Constructive memory: The ghosts of past and future. *Nature* 445, 27.

Schacter, DL; Addis, DR; Buckner, RL. (2008). Episodic simulation of future events - Concepts, data, and applications. *Year in Cognitive Neuroscience* 1124, 39-60.

Suddendorf, T; Corballis, MC. (2008). New evidence for animal foresight? *Animal Behaviour* 75, 1-3.

Suddendorf, T; Corballis, MC. (2007). The evolution of foresight: What is mental time travel, and is it unique to humans? *Behavioural and Brain Sciences* 30, 299-311.

Szpunar, K.K; Chan, J.C.K; McDermott, K.B. (2008). Contextual processing in episodic future thought. *Cerebral Cortex* 19, 201-225.

Szpunar, KK; McDermott, KB. (2008). Episodic future thought and its relation to remembering: Evidence from ratings of subjective experience. *Consciousness and Cognition* 17, 330-334.

Szpunar, KK; Watson, JM; McDermott, KB. (2007). Neural substrates of envisioning the future. *Proceedings of the National Academy of Sciences of the United States* 104, 642-647.

Quoidbach, J; Hansenne, M; Mottet, C. (2008). Personality and mental time travel: A differential approach to auto-noetic consciousness. *Consciousness and Cognition* 17, 1082 – 1092.