Investigating the Janus Hypothesis:
An fMRI Study of the Neural Substrates of Mental Time Travel

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PREFACE

This thesis was developed by me, with help from both my supervisors along the way. The topic of the thesis was determined together with my main-supervisor, based on a common interest in the cognitive neuroscience of memory. The experiment was approved by the ethics committee (REK Sør-Øst). I designed the experiment, collected the data, and performed all analyses myself.

FMRI data collection was done at the Intervention Centre, at Rikshospitalet HF, throughout October and November 2008. During the MR-scanning sessions, a radiograph performed the recordings themselves. I would like to thank Håkon Engen and Kari-Anne Hagen, for providing assistance during the MR-scanning sessions. I am also grateful to radiograph Terje Tilung, for overseeing the MR-recordings. Special thanks go to Carol Weingarten, for providing comments on the thesis.

Last but not least, I would like to express my gratitude towards my two supervisors. Special thanks go to my main-supervisor Tim Brennen, for providing invaluable input in every stage of this thesis, from start to end. I appreciate the respect you showed me and the thesis, by always being honest and exact in your supervising. I would also like to thank my co-supervisor Tor Endestad, who made it possible for me to use the MR-scanner at Rikshospitalet. The feedback you continuously provided on the methodological issues of this thesis were of great importance.

Oslo, May 4th, 2009
Lasse Bang
ABSTRACT

‘Mental time travel’ (MTT) refers to the general neurocognitive capability to re-experience past events (past MTT) and imagine future ones (future MTT). In recent years, several studies have indicated that past and future MTT are closely linked in brain and mind, a claim referred to as the ‘Janus hypothesis’. Questions pertaining to the nature of this link and its neurocognitive basis have been raised. The present study employed functional magnetic resonance imaging (fMRI) to delineate the neurocognitive processes involved in past and future MTT. Participants were scanned as they performed tasks requiring them to remember past events and imagine future ones. Whole-brain contrast analyses revealed that there were no differences in brain activity during the past and future tasks. Relative to a control task, these tasks activated regions in medial frontal, medial temporal, medial parietal (including posterior cingulate) and lateral temporoparietal areas. Analyses of functional connectivity identified four functional brain networks active during both the past and future tasks. These networks were equally modulated by both tasks, and largely replicated the regions identified in the whole-brain contrast analyses. The networks can tentatively be ascribed to processes related to the retrieval and integration of information from episodic memory. The author suggests that the observed link between past and future MTT reflect the simple fact that when imagining future events, one must draw upon past experiences. Therefore, future MTT involves the same set of processes traditionally reserved for episodic memory retrieval.
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INTRODUCTION

During the past decade, episodic memory (EM) has been reconceptualised in order to acknowledge its role in prospective processes (Atance & O'Neill, 2001; Schacter, Addis, & Buckner, 2007, 2008). From its conception, research on EM has primarily been concerned with how such memories are encoded, retrieved, and distorted. However, Endel Tulving suggested long ago that EM also plays a role in our ability to imagine future events (1985; 2002). He proposed that the EM system supports our ability to engage in ‘mental time travel’ (MTT), which refers to the general neurocognitive capability to re-experience past events (‘past MTT’), and pre-experience (or imagine) future ones (‘future MTT’, see Suddendorf & Corballis, 1997; Tulving, 2002).

In recent years, there has been an increasing interest in past and future MTT, especially regarding how they are theoretically and empirically related to each other and to EM in general (Atance & O'Neill, 2001; Boyer, 2008; Buckner & Carroll, 2007; Hassabis & Maguire, 2007; Schacter et al., 2007, 2008). Studies have revealed that past and future MTT share phenomenal characteristics and mediators (Berntsen & Jacobsen, 2008; D'Argembeau & Van der Linden, 2004, 2006; Quoidbach, Hansenne, & Mottet, 2008), develop around the same age (Atance & O'Neill, 2005; Busby & Suddendorf, 2005), have overlapping neural substrates (Addis, Wong, & Schacter, 2007; Botzung, Denkova, & Manning, 2008; Okuda et al., 2003; Szpunar, Watson, & McDermott, 2007), are equally affected in amnesia (Hassabis, Kumaran, Vann, & Maguire, 2007; Klein, Loftus, & Kihlstrom, 2002; Rosenbaum et al., 2005; Tulving, 2002) and in schizophrenia (D'Argembeau, Raffard, & Van der Linden, 2008).

This bulk of evidence has led some to suggest that past and future MTT are closely linked in brain and mind, a claim that has been referred to as the ‘Janus hypothesis’ (Dudai & Carruthers, 2005; Suddendorf & Corballis, 2007). In Greek mythology, Janus was a God with two faces, which allowed him to see both into the past and future. The evidence supporting this hypothesis is interesting, because imagining future events has traditionally not been associated with memory. Imagining future events require us to ponder and imagine the unknown future, while memory extracts and recounts already encoded information about the past. Although the Janus hypothesis is supported by the empirical literature, we do not know exactly what the link between past and future MTT consist of. Considering that both past and future MTT involves the same neural machinery, they obviously share some cognitive
processes. But what functions do these processes subserve?

Investigations of the neurocognitive basis of past and future MTT can be traced back to the study of patient K.C., who suffered anterograde and retrograde amnesia following a motorcycle accident (see Rosenbaum et al., 2005 for an extensive review of K.C.’s case). In addition to his amnesic deficits, he was also unable to imagine himself in a future event:

Thus, when asked, he cannot tell the questioner what he is going to do later on that day, or the day after, or at any time in the rest of his life. He cannot imagine his future any more than he can remember his past (Tulving, 2002, p. 14).

Endel Tulving suggested that K.C. had damaged his ability to mentally travel through time, which would equally affect his ability to remember past events and imagine future ones.

A similar case study was reported by Klein, Loftus and Kihlstrom (2002), who studied a patient with retrograde and anterograde amnesia caused by hypoxic brain damage. The patient – called D.B. – was also unable to envision future events involving himself. However, he was capable of anticipating future issues in the public domain, a process that is non-personal (and therefore non-episodic) by nature, which by some is referred to as ‘semantic future thinking’ (see Atance & O'Neill, 2001).

Thus, it appears that amnesia also disrupts the ability to engage in future MTT, although we cannot infer if this is directly related to the amnesia itself. It is also difficult to localize the deficits to a specific brain structure or system, since the brain injuries of both K.C. and D.B. are widespread, and caused by different types of trauma.

Further insights into the neural substrates of MTT come from several neuroimaging studies. These have employed analyses measuring functional specialization, which means that they statistically test if any region of the brain is more active during task A compared to task B (often a control task). Should any region be more active, one can conclude that this region is specialized for performing task A, compared to task B.

Studies of this kind have revealed that the neural substrates associated with past and future MTT are remarkably similar (Addis et al., 2007; Botzung et al., 2008; Okuda et al., 2003; Szpunar et al., 2007). That is, both past and future MTT engage much of the same network of brain regions, which suggests that there are few regions specifically specialized for
remembering past or imagining future events. The observed common network is situated mainly in medial frontal, medial temporal, medial parietal (including posterior cingulate cortices) and lateral temporoparietal regions. This MTT network has traditionally been associated with EM retrieval (Cabeza & St Jacques, 2007; Maguire, 2001; Svoboda, McKinnon, & Levine, 2006).

Buckner and Carroll (2007) point out that navigation and theory of mind (ToM) tasks activate networks similar to the MTT network. They claim that common to all these tasks is the process of projecting the self into alternative perspectives or situations. For instance, when engaging in ToM tasks, one must change the perspective from the immediate environment and into someone else’s viewpoint. In this sense, one must project the self into another person, and try to imagine what they see or what they are feeling. Similarly, when engaging in past or future MTT, one is projecting the self into situations and perspectives that is not represented in the immediate environment, but that instead are internally generated.

Hassabis and Maguire (2007) propose a different account of the observed neural overlap between the aforementioned tasks. They suggest that the common cognitive process is not self-projection, but processes related to the construction and maintenance of spatial scenes. These scenes provide the stage in which remembered or imagined events take place, and are also involved during navigation tasks (and maybe during ToM tasks as well).

In support of this, a neuroimaging study by Hassabis, Kumaran and Maguire (2007) illustrated that much of the same neural network is activated when imagining purely fictitious events, which the authors claim do not involve self-projection or a sense of subjective time. Moreover, another study showed that hippocampal amnesia were accompanied by an inability to create coherent spatial scenes (Hassabis, Kumaran, Vann et al., 2007), thus impairing the ability to engage in past and future MTT. The hippocampus is one of the brain structures activated during MTT tasks, and is a key structure subserving the EM system (Simons & Spiers, 2003).

One cognitive process common to both past and future MTT is EM retrieval, since the mental construction of future events necessarily requires the extraction of information stored in memory (Szpunar & McDermott, 2008). This expressed in the constructive episodic simulation hypothesis (Schacter & Addis, 2007; Schacter et al., 2008), which states that the imagining (or simulation) of future events involves the extraction and recombination of various elements contained in EM. This would require that the EM system is flexible and
constructive rather than reproductive, which could explain why episodic memories are prone to distortions (Schacter & Addis, 2007). Other researchers have also underlined the flexibility of the EM system (Suddendorf & Corballis, 2007). This commonality has received surprisingly little attention when attempts have been made in describing the nature of the link between past and future MTT.

Since imagining future events requires extracting information from EM without reinstating the actual memory itself, it is plausible to suggest that future MTT requires a higher degree of cognitive and mnemonic control. Thinking about one element in memory activates the full neural representation of the memory, through a process called ‘pattern completion’ (Simons & Spiers, 2003). Therefore, if the brain is to retrieve elements contained in EM without activating the whole memory itself, it has to engage in inhibitory processes, withstanding pattern completion. The prefrontal cortex (PFC) has been implicated in functions related to mnemonic/cognitive control (Cabeza & St Jacques, 2007; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Simons & Spiers, 2003) and inhibitory processes (Incisa della Rocchetta & Milner, 1993). Therefore, it is reasonable to suggest that one potential difference between past and future MTT resides in their differential engagement of the PFC. Indeed, some studies have associated future MTT with greater PFC activity (Addis et al., 2007; Okuda et al., 2003), while still others have failed to find this pattern (Botzung et al., 2008).

The present study endeavoured to further delineate the neurocognitive processes involved in remembering past events and imagining future ones, and in doing so provide a clearer picture of the neurocognitive basis of MTT. A functional Magnetic Resonance Imaging (fMRI) block-design study was performed on normal adults. Participants were scanned while remembering past events and imagining future ones. Whole-brain contrast analyses were performed, in addition to a functional connectivity analysis which identifies functional networks. Analysis of functional connectivity was performed because by investigating the neural substrates of MTT at the network level, it is easier to interpret the results and make suggestions as to what the commonalities between past and future MTT reflect. The hypotheses of the present study are derived from the Janus hypothesis, which suggests that past and future MTT are closely linked. The analyses were therefore expected to reveal overlapping brain structures and networks in both past and future MTT, relative to the control task. Any potential differences were predicted to be related to differential more engagement
of PFC regions during future MTT, due to the hypothesized greater requirement of inhibitory and control processes.

**EXPERIMENTAL PROCEDURE**

*Participants*

Eight Norwegian volunteers (five women; mean age, 25 years; range, 19-32 years) were recruited for the study. Participants reported no history of psychiatric or neurological illness. Informed written consent was acquired from all participants.

*Pre-scan interview*

Participants were individually interviewed on the day before scanning. They were told to freely generate and describe in detail 10 personal past events that had occurred during the last month, and 10 personal future events that could plausibly occur during the following month (starting with day after scanning). It was explained that the past events should be personal episodic memories specific in both time and place, and furthermore that they could have a time-frame lasting from minutes to hours, but no longer than 24 hours.

In relation to future events, participants were told to simulate plausible future personal episodic events. These events were required to involve some degree of novelty, but apart from this, involved the same criteria as for past events. To further explain the concept of future MTT, and to separate it from other prospective thought processes (e.g. planning), future events were compared to the concept of simulations. A simulation was explained as a hypothetical scenario involving oneself. In this sense, one simulates the future, imagining what happens, where, and when.

During the interview, the interviewer initially took a passive role, telling the participants to freely start generating events, starting with 10 past ones. Furthermore, they were told that the interviewer would cue them (e.g. “what did you do there”), if the generated events did not satisfy the criteria for specificity in time and place. In some instances, the interviewer had to take a more active role, and directly try to get the participants to think about an event (e.g. “what have you done during the last week? Any events from the past month you remember especially well?”).
Events were accepted only if they were considered episodic in nature, which involved being personal and specific in time and place. Major life events or other obviously highly emotional events were not accepted. Future events that exclusively involved routine activities (e.g. “taking the bus”) were also not accepted. The interview continued until 10 past and 10 future events had been generated. Examples of accepted and rejected events can be found in Appendix A.

Each event was given an appropriate cue-word by the participants themselves, consisting of 2-4 separate words (e.g. “Letter - Perfume”). Participants were told that during scanning, they would be presented with their self-generated set of cue-words, and that it was therefore important that they remembered which cue-word was associated with which event, and so they were encouraged to produce cue-words that were unambiguous. The interviewer wrote down short descriptions of each event, and after the participants had generated all 20 events, these descriptions were read aloud to them.

Scanning

On the day of scanning, participants were carefully instructed. They were shown the experimental paradigm on a computer, and briefed about the different tasks. The participants first completed a closed-eyes resting state functional series (≈ 5 minutes). However, data from this series were not analysed for the present study. Then another functional series was run (≈ 14 minutes), at which point the experimental paradigm was presented to the participants in the scanner. At the end of the paradigm, an anatomical scan was run (≈ 10 minutes). Total scan time for each participant was ≈ 30 minutes.

All visual stimuli were presented through vision-correcting goggles, and auditory stimuli were presented through headphones. Stimuli was presented and timed with the E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA). All visual stimuli were presented in white text on a black background (Courier New font, size 25).

Tasks

The experimental paradigm consisted of three tasks, called: ‘past’, ‘future’ and ‘control’. The past and future tasks are referred to as the ‘MTT tasks’. These were presented 10 times each, while the control task was presented 20 times (totalling 40 trials). The experiment
cycled through the tasks in a sequential order, so that the control task was always presented between the MTT tasks (e.g. control – past – control – future).

**MTT tasks.** The MTT tasks consisted of total 20 cue-words (10 past and 10 future events) generated by the participants during the interview. During ‘past’ trials, one random cue-word from the participants’ past cue-word list was presented. Participants were required to retrieve and visualize – or “play through” – the memory of the event signalled by the cue-word. They were instructed not to think about the interview, but to think about the original event, as they described it during the interview. In other words, they were told not to worry about what they said (i.e. how they described each event) during the interview, but to concentrate on the original events.

During ‘future’ trials, one random cue-word from the participants’ future cue-word list was presented, in which the participants were required to imagine and simulate the target event. Participants were told to simulate the *same events*, but the manner in which these were simulated did not have to match the simulations made during the interview. This was emphasized to reduce the chance of them trying to recall exactly what they said and imagined during the interview. Verbal instructions were given to encourage them to view the past and future events from a field-perspective (1st person), and in as much detail as possible.

The MTT tasks began with a fixation cross, followed by an instruction cue defining the task (“past” or “future”). Then one of the cue-words was presented, together with the instruction to “close your eyes.” This marked the beginning of the visualization period, which lasted for 16.5 seconds. After this, a loud ringing sound was presented, accompanied by on-screen instructions to “**open your eyes**.” This marked the end of the trial. The MTT tasks lasted for a total of 23 seconds each.

**Control task.** The control task consisted of a word-generation task (a semantic memory task). Participants were presented with a single letter (e.g. “A”), and were required to silently generate as many words as they could, starting with that specific letter. It was emphasized that this word-generation should be done without moving the lips. As in the MTT trials, each control trial began with a fixation cross, followed by the instruction “**semantic**.” Then a randomly selected letter was presented, followed by the “**close your eyes**” instruction. The following generation period was shorter than in the MTT tasks, lasting 10.5 seconds. The end of this period was marked by the onset of the ringing sound, and the “**open your eyes**” instruction. The control trials lasted a total 19.5 seconds each.
Post-scan questionnaire

Immediately following the scanning session, participants filled out a questionnaire. They responded to questions regarding the detail-richness (“To what degree would you say that the visualized event was rich in detail?”), emotionality (“To what degree would you say that the visualized event was emotional?”), and difficulty (“To what degree would you say that it was difficult to visualize the event?”) of each event. The response alternatives for these scales were in a 7-point Likert scale format, where 7 indicated the highest value (i.e. “very rich in detail,” “very emotional,” and “very difficult”), and 1 the smallest value (i.e. “few details,” not emotional,” and “very easy”).

They were further required to respond to the question: “Did you see the event mainly from a field- (through your own eyes, 1st person) or observer-perspective (through someone else’s eyes, 3rd person)?” Response to this question was given by checking one of two boxes. The last question concerned the visualized event: “When you visualized the event, did you visualize the original event (as you described it during the interview) or did you visualize the interview itself (and the memory of this?)” Participants made their response by ticking one of two boxes.

In addition to these ratings, participants also gave short descriptions of each event, in cue-word form. These were required to capture the gist of the event, and thus length was not emphasized. These descriptions would later be compared to the descriptions of each event the interviewer made the day before scanning, to ensure that the events participants thought about during scanning were the same as the ones generated in the interview.

FMRI IMAGE ACQUISITION AND ANALYSIS

Image acquisition

Images were acquired on a 3 Tesla Philips Sonata MRI scanner. Anatomical T1 weighted images were collected using a fast field echo sequence (TR = 8.5 ms, TE = 2.3 ms). Functional, or Blood-Oxygen-Level-Dependent (BOLD) data was obtained using a T2* weighted echo planar imaging (EPI) sequence (TR = 3000 ms, TE = 40 ms, FOV = 224 mm, flip angle = 80°). Thirty-six axial slices (3 mm thick) were acquired along the AC-PC line.
The first functional images were discarded to allow scanner equilibrium.

Pre-processing

All pre-processing were performed using the MatLab toolbox SPM5 (Wellcome Department of Cognitive Neurology, London, UK). Standard pre-processing steps was performed, and involved rigid-body motion correction, spatial normalisation to the MNI template, and spatial smoothing using an 8 mm FWHM Gaussian kernel. All data were high-pass filtered with a cut-off value of 128 seconds, so that low-frequency drifts longer than this was removed.

Whole-brain contrast analyses

Each of the three experimental tasks was modelled using SPM5’s canonical hemodynamic response function (HRF). Additional regressors were included to control for the effects of head movement. For each subject, a fixed-effects (1st level) model was specified using the onset times of the past, future and control tasks. The onset times of the MTT tasks were set to 2 seconds after stimulus presentation (the cue word), to take into account that the subjects had to read the cue word and close their eyes. For the control tasks, the onset time was set to 1.5 seconds after stimulus onset (the cue letter). The MTT task epochs lasted 14 seconds, while the control epoch lasted 8.5 seconds. The following t-contrasts were entered into the model: past > control; past > future; future > control; and future > past.

The contrast images from the fixed-effects model was entered into a random-effects model (2nd level), and analysed with a one-sample t-test in SPM5. All activation maps was thresholded at $p < .05$ FDR (False Discovery Rate) corrected, with a minimum cluster size of 20 voxels.

For all analyses, peak voxels from each cluster were converted to Talairach space using the icbm2tal conversion (see Lancaster et al., 2007), and labelled using the Talairach Client software (Lancaster et al., 2000), which is based upon the stereotaxic atlas described by Talairach and Tournoux (1988). Where coordinates are provided, these are in Talairach space.
An independent component analysis (ICA) was run on all participants using the GIFT toolbox (http://icatb.sourceforge.net). ICA is a data-driven (model-free) approach to fMRI analysis, which seeks to separate a mixed signal (the BOLD signal – as collected by the functional series of the MR-scanning) into a set of underlying source signals, called components (see Calhoun, Adali, Hansen, Larsen, & Pekar, 2003). The components consist of voxels that covary over time, and that are maximally independent of each other. This approach provides a measure of functional connectivity, which is defined as the temporal “correlations between spatially remote neurophysiological events” (Friston, Frith, Liddle, & Frackowiak, 1993). The ICA analysis produces a predefined number of components, each with its own spatial map and timecourse – averaged over participants. Voxels grouped together into a single component are considered functionally connected, which may indicate that they support the same cognitive process. For another example of an ICA analysis employed on complex tasks, see Calhoun and colleagues (2002).

The purpose of the ICA analysis in the present study was to investigate the functional brain networks involved during the past and future MTT tasks, and whether or not different functional networks were engaged during these tasks. Note that this is different from the contrast analyses performed in SPM5, which show regions statistically more active in one epoch compared to another. This is a measure of functional specialization. Also, a benefit of an ICA analysis is that since no model is needed, it can identify brain networks without the need for a priori assumptions about the cognitive processes involved.

The optimal number of components was determined to be 31, based on the minimum description length (MDL) algorithm, as implemented by the GIFT software. The ICA analysis was run on all eight participants using the Infomax algorithm. Results were scaled to represent z-scores. For an overview of the steps and algorithms involved in an ICA analysis, see Calhoun and colleagues, 2003.

Selection of components. Of the 31 components extracted, only some will be related to the experimental tasks. The rest will be a mixture of physiologically meaningful but - for this study - uninteresting components (e.g. visual networks), and artifacts (e.g. movement artifacts). Therefore, additional steps must be performed in order to select only a subset of the components which are deemed task-related.

To aid in the selection of components, they were temporally sorted through a multiple
regression analysis model. The ‘past’ and ‘future’ task conditions from the GLM design matrix (specified in SPM5) were used as regressors. This analysis provides a set of beta weights for the regressors associated with each component. These beta weights indicate how strongly the regressors (the past and future tasks) modulate the component timecourses. In other words, the higher the beta weight value of a particular regressor, the stronger the modulatory effect on the component timecourse. Selection of the task-related components was from here on determined by three criteria.

First criterion. First, the beta weights from the multiple regression analysis for the past and future regressors were analyzed separately with a one-sample t-test (results considered statistical significant if \( p < .05 \)). This tests whether the beta weights for the past and future regressors were statistical significant in predicting the specific component timecourses, at the random-effects level. A statistical significant result in these tests indicate that the experimental onsets (past and future tasks) modulate the respective component timecourses, and further that these components are likely task-related. In instances were a specific component was not significantly modulated by neither past or future event onsets, the component was considered uninteresting and excluded from further consideration. If a component was shown to be modulated by either (or both) past or future event onsets, the second criterion was considered.

Second criterion. The second criterion involved inspecting the individual component timecourses, to check for the task-relatedness of the components. Although the regression analysis might indicate through a high \( R^2 \) value and significant beta values that a component is modulated by the MTT tasks, the component might not be exclusively involved in these tasks. For instance, visual networks are modulated by the instructions on the screen, and so could be considered task-related in accordance with the first selection criterion, although it is modulated similarly by all conditions and are therefore not of interest in the present study. Components whose timecourses did not show differential activation in relation to the MTT tasks (separately or collectively) or control tasks, were excluded from further consideration. This could easily be determined because of the block-design and the length of each epoch.

Third criterion. The third and last criterion involved inspecting the remaining components’ spatial maps. Components consisting of obvious artefacts (e.g. activations in cerebrospinal fluid, white matter or around the edges of the brain) were excluded. Other physiologically meaningful but uninteresting activations (such as purely thalamic activations)
were also excluded. The remaining components were classified as being either MTT-related (past and/or future), or control-related, with all other components dropped from further consideration. This classification was performed on the basis of prior knowledge of the activations associated with the specific tasks, as well as their timecourses which was inspected during the selection process.

Analysis of timecourses and spatial maps. The MTT-related components were then further analyzed. This involved taking the beta weights from the past and future regressors from the regression analysis, and performing a Wilcoxon Signed Rank test. This tests whether the modulatory effects of the past and future event regressors on the component timecourses were significantly different from each other. In other words, it tests if one of the functional networks was more strongly modulated by either the past or future MTT tasks.

Furthermore, MTT-related components’ spatial maps were analyzed at the random-effects level with a one-sample t-test in SPM5. Activation maps were thresholded at $p < .05$ FDR, with a minimum cluster size of 20 voxels. This was done in order to identify the brain regions associated with each component. Note that significant results in this test do not say anything about the task-relatedness of each component. Instead, this test seeks to investigate which voxels show a statistical significant contribution to the component timecourses across participants.

RESULTS

Behavioural data

Post-scanning ratings revealed that in 95.6% of the MTT tasks, the participants were able to visualize the original event and not the interview itself. Also, a vast majority of every MTT task was visualized mainly through a field-perspective (80.6%) rather than an observer-perspective (17.5%).

By subjectively comparing descriptions of the events from before and after scanning, it was evident that for seven of the participants, the events they thought about in the scanner were the same as the ones generated during the interview (excluding 3 missing values). The remaining participant did not complete the post-scanning event descriptions, so a comparison was not possible.

Results of three Wilcoxon Signed Rank tests revealed significant differences in
phenomenological qualities across past and future conditions. Past events were more detailed ($Z = -10.52, p < .0001$), more emotional ($Z = -9.58, p < .0001$), and rated as less difficult to visualize ($Z = -5.18, p < .0001$, see Figure 1).

![Figure 1](#)

*Figure 1.* Mean and standard error values of detail-richness, emotionality, and difficulty for past and future events, as rated in the post-scanning questionnaire.

**Whole-brain contrast analyses**

Contrast analyses at the random-effects level revealed that remembering past events relative to the control task activated a brain network situated in medial frontal, medial parietal (including posterior cingulate), and lateral temporoparietal regions (see Figure 2 and Table 1). Note that the descriptions of the activations below include regions not necessarily identified in Table 1. This is because, since the cluster size was so large (20 voxels), and since the Table only lists the maximally activated voxel within each cluster, some regions are left out of the Table, even though they were part of the activation cluster.

The past MTT network involved the bilateral posterior cingulate, bilateral precuneus, left middle temporal gyrus, left parahippocampus, right fusiform gyrus, right hippocampus, right middle cingulate gyrus, bilateral medial and superior frontal gyri, left middle frontal gyrus, and right inferior frontal gyrus.

In future tasks relative to the control tasks, the same distributed network was activated (see Figure 2 and Table 1). This network included the bilateral precuneus, bilateral posterior cingulate, right anterior cingulate, right middle cingulate gyrus, left parahippocampus, right fusiform gyrus, bilateral middle temporal gyrus, left superior occipital gyrus, right postcentral
gyrus, left caudate head, left superior, right middle, and right inferior frontal gyri.

Contrast analyses between the past and future conditions failed to reject the null hypothesis. This shows that the neural substrates of past and future MTT in the present study are no different from each other, in terms of functional specialization. That is, no regions of the brain can be said to be specialized for future MTT relative to past MTT, and vice versa.
<table>
<thead>
<tr>
<th>Brain Region</th>
<th>Coordinates (x, y, z)</th>
<th>Z-score</th>
</tr>
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<tbody>
<tr>
<td><strong>Past &gt; Control</strong></td>
<td></td>
<td></td>
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<tr>
<td>L/R. Posterior Cingulate (BA 31)</td>
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<td>R. Middle Frontal Gyrus (BA 6)</td>
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<tr>
<td>R. Inferior Frontal Gyrus (BA 13)</td>
<td>36 11 -16</td>
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L. Parahippocampus (BA 36) -29 -36 -8 3.53
R. Fusiform Gyrus (BA 20) 44 -27 -11 4.48
L. Middle Temporal Gyrus (BA 21) -56 -2 -13 3.17
R. Middle Temporal Gyrus (BA 39) 32 -60 18 4.45
R. Middle Temporal Gyrus (BA 21) 51 -4 -17 3.23
L. Superior Occipital Gyrus (BA 19) -39 -75 24 4.20
R. Postcentral Gyrus (BA 3) 19 -27 48 3.44
L. Caudate 1 4 2 3.59

Note. All activations significant at $p < .05$, FDR corrected; with a minimum cluster size of 20 voxels. Talairach coordinates from the maximally activated voxel within each cluster are reported.

L, Left; R, Right; BA, Brodmann area.

aThis cluster includes parts of the parahippocampus.
bThis cluster includes parts of the precuneus.

Figure 2. Brain activations (thresholded at $p < .05$ FDR, cluster size of 20) associated with the past and future MTT tasks. Activations are overlaid on a single subject’s T1 scan. For coordinates, see Table 1.
**Independent component analysis**

A total of six components survived the three selection criteria: 5, 18, 21, 25, 28 and 29. Of these, components 5, 18, 25 and 29 were classified as being MTT-related, while components 21 and 28 were classified as control-related.

*Timecourses*. The timecourses for the MTT-related and control-related components peaked in an interleaved fashion, and their spikes were perfectly related to the experimental design (20 peaks for the MTT tasks, and 20 for the control tasks, see Figure 3). Inspection of the timecourses indicated that none of the MTT-related components was exclusively related to either the past or future tasks. This was confirmed by Wilcoxon Signed Rank tests of the beta weights associated with the past and future events, which revealed no significant differences. Thus, the four functional networks identified as MTT-related are similarly modulated by both the past and future tasks.

*Spatial maps*. Results from the random-effects level one-sample t-test in SPM5 of the spatial maps of the MTT-related components are shown in Figure 4 and Table 2. As already mentioned, the voxels within these maps represent those which show a statistically significant contribution to the respective component timecourses across participants.

Component 5 consisted of the left superior and temporal gyrus, left precuneus, left posterior cingulate, left fusiform gyrus, right inferior parietal lobule, and bilateral frontal regions centred around the middle and superior gyri. Some cerebellar activity was also evident.

Component 18 comprised of the posterior cingulate/retrosplenial cortex, hippocampus, parahippocampus, and precuneus, all bilaterally. The network also included the right middle cingulate gyrus, the left middle/medial and right superior frontal gyri, and bilateral temporal cortices.

Component 25 involved the bilateral precuneus, left anterior cingulate gyrus, left middle/superior temporal gyrus, and right medial frontal gyrus.

Lastly, component 29 comprised a network including the left superior/inferior frontal gyri, bilateral posterior cingulate, right fusiform gyrus, left middle/superior temporal gyrus. Some activity in the cerebellum was also evident.
Table 2.

*Results of a One-Sample T-Test of the MTT-Related Components’ Spatial Maps*

<table>
<thead>
<tr>
<th>Component</th>
<th>Coordinates (x, y, z)</th>
<th>Z-score</th>
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<td>R. Cerebellum</td>
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<td>R. Cerebellum</td>
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<td>L. Middle Frontal Gyrus (BA 8)</td>
<td>-24 17 41</td>
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\(^a\) Only one hemisphere is listed for bilateral components.
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<td>3.91</td>
<td>3.70</td>
<td>3.57</td>
<td>3.71</td>
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*Note.* All activations significant at \( p < .05 \), FDR corrected, with a minimum cluster size of 20. Talairach coordinates from the maximally activated voxel within each cluster are reported.

L, Left; R, Right; BA, Brodmann area.

"This cluster extends into the right hemisphere, and includes right hippocampus / parahippocampus, as well as the retrosplenial cortex."
Figure 3. Timecourses of the (1) control-related, and (2, 3) MTT-related components, in percent signal change. Yellow boxes represent the past and future task epochs.
Figure 4. Spatial maps of the MTT-related components, thresholded at $p < .05$ FDR, minimum cluster size of 20 voxels. Only t-values within the range 5-15 are displayed. Activations are overlaid on a single subject’s T1 scan. For coordinates, see Table 2.
DISCUSSION

The present study sought to investigate the neurocognitive basis of the link between past and future MTT. Participants were scanned as they remembered past personal events and imagined future ones. Behavioural results revealed that relative to future events, past events were more detailed, more emotional and easier to visualize. Additionally, the post-scan questionnaire indicated that participants were able to visualize all events, and that they visualized the original events, and not the interview itself.

Analyses of functional specialization and functional connectivity were performed, and these converged on the notion that remembering past events and imagining future ones are closely linked, thus providing further support for the Janus hypothesis. Specifically, the results revealed that past and future MTT share a remarkable neural overlap in medial frontal, medial parietal (including posterior cingulate cortices), lateral temporoparietal and medial temporal lobe regions. Previous studies of MTT have revealed a similar neural overlap between past and future MTT (Addis et al., 2007; Botzung et al., 2008; Szpunar et al., 2007). The regions in this network have traditionally been linked with EM retrieval (Cabeza & St Jacques, 2007; Maguire, 2001; Svoboda et al., 2006). Additionally, no region was exclusively associated with either past or future MTT, thus failing to reject the null hypothesis.

Furthermore, functional connectivity analyses revealed six task-related functional networks underlying the BOLD signal fluctuations, in which four of these were related to both past and future MTT. Each of these four networks was shown to be modulated equally during engagement in either past or future MTT. No functional network was identified as being exclusively related to either past or future MTT tasks.

These results support the Janus hypotheses, as predicted. However, no evidence of more PFC activity during future MTT was evident, contrary to preliminary hypothesis. The results provide important clues to the neurocognitive basis of the link between remembering past events and imagining future ones. By examining the neural substrates of past and future MTT, it is possible to provide tentative interpretations regarding the cognitive processes they reflect and share.
Neural substrates of past and future MTT

Functional specialization. All studies on past and future MTT have identified an activation pattern similar to the one found in the whole-brain contrast analysis of the present study (Abraham, Schubotz, & von Cramon, 2008; Addis et al., 2007; Botzung et al., 2008; Okuda et al., 2003; Szpunar et al., 2007). This pattern has traditionally been implicated in EM retrieval (Cabeza & St Jacques, 2007; Maguire, 2001; Svoboda et al., 2006), and includes the posterior cingulate, medial parietal, medial temporal, medial frontal, and lateral temporoparietal regions, all bilaterally.

The contrast analyses in the present study found no differences between past and future MTT. This failure to reject the null hypothesis has also been reported in a previous study (Botzung et al., 2008). However, several other neuroimaging studies have found discernable differences between past and future MTT (Abraham et al., 2008; Addis et al., 2007; Okuda et al., 2003; Szpunar et al., 2007). The specific nature of the control tasks vary between studies, and because of this, the specific commonalities and differences vary.

The behavioural data indicated some phenomenological differences between past and future MTT. One might have suspected that these differences would be reflected in the contrast analyses, which they were not. It might be that the differences were not large enough to be detected in these analyses. It could also be that these differences are reflected in the relative activity of the brain regions. Analyses of percent signal change was not performed in the present study, but such analyses might have picked up subtle differences between past and future MTT, that is attributable to the phenomenological differences between past and future events. However, note that interpretations of percent signal change analyses is particularly problematic in studies of MTT given that the same brain regions have been found to display spontaneous fluctuations in activity during passive, or resting-state periods (see Buckner, Andrews-Hanna, & Schacter, 2008; Buckner & Carroll, 2007). Potential reasons for failing to detect a difference between past and future MTT in the contrast analyses will be discussed in more detail later.

Functional connectivity. ICA analysis is an ideal tool to use when attempting to determine the cognitive processes the neural substrates of MTT reflect. By splitting activations into functionally connected networks, the neural activity is easier to interpret, and may yield different neural dynamics than the ones identified with a whole-brain contrast analysis. The present study employed such an analysis, which revealed four functionally connected
networks, all active and modulated to the same degree by past and future MTT.

Each of these can be interpreted as playing a specific role in EM retrieval, which traditionally have been thought to involve processes related to self-reflection, visual imagery, attention, executive functions, and mnemonic control (Cabeza & St Jacques, 2007; Svoboda et al., 2006). Since no functional network was uniquely associated with past or future MTT, we can conclude that regardless of what the cognitive processes these networks reflect, they are present in both past and future MTT. It is important to note that the components may not reflect a unitary cognitive process, but could contain several. Since the ICA analysis provides a measure of functional connectivity, the interpretation of each component is done in a holistic manner, considering all the brain regions in each component together.

Component 5. This functional network (see Figure 4 and Table 2) predominantly includes regions around or near the bilateral dorsolateral prefrontal cortex (DLPFC) and bilateral dorsolateral temporal cortex, which both are associated with working memory processes (Baddeley, 2003; Constantinidis & Wang, 2004). Specifically, these regions have been implicated in spatial working memory, which is an essential part during the retrieval of rich contextual memories, such as memories of events. These regions could also reflect the workings of the episodic buffer, which Baddeley proposed as a subcomponent responsible for the integration of the multi-modal constituents of episodic memories (Baddeley, 2003). Some have implicated the ventral parietal cortex (close to BA 39 and 40, both which is part of component 5) as the site of the episodic buffer (Cabeza, Ciaramelli, Oslon, & Moscovitch, 2008).

This component also involves activation in the fusiform gyrus and the precuneus. This further supports the notion that this network processes visuospatial information, as the fusiform gyrus is known for its function in processing faces (McCarthy, Puce, Gore, & Allison, 1997), and the precuneus for its role in visual imagery (Byrne, Becker, & Burgess, 2007; Cabeza & St Jacques, 2007; Cavanna & Trimble, 2006; Fletcher et al., 1995; Wagner, Shannon, Kahn, & Buckner, 2005).

This component also involves activity in the left ventrolateral and dorsomedial prefrontal cortices. The role of these regions in the present context is not as easily interpretable, since they have been associated with a wealth of cognitive processes, and are not prototypically correlated with working memory processes. It could be that they serve functions directly related to working memory, but they could also reflect other high-level cognitive processes.
such as cognitive and mnemonic control.

The retrieval of complex multi-dimensional episodes requires the temporary integrated storage of this information, so that it may be inspected. The brain network of component 5 might reflect final or transitional processes related to this temporary storing. It is worth noting that this component was identified as related to the past and future MTT tasks, which means that it is not active during the semantic task. This might suggest that the specific working memory processes this component reflects are related to spatial and otherwise multi-modal information.

Component 18. The network within component 18 involves the hippocampus/parahippocampus, retrosplenial/posterior cingulate (extending partly into the precuneus), lateral temporoparietal and superior frontal cortices, all bilaterally (see Figure 4 and Table 2). This pattern of activation contains all the regions traditionally associated with EM retrieval (Cabeza & St Jacques, 2007; Maguire, 2001; Svoboda et al., 2006), which makes sense since one would expect that all these regions operate in temporally close conjunction with each other, which would predict that they be grouped together in a functional connectivity analysis.

Damage to the retrosplenial cortex has been shown to cause amnesia (Valenstein et al., 1987), as has damage to the medial temporal lobe (Steinvorth, Levine, & Corkin, 2005). The hippocampus and parahippocampus are both crucial structures subserving EM (Bird & Burgess, 2008; Eichenbaum, 2000; Simons & Spiers, 2003; van Strien, Cappaert, & Witter, 2009). The hippocampus is thought to serve an integrative function in EM, linking together the various features that make up episodic memories (Eichenbaum, 2000; Simons & Spiers, 2003). This function is achieved through the process of pattern completion, which refers to the reactivation of a stored neural representation cued by the firing of a subset of that neural pattern (Simons & Spiers, 2003). The role of the hippocampus has also been implicated in spatial processing (Bird & Burgess, 2008; Lee et al., 2005; Maguire, Nannery, & Spiers, 2006; Rolls, Stringer, & Trappenberg, 2002), which is also an essential part of EM retrieval.

The activation of the lateral temporoparietal cortices could reflect the retrieval of modality-specific information, which occurs during the reinstating of neural patterns (Buckner & Wheeler, 2001). These areas may store the visuospatial details of the memory, a function that may be partly shared with the precuneus. As discussed, the retrieval and integration of this stored information is governed by the hippocampus, which together with the parahippocampus binds together the various feature of the memory, creating a spatially
coherent scene.

Bilateral PFC is also part of the network in component 18. During memory retrieval, the role of the PFC has been attributed to mnemonic control processes. This involves the strategic search of memories, the verification and monitoring of retrieved information, and inhibition processes (Incisa della Rocchetta & Milner, 1993; Simons & Spiers, 2003). Considered together, it seems that component 18 reflects a network dedicated to the retrieval and integration of information from memory. However, other components probably reflect the active representation (and manipulation) of this information.

Component 25. The pattern of activations involved in this component is mainly centred on the posterior cingulate and precuneal midline walls, but includes activations in the left frontal pole, left lateral temporal cortices and right superior parietal lobule (see Figure 4, Table 2). As already mentioned, the precuneus is known to be involved in visuo-spatial imagery (Cabeza & St Jacques, 2007; Fletcher et al., 1995; M. E. Wheeler, Petersen, & Buckner, 2000). It has been implicated in EM retrieval, along with the surrounding areas of the posterior cingulate (Cabeza & St Jacques, 2007; Maguire, 2001). However, unlike posterior cingulate and retrosplenial cortices, lesions to parietal areas (including the precuneus) do not lead to amnesia, which have led some to propose it has a more indirectly function in memory retrieval through its role in attentional processes (Cabeza et al., 2008).

The superior parietal lobule (or more broadly referred to as the posterior parietal cortex) has been shown to exhibit sensory-specific reactivation during remembering (Buckner & Wheeler, 2001). Some have also proposed that this structure serves working memory and attentional functions as well (Wagner et al., 2005). Considered with the other regions, this could suggest that this network is foremost dedicated to the direction of attentional resources toward the internal representations extracted from memory. It could also be that this network actively stores some of the retrieved memories, perhaps in the precuneus or in the superior parietal lobule. Given these functions, this network would then be expected to work in close temporal conjunction with the network responsible for the extraction of information. Indeed, a visual inspection of the component timecourses indicate that component 25 and 18 (hypothesized to support memory retrieval and integration) have similar temporal characteristics.

What remains unclear is how this network – if indeed subserving function relating to the holding and inspection of information retrieved from memory, relates to the network in
component 5, which is hypothesized to support working memory functions. Inspection of the component timecourses suggest that component 5 sustains activity over time, while component 25 has sharp spikes of activity. This supports the notion that component 5 contains working memory functions, but the reason for the spiking activity in component 25 is unclear.

The role of the frontal pole and temporal cortical areas within this network in the proposed function is elusive. They might play a part in the process of holding and inspecting the retrieved memories, but they may also support different functions altogether.

**Component 29.** This network consists mainly of bilateral frontal pole activation, extending posterior along the midline walls to the anterior cingulate, and dorsally along the superior frontal gyri. Activation is also evident in the bilateral precuneus, and in the right fusiform gyrus and hippocampus/parahippocampus (see Figure 4 and Table 2).

The PFC is implicated in many higher-level cognitive processes. Anterior parts of the PFC (the frontal pole) has been implicated in mnemonic control operations (Simons & Spiers, 2003), in cognitive control functions (Ramnani & Owen, 2004), and in mentalizing tasks (Gilbert et al., 2006). Medial PFC have been shown to be active during cognitive control (Ramnani & Owen, 2004; Ridderinkhof et al., 2004), and during self-referential processing (Gusnard, Akbudak, Shulman, & Raichle, 2001; Northoff et al., 2006). The network reflected in this component is most likely linked to several cognitive processes, given the functional complexity of these frontal structures.

The prefrontal cortices in this network (especially the medial cortices) might subserve the phenomenal properties of MTT (self-awareness in subjective time), or what Tulving called autonoetic consciousness (Tulving, 1985, 2001). In support of this, the frontal lobes have been hypothesized to be the seat of autonoetic consciousness (A. M. Wheeler, Stuss, & Tulving, 1997). Moreover, the midline structures of the brain have been implicated in self-referential processing (Northoff et al., 2006), and component 29 is the only network containing both frontal and parietal midline structures. This might suggest that at least one function of this network lies in mediating the self-awareness crucial for the engagement in MTT. Furthermore, the ventromedial PFC has been hypothesized to be related to the subjective feeling of remembering accompanying episodic retrieval (Cabeza & St Jacques, 2007), which is also related to processes pertaining to self-awareness.

Another role of the frontal regions may be in supporting the active maintenance of the retrieved episodes. It might exert influence over other areas (or networks) actively containing
or inspecting this information, which would be plausible considering these areas’ role in cognitive/mnemonic control processes and executive functions. In support of this, the timecourse of this component indicates a sustained activity throughout the epoch, much like component 5.

The roles of the right fusiform gyrus and right hippocampus/parahippocampus in this network are elusive. The engagement of these structures might indicate that memory-processes are involved. It could indeed be that this component also reflects encoding processes, which also would involve the frontal lobes. However, we would then also expect to see more lateral frontal regions, as predicted by the HERA model (Habib, Nyberg, & Tulving, 2003; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994).

Integrating the components. Considered together, the components reproduce the activation pattern of the contrast analyses, and they also include some additional activations not present in the contrast analyses. The components can be ascribed processes that are crucial for EM retrieval, such as working memory, memory extraction, mnemonic control, visual imagery, attention and self-reference.

The cognitive functions subserved by component 18 probably reflect the actual retrieval and integration of the episodic memories. Component 5 is hypothesized to support working memory related functions, especially related to spatial scenes. It might be that information retrieved and assembled by component 18 are brought to the network within component 5, which then temporarily stores this information so that it is accessible to conscious inspection and manipulation. This function might also be partly served by component 25. However, this component was also associated with attentional processes. It could be that components 5 and 25 actively maintain different types of information, with component 25 serving additional functions related to the direction of attention to the internal representations maintained by either component 5 or 25. Amidst all this, component 29 probably reflects processes related to self-reference, which would contribute to the conscious awareness of subjective time. This network might also exert influence over the other networks, or in some way coordinate the efforts involved in MTT.

The findings of the ICA analyses can also be integrated with earlier theories regarding the specific nature of the commonalities underlying past and future MTT. Component 18, which is hypothesized to involve memory retrieval and spatial-related processes, probably reflect some of the scene-construction processes that Hassabis and Maguire (2007) suggested was the
basis of the similarity in neural activation between past and future MTT. Indeed, several researchers have underlined the role of the hippocampus in this regard (Hassabis, Kumaran, Vann et al., 2007), and some have also identified a network quite similar to the one in component 18 that is related to retrieving and imagining spatial scenes (Burgess, Maguire, Spiers, & O'Keefe, 2001; Hassabis, Kumaran, & Maguire, 2007).

Components 25 and 29 could reflect processes related to self-projection, which Buckner and Carroll (2007) proposed was the common process when remembering past events and imagining future ones, given that these networks have been implicated in self-referential processing. These components resemble the neural networks identified in relation to ToM tasks as well (Gallagher & Frith, 2003; Saxe & Kanwisher, 2003), which also involves self-projection processes (see Buckner & Carroll, 2007).

**Episodic memory as the link**

Thus far, I have documented that past and future MTT both rely on the same neural machinery. Also, I have suggested that this machinery reflects processes involved in EM retrieval. The question that remains is “why doesn’t future MTT involve a different set of neural correlates?” After all, past and future MTT are at face value quite different. Remembering past events involves retrieving information from memory, by reactivating neural firing patterns. Imagining future events on the other hand, involves more constructive processes related to the imagination of how things may transpire.

The remainder of this discussion will focus on providing an explanation of why past and future MTT are so closely linked in the brain. I propose that this link can be understood by regarding both past and future MTT as being essentially the same process, involving the search, retrieval and integration of information stored in memory.

The retrieval of episodic memories involves accessing information stored in neural networks, in concordance with some task-parameter, temporarily holding it within consciousness, and then directing attention towards this information in order to perform the task. A simple task requiring participants to retrieve a personal event from when they were 14 years old involves a cascade of processes related to long-term memory retrieval, (spatial) working memory, mnemonic control, visual imagery, and self-reference (or awareness).

All these processes are obviously part of EM retrieval. However, they are also an essential
part of imagining future events. When constructing complex mental images like the ones involved when imagining future events, one must access and retrieve information from the same databases making up our long-term memory system. After all, we cannot build such mental episodic scenes without some form of raw-material, which of course is provided by the cumulative storage of information, both in semantic and EM systems. This is similar to the constructive episodic simulation hypothesis (Schacter & Addis, 2007; Schacter et al., 2008) mentioned earlier, which states that one crucial function of memory is to allow us to simulate the future.

The results from the present study support this notion. Not only did the contrast analyses reveal that no brain regions were specifically activated during either past or future MTT, the ICA analysis also showed that the various networks are equally modulated by the engagement in past and future MTT. Additionally, the discussion of these networks has shown that they can be tentatively mapped onto cognitive processes traditionally considered to be involved in EM.

One potential difference between past and future MTT pertaining to memory processes is related to the integration of elements stored in memory and the control of these. As discussed earlier, when thinking about one specific element of a memory, the full neural representation of the memory will be activated (if the element is specific enough to separate between different episodic memories) through the process of pattern completion. In this sense, when retrieving a memory of an event we already have a ‘recipe’ for how the various elements defining the event is to be combined (although this recipe might be faulty and lead to memory distortions).

When imagining future events on the other hand, we have no ‘recipe’ for how to combine the various elements, like in memories. Since this calls for a more flexible retrieval of elements contained in memory, it requires withstanding pattern completion, which again requires a greater degree of inhibition and control processes. Consider the hypothetical future scenario of going to the dentist. Your tooth hurts, and you know that the dentist has to pull it. When imagining this event, one would have to draw on elements contained in memory (i.e. memories of experiences going to the dentist), without reinstating pattern completion. After all, if pattern completion is successfully completed, this would bring up the memory of a past event instead. Therefore, imagining future events requires one to extract individual elements contained in EM, and combine them into a novel personal event.
On the basis of this, one would expect that the memory related processes during past and future MTT is similar, with the exception that future MTT requires a greater degree of mnemonic control processes, such as strategic retrieval, inhibition and monitoring. As mentioned earlier, these processes reside within the PFC (Cabeza & St Jacques, 2007; Incisa della Rocchetta & Milner, 1993; Ridderinkhof et al., 2004; Simons & Spiers, 2003). The additional processes associated with this would be more evident during the initial phases of a future MTT task, since it is during this time that the retrieval and combination of elements occurs. When the future event has been created, it is probably held in the temporary conscious storage in much the same way as past memories.

In support of this, Addis and colleagues (2007) found several regions within the frontal lobes activated during future MTT but not during past MTT, when participants were engaged in mentally constructing the events. Importantly, these differences were not present when participants were elaborating on the events. Also, percent signal change estimations showed a greater degree of activity during future MTT within frontal areas.

Furthermore, in the study by Okuda and colleagues (2003), the anteromedial frontal pole was found to be more active when participants were thinking about the future relative to the past. As already mentioned, the frontal pole has been associated with higher cognitive functions such as mnemonic control (Simons & Spiers, 2003), cognitive control in general (Ramnani & Owen, 2004), and mentalizing (Gilbert et al., 2006). The results of the studies by Addis and Okuda are in concordance with the hypothesis that future MTT requires a greater degree of mnemonic control.

However, the present study and a previous one (Botzung et al., 2008), found no differences in the contrast analyses between past and future MTT. The reason for this is probably due to two factors common to both studies: the usage of a pre-scan interview, and the collapse of both construction and elaboration processes into one single block.

By using a pre-scan interview to acquire the events and their associated cue-words, one removes the sort of spontaneous generation that is required when being presented with novel cue-words. Such spontaneous generation of events puts a greater toll on processes related to the construction of the events. When participants know which future event a specific cue-word signalizes, this demands less constructive processes related to the novel combination of elements contained in memory. Moreover, it is possible that the participants thought about the pre-scan interview during the future trials, in which case the future events would be
remembered instead of imagined. However, this is unlikely to have happened considering they were specifically instructed to not worry about what they said during the interview, and in light of the responses in the post-scan questionnaire.

Additionally, the present study and the study by Botzung and colleagues did not separate between construction and elaboration processes, such as Addis and her colleagues (2007) did. This might have lead to a Type-II error, by reducing the statistical power of the tests. However, if there were indeed differences in the neural substrates during the construction of past and future events, this should have been picked up by the ICA analysis, since this type of analysis operates independently of the experimental design. However, no such difference was detected.

Limitations and future directions

I have already noted on some of the limitations of the experimental design, related to the use of a pre-scan interview and block design. Some technical limitations of the analyses are also worth noting.

ICA analysis is a fairly new way of analysing fMRI data, and there is not yet a straightforward way of performing and interpreting such analyses. The present study relied on the MDL criteria when selecting the number of components. This order might have been too high, which results in functional networks being split up into several. However, the present study only identified a total of six task-related components, and this number does not in any way seem to be excessive, considering the complex nature of the tasks. Moreover, the present study did not do analyses on the component timecourses. There might be differences in the temporal characteristics of the timecourses during past and future MTT, which is not apparent by visually inspecting the timecourses.

Future studies will benefit from a shift of focus away from exploratory analyses of MTT, to directly testing hypothesis regarding the commonalities and differences between past and future MTT. For instance, the present study, as well as previous ones (e.g. Addis et al., 2007; Okuda et al., 2003), have suggested that the one difference between past and future MTT lies in the construction of the events, in which future MTT requires more mnemonic control, in order to inhibit pattern completion and constructively combine elements from memory in novel ways.
The conjoint study of past and future MTT has great theoretical implications. For many years now, researchers have separated between memory and prospection. Memory researchers have focused on the encoding and retrieval of memories, while those within the field of judgment and decision-making have focused on how people make inferences about the world, which often, concerns the future. However, one vital aspect of memory is to allow us to better cope with the future, and conversely, making inferences about the world is often (if not always) based on knowledge or experiences contained in memory. The Janus hypothesis, and studies of MTT, indicates that the past/future, or memory/prospection distinction is somewhat artificial. Researchers have a lot to gain by bridging the gap between the past and the future. The close link between memory and processes oriented toward the future tells us that memory is not only a system concerning the past, it is also essential for the future. In the words of the British poet Lord Byron: “the best of prophets of the future is the past.”
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APPENDIX A. EXAMPLES OF ACCEPTED AND REJECTED EVENTS

This section will give examples of rejected and accepted past and future events. Each event is from different participants. Rejected events were considered to lack the episodic specificity, and/or personal involvement needed in order to be categorized as ‘episodic’. Episodic specificity refers to the event having a clear temporal timeframe (i.e. from minutes to hours), and to involve a clear visuospatial context.

Accepted past event

Last Tuesday, I was going to a band meeting at our rehearsal place, near Ullevål. I had just gotten a new instrument, so I was excited. Me and fourteen others showed up, only to discover that we didn’t have a key to the building where we rehearse. We had to wait for someone to bring a key, and in the meantime, we just sat around waiting. Then we started to play games, and it turned out that we actually had a lot of fun just waiting and playing games! After about forty-five minutes, someone showed up and locked us in.

Accepted future event

It’s my friend’s birthday next week. I envision a bunch of us going out to dinner, maybe on Saturday. Since it’s probably only my Turkish friends there, I imagine that the mood is quite casual. We talk and laugh out loud. I imagine we go and catch a show afterwards. Maybe the stand-up show with Anne K. Hærland. I’ve never seen her, but I imagine we’re all having a good time, and laughing.

Rejected past event

A few days ago, I was waiting for the train to school. I remember the train coming, and once on the train I was reading a newspaper, the same one I always read on my way to school. It was crowded as usual.

Rejected future event

We’re going to Sydney in a few weeks, to visit some relatives I have over there. I envision that the trip will be nice, and that we’ll all have a good time together. We bathe a lot in the ocean, eat a lot of good food.