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Research Report

Thinking about the future versus the past in personal and non-personal contexts

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ABSTRACT

The ability to ponder the future is a hallmark of human imagination. Neuroimaging research so far has focused on episodic prospection, or thinking about hypothetical future personal events. What has received no attention is semantic prospection or contemplating hypothetical future world events. Using functional magnetic resonance imaging (fMRI), we show a number of functional dissociations in the brain when comparing future and past thinking across personal and non-personal conceptual domains. In the prefrontal cortex, the processes of information integration and self-referential thinking in the anterior medial prefrontal cortex were differentiated from those pertaining to generative construction along the dorsal medial prefrontal cortex and adjoining regions in the superior frontal gyrus. Dorsal parts of the lateral inferior parietal lobe showed lateralization effects as a function of the divergent or convergent nature of the retrieval process corresponding to whether the accessed information referred to hypothetical or real events. While ventral parts of the bilateral inferior parietal lobe were preferentially engaged during both personal past and personal future thinking, dissociations between the areas involved in personal past versus personal future thinking were found along the medial parietal wall. All in all, these findings provide novel and critical insights into the complex interactions between different processes involved in prospective and retrospective thought as modulated by the type of processed content.

1. Introduction

The idea that our ability to contemplate our futures is necessarily linked with remembering our pasts (Ingvar, 1985; Tulving, 1983, 2005), which has long been indicated by neuropsychological data (Klein et al., 2002; Rosenbaum et al., 2005; Tulving, 1985), has recently received empirical support from a number of neuroimaging studies (Addis et al., 2007; Botzung et al., 2008; Okuda et al., 2003; Szpunar et al., 2007). Diverse areas of the brain that are involved in retrieving autobiographical episodic memories, or memories of events involving oneself that occurred in the past, were also shown to be responsive when thinking about possible personal events that could take place in the future.

Attempts to explain the considerable overlap between the brain regions involved in both types of episodic thinking as well as certain types of mental simulation has resulted in broader conceptualizations concerning this network's global function as necessitating self-projection (Buckner and Carroll, 2007), mental scene construction (Hassabis et al., 2007a; Hassabis and Maguire, 2007) constructive simulation (Schacter and Addis, 2007; Schacter et al., 2007) or proactive associative

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processing (Bar, 2007; Bar et al., 2007). Although the extensive activation overlap during episodic past and future thinking suggests the involvement of several common mental operations, only few efforts have been directed at understanding the functional differences between the many brain regions (D'Argembeau et al., 2008; Hassabis et al., 2007a).

One approach to glean functional differences would be to focus on factors that are common to episodic future and past thinking and vary them selectively within a different comparison variable. The recall of episodic memories can be conceptually broken down into many component processes such as self-processing, a subjective sense of time, narrative structure, retrieval of multimodal details, and a feeling of familiarity (Hassabis et al., 2007a). Of these, two factors that lie at the root of both episodic past and future thinking, are that they are inherently and explicitly self-referential, and that both entail the (re)construction of the personal event in question. What is meant by construction is that during episodic future thinking, constructive simulation of hypothetical events enables us to pre-experience the future, whereas during episodic past thinking constructive simulation comes into play when we remember personal events that we have experienced in the past (Gilbert and Wilson, 2007). As such, our ability to mentally simulate episodic past or future events is possible because episodic memory is constructed rather than reproduced (Schacter et al., 1998; Schacter and Addis, 2007), which is why it tends to be liable to distortions and errors (Schacter and Slotnick, 2004).

In an effort to differentiate between areas that are involved in the constructive aspects of episodic thinking from its inherently self-referential aspects, we created a novel event-related fMRI experimental design where episodic (or personal) past and future thinking were investigated together with semantic (or non-personal) past and future thinking. Semantic memory refers to memory of fact based world knowledge that is not bound to a specific learning event. As human beings, we not only have the ability to think about our personal pasts and possible futures, we are also able to contemplate past world events and make informed guesses about future happenings in the world. The contemporary debate on global climate change is an ideal example of our capacity to engage in theoretical issues about what could happen to our planet in the future, regardless of whether we will be around to experience it firsthand. So the inclusion of semantic thinking into the discussion on prospection is not only timely, it also allows for a better characterization of the functions of different brain regions involved in episodic thinking.

We would predict, for instance, that brain areas involved in the constructive and flexible recombination of representations from memory should be highly activated in the case of episodic past, episodic future and semantic future thinking.[1] This is because semantic future thinking relative to the semantic past thinking would also involve accessing and manipulating a wider extent of representations that need to be weighed and integrated in order to predict the likelihood of the occurrence of a hypothetical world event. After all, generating new content necessarily requires having to combine and recombine existing elements in memory (Schacter and Addis, 2007; Suddendorf and Corballis, 2007).

These brain areas should be dissociable from other regions, that are specifically involved in self-referential processing as such regions would be only highly activated for the two episodic thinking conditions and not the semantic thinking conditions. In fact, one neuropsychological study has demonstrated a double dissociation in these declarative memory domains to encompass both future and past thinking such that the patient's capacity to engage in semantic past and future thinking was preserved, but his episodic past and future thinking were severely affected (Klein et al., 2002). The literature thus far indicates that the anterior medial prefrontal cortex (BA 10) plays a role both in the components of self-referential processing (Hassabis et al., 2007a) as well as constructive processes (Addis et al., 2007). The design of present study which allows for the disentanglement of these two processes should render it possible to shed more light on the precise function of this area.

Furthermore, uncovering which brain regions are generally responsive to representations that refer to the future, the past, or semantic content, and which are preferentially engaged by the single conditions would also help ascertain other specific functional contributions of the network of regions that includes the hippocampal formation, the lateral posterior parietal cortex, and the posterior cingulate cortex. Areas that are most strongly activated during both episodic future and semantic future thinking, for instance, could be regarded as being involved in more open-ended or divergent retrieval processes, as there is no objective correct or incorrect answer associated with the response in these conditions. By the same token, more convergent retrieval processes could be said to be operating in the areas most strongly involved during episodic past and semantic past thinking, as there is an objective true/false response associated with these conditions. Also, the functional differences between the areas involved in episodic future versus episodic past thinking could also be more clearly interpreted depending on the pattern associated with the semantic thinking conditions in the implicated brain regions. The latter would help indicate which combination of self-referential, constructive and/or open- versus close-ended retrieval components is at play.

The experimental design (Fig. 1) thus comprised of four experimental conditions (personal future, non-personal future, personal past and non-personal past). Stimuli used both in the personal past and future thinking conditions referred to events related to oneself, whereas stimuli in the non-personal past and future thinking condition referred to happenings in the external world. We employ the terms "personal" and "impersonal" in place of "episodic" and "semantic" respectively. This is because unlike in previous paradigms, where retrieval success of a particular episodic memory was checked in relation to the phenomenology and imagery associated with the recall (Addis et al., 2007; Botzung

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[1] We make no claims regarding the "simulative" aspect of these constructive processes. Presumably, simulation is only possible in relation to episodic memory as it involves recalling event-specific details. Constructive processes, however, insofar as they involve the flexible recombination of representations from memory, are required in many non-episodic situations, such as during analogical reasoning and creative thinking.

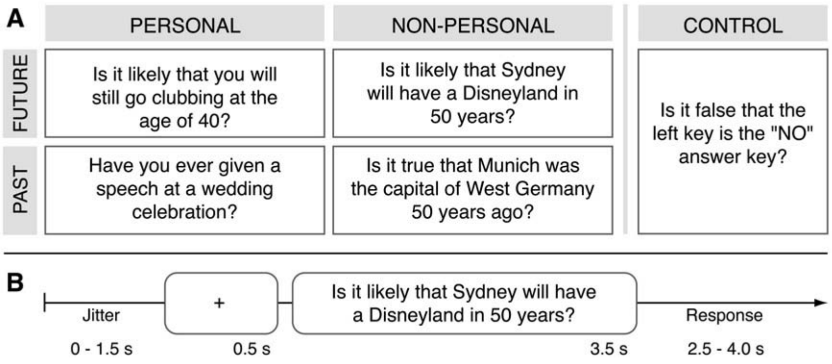

Fig. 1 – (A) The experimental design included four experimental conditions and one control condition. Examples of stimuli for each condition are provided. Past events related to the person (personal past) or the world (non-personal past), and future happenings referred to hypothetical personal events (personal future) or hypothetical world events (non-personal future). Statements concerning the coding of response keys were presented in the control condition. (B) A schematic representation of the sequence of events in a trial (trial length: 8 s).

et al., 2008), the current speeded paradigm does not stress this facet of episodic memory retrieval. Our aim was to investigate thinking about the future versus the past in both semantic and episodic domains. Both domains are not comparable in terms of associated imagery because semantic memory per definition has far less associated multimodal detail as it refers to fact knowledge that is not cued to a given time or place. Given the study's objective, the experimental trials for both semantic and episodic thinking were made comparable to avoid problems associated with contrasting conditions that contain dissimilar stimulus events within a trial or have fMRI trials of differing lengths. This of course does not rule out the possibility that episodic thinking relative to semantic thinking could automatically trigger, even in a speeded paradigm with short trial durations, richer visual imagery and the retrieval of greater volume of content.

In order to discount possible unspecific effects arising from behavioral differences, such as perceived difficulty of the conditions, an unrelated control condition was also included where participants were required to make accuracy judgments about the coding of their response keys. A variation of this control task was used in a previous study (Abraham et al., 2008a).

2. Results

2.1. Behavioral findings

Participants took longer to respond to statements referring to non-personal information compared to personal information (Main effect: context type; $F_{1,\ 19}=46.62$, $P<.001$) and to statements referring to the future relative to those referring to the past (Main effect: time period; $F_{1,\ 19}=12.5$, $P=.002$). Longer reaction times were associated with the non-personal future condition relative to the non-personal past condition ($t_{19}=2.82$, $P=.01$), and the personal future condition relative to the personal past condition ($t_{19}=4.29$, $P<.001$). Compared to the speed of their responses to the control condition statements, participants responded slower to statements referring to the non-personal future ($t_{19}=5.72$, $P<.001$), the non-personal past ($t_{19}=3.54$, $P<.001$), and the personal future ($t_{19}=2.56$, $P=.019$). So participants were slowest when answering statements about the non-personal future (mean ± s.e.: 3206 ± 100 ms), followed by that of the non-personal past (3094 ± 115 ms) and then the personal future (2995 ± 109 ms). They were fastest when responding to personal past (2847 ± 116 ms) and control statements (2832 ± 119 ms). So participants were more readily able to provide answers to self-referential questions (personal) compared to world knowledge related questions (non-personal). They were also faster when responding to questions that were associated with an objective yes-or-no response (past) compared to open-ended questions where there were no correct/incorrect answers (future).

The analyses of the fMRI data were performed using inclusive mask analyses where the contrasts with the control condition were employed as inclusive masks when comparing the experimental conditions. This allows overruling the argument that the areas activated during episodic thinking only reflect the operation of the default mode of brain function (Raichle et al., 2001), as might have otherwise been claimed because the reaction times during episodic past and future thinking were faster than during semantic past and future thinking.

2.2. *fMRI findings*

2.2.1. *Experimental conditions versus control condition*

To determine which brain regions were activated in all experimental conditions (personal past, personal future, non-personal past and non-personal future) relative to the control condition, a conjunction analysis of all four contrasts was carried out. The results revealed overlapping activations between the contrasts in the medial prefrontal cortex, posterior cingulate and retrosplenial regions, temporo-parietal junction, temporal poles, lateral temporal gyri and medial temporal lobe structures (Table 1).

2.2.2. *Personal versus non-personal*

Inclusive masked analyses were carried out when comparing the experimental conditions. The inclusive masks within each

Table 1 – Activations resulting from the conjunction analysis of the Personal past>Control, Non-personal past>Control, Personal future>Control and Non-personal future>Control contrasts

Area	x	y	z	BA	mm^3	Z-max
Dorsal medial PFC	−8	46	36	8/9/10/32	16,929	5.59
Dorsal medial PFC	4	49	18	9/10/32	..	4.86
Superior frontal gyrus	19	22	39	8	..	4.62
Ventral medial PFC	−5	52	−9	10/11/12	3942	4.49
Subgenual ACC	1	22	−9	24/25	1296	4.04
PCC/RSC	−8	−50	9	29/30/23	10,287	5.59
Inferior parietal lobule/TPJ	−47	−62	27	39	2160	4.69
Inferior parietal lobule/TPJ	43	−62	30	39	1647	4.78
Hippocampal formation	19	−14	−18	–	5427	4.75
Hippocampal formation/PHG	22	−26	−15	–	..	4.70
Inferior temporal gyrus/PHG	34	−14	−24	36/37	..	3.90
Hippocampal formation/PHG	−26	−35	−12	–	6723	5.15
Middle and inferior temporal gyrus	58	−8	−12	20/21	3159	4.89
Temporal poles	43	7	−30	38	6372	5.16
Temporal poles	−41	13	−24	38	17,091	5.36
Inferior frontal gyrus	−44	28	−12	47	..	5.17
Middle and inferior temporal gyrus	−53	−11	−12	20/21	..	4.96
Cerebellum	4	−53	−39	–	1323	4.76

The list includes anatomical specification, Talairach co-ordinates (*x*, *y*, *z*), Brodmann area (BA), maximum *Z* value and volume (mm^3). All activations passed a False Discovery Rate (FDR) threshold of $P<0.05$ and a minimal cluster size of 216 mm^3 (see abbreviations in Table 2).

Table 2 – List of activations resulting from the contrast of personal thinking relative to non-personal thinking

Area	x	y	z	BA	mm^3	Z-max	Pattern
Anterior medial PFC	−5	46	0	10/32	35,802	6.73	a3, b1, c1
Left superior frontal gyrus	−20	28	42	8/9	..	6.02	a1
Subgenual ACC	−5	19	−6	24/25	..	4.94	b3, –
Right dorsomedial PFC	19	43	36	9	1728	4.22	c1
Right superior frontal gyrus	19	28	39	8	..	4.72	a1, c1
Precuneus/PCC	−5	−53	33	31	13,392	5.97	a3
Left RSC/PCC	−11	−50	9	29/30/23	..	5.21	a2, b3
Left parahippocampal gyrus	−20	−38	−9	36/37	1755	3.88	b3
Right RSC/PCC	13	−47	9	29/30	216	3.54	b3
Right hippocampal formation[a]	16	−17	−12	–	–	3.11	b3
Right MTG	46	−14	−15	21	1836	4.41	a3
Right MTG	55	−5	−6	21	..	3.75	a3
Left MTG	−59	−11	−21	21	1107	3.75	a3
Left MTG	−56	−26	−6	21	243	3.58	a3
Left temporal pole	−35	7	−33	38	1377	3.66	a3
Left ITG	−44	−8	−39	20	..	3.66	b1, c1
Left TPJ and IPL	−41	−56	24	39	3834	5.32	a3
Right TPJ and MTG	49	−62	24	39	864	5.03	a3
Left hippocampal formation	−20	−14	−21	–	837	3.54	a3
Left uncus	−17	10	−24	–	405	3.94	a3
Left IFG/MFG/OFC	−29	31	−18	47/11	2079	4.27	a3
Right IFG/OFC	25	16	−21	47/11	999	4.25	a3
Right temporal pole[a]	31	4	−27	38	–	3.30	–
Cerebellum	28	−80	−24	–	594	3.98	a3
Cerebellum	4	−56	−42	–	1701	5.20	a3

Anatomical specification, Talairach co-ordinates (*x*, *y*, *z*), Brodmann area (BA), maximum Z value and volume (mm^3) of the significantly activated areas in the Personal>Non-personal contrast (inclusive mask: Personal>Control). All activations passed a False Discovery Rate threshold of $P<0.01$ and a minimal cluster size of 216 mm^3. The last column presents the general pattern(s) of activation in each area as determined by the percentage signal change (PSC) response for each condition (see abbreviations below).

Abbreviations—Brain Areas: ACC—anterior cingulate; IFG—inferior frontal gyrus; IPL—inferior parietal lobule; ITG—inferior temporal gyrus; MFG—middle frontal gyrus; MTG—middle temporal gyrus; OFC—orbitofrontal cortex; PCC—posterior cingulate; PHG—parahippocampal gyrus; PFC—prefrontal cortex; RSC—retrosplenial cortex; TPJ—temporo-parietal junction.

Abbreviations—Activation patterns: a1: Future (PF and NPF > PP and NPP); a2: Past (PP and NPP > PF and NPF); a3: Personal (PF and PP > NPF and NPP); a4: Non-personal (NPF and NPP > PF and NPP); b1: Personal future (PF > all); b2: Non-personal future (NPF > all); b3: Personal past (PP > all); b4: Non-personal past (NPP > all); c1: Constructive generation (PF and NPF and PP > NPP); –: Other complex patterns that were beyond the scope of this paper.

[a] These regions survived a FDR correction threshold of $P<0.05$.

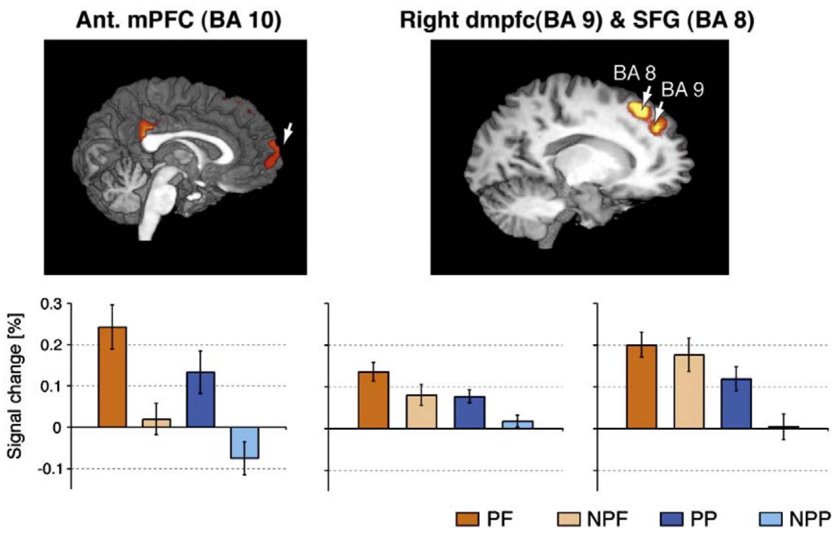

Fig. 2 – Construction and flexible recombination: Significant greater activations associated with personal future (PF), personal past (PP) and non-personal future (NPF) thinking relative to non-personal past (NPP) thinking in the anterior mPFC [PSC: 4, 61, 18], right dorsal mPFC [16, 40, 30] and right SFG [16, 31, 45] (Contrast: Future>Past) (FDR threshold $P<0.05$).

analysis were the experimental-versus-control condition contrasts. No brain region was found to be selectively activated for both non-personal conditions relative to both personal conditions (Contrast: Non-personal>Personal). In contrast, thinking about past or future events in relation to oneself (Contrast: Personal>Non-personal; Table 2) led to activations in several regions of the brain including the anterior medial prefrontal cortex (mPFC: BA 10; Fig. 2), the left hippocampal formation (Fig. S2 in Supplementary material), bilateral anterior middle temporal gyrus (BA 21), left temporal pole (BA 38), bilateral temporo-parietal junction/posterior middle temporal gyrus (BA 39; Fig. 4), and the posterior cingulate/precuneus (BA 31/7).

2.2.3. *Past versus future*

When contemplating scenarios that may have occurred in the past either with reference to oneself or to the world at large (personal past and non-personal past), regions in the right parahippocampal gyrus (BA 36/37) as well as the right retrosplenial (RSC) and ventral posterior cingulate cortices (PCC) (BA 23/29/30) were significantly more responsive (Contrast: Past>Future; Table 3).

This right RSC/vPCC region (Fig. 3) was additionally most strongly associated with personal past thinking (Table 3) as were the left RSC/vPCC (Fig. 3), the right hippocampal formation, the left parahippocampal gyrus (BA 36/37), the left angular gyrus (BA 39) (Fig. 4), and the subgenual anterior cingulate cortex (Fig. S1 in Supplementary material). In the right hippocampus (Fig. S2 in Supplementary material), for instance, activations were highest in the personal past condition relative to the non-personal past ($t_{19}=3.75$, $P=.001$), the non-personal future ($t_{19}=2.93$, $P=.009$) and the personal future ($t_{19}=2.16$, $P=.044$) conditions. This pattern was also true for the other aforementioned regions ($t_{19}>2.09$, $P<.05$ in all contrasts). Only one region in the brain was exclusively activated when thinking about the non-personal past (Table 4; Fig. S1 in Supplementary material), namely the right inferior frontal gyrus (BA 47), where the brain's response was highest relative to the personal past ($t_{19}=3.79$, $P=.001$), the non-personal future ($t_{19}=3.12$, $P=.006$) and the personal future ($t_{19}=5.18$, $P<.001$) conditions.

Table 3 – List of activations resulting from the contrast of past thinking relative to future thinking

Area	x	y	z	BA	mm^3	Z-max	Pattern
Left angular gyrus	35	74	33	39	675	4.3	b3
Subgenual ACC	5	16	0	24/25	594	4.1	b3,
Right parahippocampal gyrus	28	35	12	36/37	1080	4.65	a2
Left parahippocampal gyrus	23	38	9	36/37	9018	4.93	b3
Left RSC/PCC	14	50	9	29/30/23	..	4.9	b3
Right RSC/PCC	10	47	9	29/30	..	4.81	a2, b3
Left inferior frontal gyrus	29	28	6	47	270	3.63	–
Right inferior frontal gyrus	34	25	6	47	621	4.7	b4, –

Anatomical specification, Talairach co-ordinates (x, y, z), Brodmann area (BA), maximum Z value and volume (mm^3) of the significantly activated areas in the Past>Future contrast (inclusive mask: Past>Control). All activations passed a FDR threshold of $P<0.05$ and a minimal cluster size of 216 mm^3. The last column presents the general pattern(s) of activation in each area as determined by the PSC response for each condition (see abbreviations in Table 2).

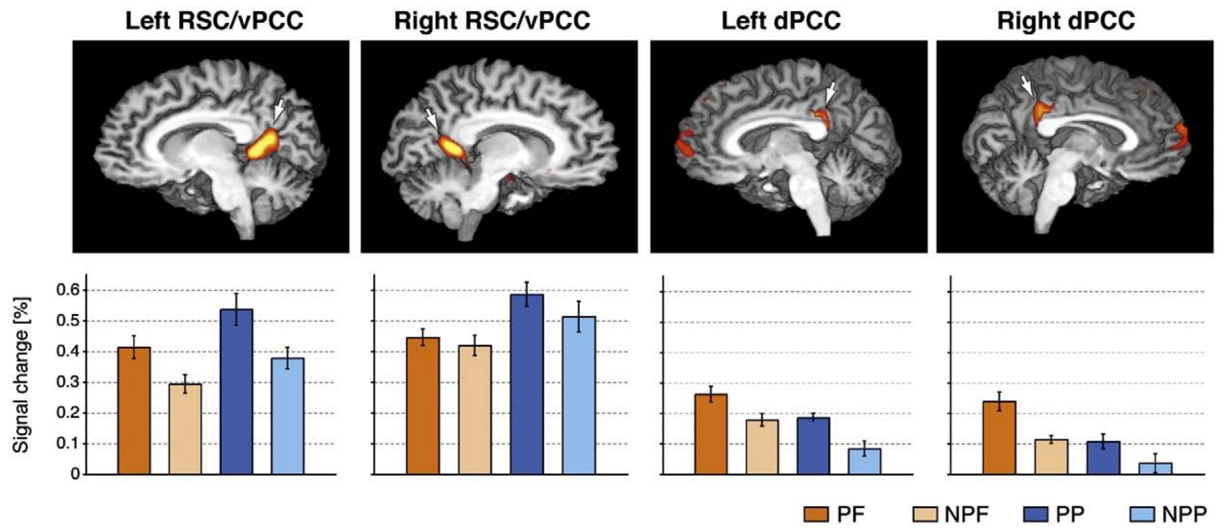

Fig. 3 – Medial parietal activations: Significant activations associated with personal future thinking (PF) in the left dorsal PCC [−5, −35, 30] and the right dorsal PCC [7, −41, 27] (Contrast: Future > Past, FDR threshold $P < 0.05$); and personal past thinking (PP) in the left retrosplenial cortex (RSC)/ventral PCC [−14, −50, 9] and the right RSC/ventral PCC [10, −47, 9] (Contrast: Past > Future, FDR threshold $P < 0.05$).

2.2.4. *Future versus past*

The brain regions that were responsive during both personal and non-personal future thinking (Contrast: Future > Past; Table 4) were the right angular and supramarginal gyri (BA 39/40; Fig. 4), the anterior part of the right inferior temporal gyrus (BA 20) as well as regions in the bilateral superior frontal gyrus (SFG: BA 8; Fig. 2. Fig. S1 in Supplementary material).

While no brain region was found to be selectively activated for non-personal future thinking, areas that were most highly responsive during personal future thinking relative to all other conditions included the left and right posterior cingulate cortices (PCC: BA 31; Fig. 3), the anterior mPFC (BA 10; Fig. 2) and the anterior portion of the left inferior temporal gyrus (ITG: BA 20) ($t_{19} > 2.09$, $P < .05$ in all contrasts). The anterior mPFC was mentioned earlier as one of the areas that was more highly activated for both personal past and future thinking relative to both non-personal past and future thinking. In addition to this, the activation of this region was highest for the personal future condition relative to the personal past ($t_{19} = 2.68$, $P = .015$), non-personal future ($t_{19} = 4.61$, $P < .001$) and non-personal past ($t_{19} = 5.14$, $P < .001$) conditions.

In order to determine which brain regions were involved in the more constructive and flexible aspects of manipulating and combining representations from memory, we carried out

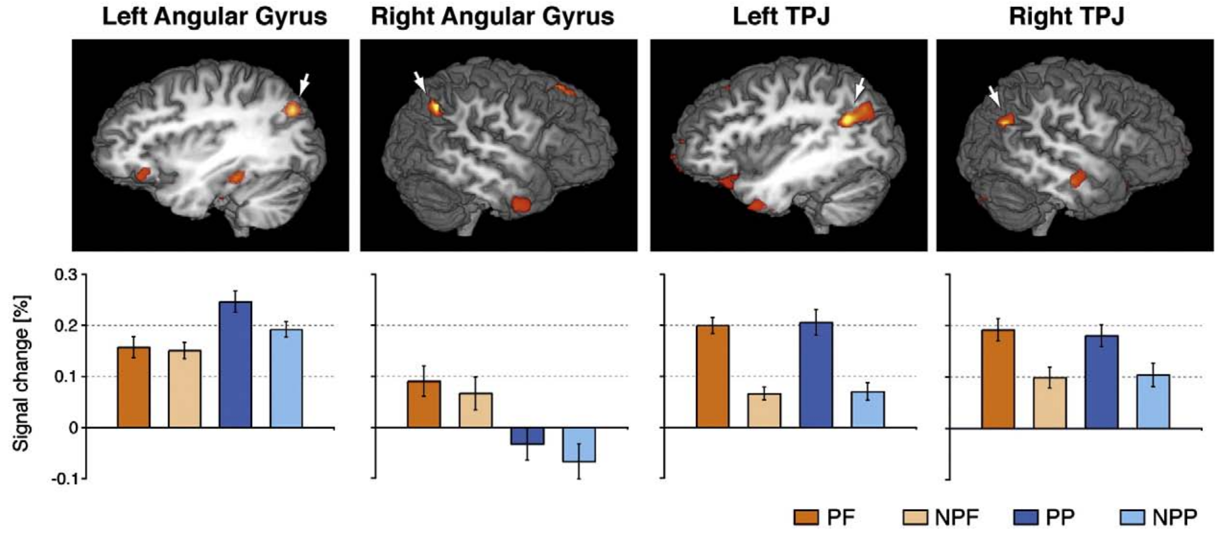

Fig. 4 – Lateral parietal activations: Significant activations associated with personal thinking (PF and PP) in the left temporoparietal junction/ventral inferior parietal lobule [left TPJ/vIPL: −41, −56, 24] and the right TPJ/vIPL [49, −62, 24] (Contrast: Personal > Non-personal, FDR threshold $P < 0.01$); future thinking (PF and NPF) in the right angular/supramarginal gyri [55, −56, 36] (Contrast: Future > Past, FDR threshold $P < 0.05$); and personal past thinking (PP) in the left angular gyrus [−35, −74, 33] (Contrast: Past > Future, FDR threshold $P < 0.05$).

Table 4 – List of activations resulting from the contrast of future thinking relative to past thinking

Area	x	y	z	BA	mm^3	Z-max	Pattern
Left superior frontal gyrus	−11	34	51	8	3402	4.76	a1
Right superior frontal gyrus	16	31	45	8	3591	5.01	c1
Right dorsomedial PFC	16	40	30	9	..	4.15	c1
Anterior medial PFC	4	61	18	10	324	3.41	a3, b1, c1
Right inferior parietal cortex	52	−56	36	39/40	513	4.67	a1
Left posterior cingulate	−5	−35	30	31	1620	3.92	b1, c1
Right posterior cingulate	7	−41	27	31	..	3.92	b1, c1
Left inferior temporal gyrus	−44	−2	−30	20	324	3.59	b1, c1
Right inferior temporal gyrus	46	−5	−30	20	945	3.79	a1

Anatomical specification, Talairach co-ordinates (x, y, z), Brodmann area (BA), maximum Z value and volume (mm^3) of the significantly activated areas in the Future>Past contrast (inclusive mask: Future>Control). All activations passed a FDR threshold of $P<0.05$ and a minimal cluster size of 216 mm^3. The last column presents the general pattern(s) of activation in each area as determined by the PSC response for each condition (see abbreviations in Table 2).

t-tests on the mean percentage signal change values of the conditions in the significantly activated brain areas from the contrast of the future versus past conditions to ascertain which areas were more highly responsive during personal past, personal future and non-personal future thinking relative to non-personal past thinking. Two adjoining areas in the prefrontal cortex (Fig. 2) were implicated in this respect. The activated area encompassed the lateral right SFG (BA 8), which was previously mentioned as being the most responsive for both future thinking conditions, and spread rostrally into the right dorsal mPFC (BA 9). This latter region was more significantly activated during non-personal future thinking ($t_{19}=2.73$, $P=.013$), personal future thinking ($t_{19}=4.48$, $P<.001$) and personal past thinking ($t_{19}=3.38$, $P=.003$) relative to non-personal past thinking. The right SFG also showed the same pattern ($t_{19}>2.8$, $P<.015$ in all contrasts). The pattern of findings in the anterior mPFC (Fig. 2), however, was unique in that it revealed significant differences such that activations when thinking about the Personal future>Personal past>Non-personal future>Non-personal past ($t_{19}>2.1$, $P<.05$ in all contrasts) (refer to Supplementary material for alternative confirmation analyses).

3. Discussion

Neuroimaging studies have investigated mental time travel with reference to episodic memory and prospection or thinking about one's own personal past or personal future. The aim of the present study was to further elucidate the functional roles of the brain regions that are activated when we engage in mental time travel by introducing the semantic memory or non-personal domain into this context. As a first step, similarities between the experimental conditions relative to the unrelated control condition were assessed. The overlapping network of regions that were implicated in this respect included the frontomedian wall, parietomedian wall, inferior parietal cortex, lateral temporal cortex, temporal poles and the medial temporal lobe. This is to be expected as thinking about personal and non-personal contexts, compared to unrelated contexts in which arbitrary rules are presented, requires retrieving and manipulating conceptual knowledge from long-term memory stores. Such tasks thereby engage declarative memory systems (episodic and semantic), which are commonly dependent on many of these brain regions (e.g., Eichenbaum, 2004; Patterson et al., 2007; Squire et al., 2004). Differences between the experimental conditions in these regions therefore indicate which parts of the general network are preferentially more engaged by a certain content type.

3.1. *Thinking about oneself*

Thinking about past or future events in relation to oneself activated several brain areas including the anterior mPFC, PCC/precuneus, and the left hippocampal formation. These areas have been routinely reported to be involved in autobiographical episodic memory retrieval (Cabeza and St Jacques, 2007; Maguire, 2001; Svoboda et al., 2006; Wagner et al., 2005). Of these, regions along the medial wall of the brain such as the anterior mPFC and the PCC/precuneus are also known to be involved during self-referential processing (Cavanna and Trimble, 2006; Gilbert et al., 2006; Northoff et al., 2006), which is of course closely related to autobiographical memory retrieval. No brain region was, however, found to be selectively activated for both non-personal past and non-personal future conditions.

3.2. *Pondering the past*

When contemplating scenarios that may have occurred in the past either with reference to oneself or to the world at large (personal past and non-personal past), regions in the right retrosplenial (RSC) and ventral posterior cingulate cortices (vPCC) were significantly more responsive. This right RSC/vPCC region was additionally most strongly associated with personal past thinking just as were the left RSC/vPCC, the right hippocampal formation, the left angular gyrus, and the subgenual anterior cingulate cortex. This fits well with much of the published literature which have for long indicated that these brain regions, particularly the hippocampal formation, play a critical role in retrieving episodic memories of the past (Cabeza and St Jacques, 2007; Maguire, 2001).

The only region in the brain that was exclusively activated when thinking about the non-personal past was the right inferior frontal gyrus. While anterior portions of the left inferior frontal gyrus have been linked to processes such as controlled semantic retrieval (Badre and Wagner, 2007), the function of this region in the right hemisphere is less clear. As some studies have indicated a role played by this area in semantic ambiguity resolution (Rodd et al., 2005; Zempleni et al., 2007), activations seen in this region may reflect the greater recruitment of resources to retrieve specific details of stored semantic memories.

3.3. *Contemplating the future*

Thinking about personal and non-personal happening in the future led to activations in the angular and supramarginal gyri in the right hemisphere as well the bilateral superior frontal gyrus. No brain region was found to be selectively activated for non-personal future thinking. In contrast, areas that were most highly responsive during personal future thinking included the bilateral PCC and the anterior mPFC. So the anterior mPFC was not just generally more highly activated for personal relative to non-personal thinking, the activation of this region was additionally highest during personal future thinking. This pattern of higher activation during personal future thinking compared to personal past thinking in the anterior mPFC has also been reported in other studies on episodic prospection and memory (Addis et al., 2007; Okuda et al., 2003).

3.4. *Flexible construction and recombination of associations from memory*

Episodic or personal past and future thinking are held to inherently entail constructive processes such as the flexible recombination of conceptual representations in memory. That semantic or non-personal future thinking would also involve a higher degree of constructive operations relative to semantic non-personal past thinking is conceivable because generating new content when mentally projecting hypothetical possibilities necessarily requires having to combine and recombine existing conceptual elements from memory (Suddendorf and Corballis, 2007). Indeed, longer reaction times during non-personal future relative to non-personal past thinking point to the recruitment of more extensive cognitive processing resources in the former.

Regions in the bilateral superior frontal gyrus (BA 8 and 9) appear to subserve such recombinatory processes as they were found to be more strongly activated during personal future, personal past and non-personal future thinking relative to a the non-personal past thinking conditions. These prefrontal areas, which in accordance with maps delineated by Petrides and Pandya (1999) would be classified as areas 9 and 8B, are dorsal to the areas 9/46d, 9/46v, 8Ad and 8Av along the middle frontal gyrus, parts of which are customarily referred to as the dorsolateral prefrontal cortex (Petrides and Pandya, 1999), and extend into the medial wall of the frontal lobe up to the paracingulate sulcus. These areas are architectonically similar, have bidirectional connections with one another, and receive afferent inputs from the posterior cingulate cortex (PCC), the retrosplenial cortex (RSC), the parahippocampal gyrus and multimodal areas of the posterior superior temporal sulcus (Petrides and Pandya, 1999).

The dorsomedial BA 9 region has been widely reported in association with mental state reasoning, although its underlying role remains disputed (Frith and Frith, 2006; Saxe, 2006). One study has shown that this region was not only specifically involved during mental state reasoning but also more generally when generating inferences to detect the presence of coherency between distinct contexts (Ferstl and von Cramon, 2002). In this study, when presented with two either indirectly related coherent sentences or unrelated incoherent sentences, processing coherent contexts gave rise to activations in the dorsomedial PFC. To be able to successfully carry out this task, the pertinent information provided by the two different contexts must be held in working memory and the relevant world knowledge from long-term memory must be retrieved and integrated with the contextual information in order to permit inference generation (Ferstl and von Cramon, 2002).

Activations close to or in the superior frontal gyrus area 8 have been reported, though rarely discussed, in tasks that require greater flexibility or generativity such as inductive reasoning (Goel et al., 1997), verbal fluency (Phelps et al., 1997) and creative story generation (Howard-Jones et al., 2005). A recent neuropsychological study on working memory has in fact pointed out that posterior aspects of lateral superior frontal gyrus are critical for monitoring and manipulative processes in working memory (du Boisgueheneuc et al., 2006). Activations along the superior frontal gyrus (BA 8 and BA 9) have also been reported in episodic prospection studies (Addis et al., 2007; Okuda et al., 2003; Szpunar et al., 2007). All these findings together indicate that these areas are involved in the more generative or constructive aspects of prospection and memory.

3.5. *Anterior mPFC: a combination of processes?*

The inclusion of the non-personal future thinking condition in the current paradigm has enabled new insights to be gained about the functional significance of this region (Fig. 2). Not only was the anterior mPFC more highly activated for during personal thinking in general and most strongly activated for personal future thinking in particular, it was also more activated during personal future, personal past and non-personal future thinking compared to non-personal past thinking, which indicates a role for this area in the constructive aspects of cognition. But the pattern of the findings was unique as the activations were proportionally highest during personal future thinking, followed by that of personal past thinking and then non-personal future thinking, all relative to non-personal past thinking. This blend of different processes at play in the anterior mPFC may be indicative of its role in integrative aspects of information processing over and above flexible construction and self-referentiality.

Previous findings of greater activation in the anterior mPFC in episodic future thinking compared to past thinking have been interpreted in terms of the role of this area in prospective memory (Addis et al., 2007). However, the fact that this area is more active when thinking about the episodic or personal past than the semantic or non-personal future in the current study speaks against a primary role for this region in simple prospective thought. More importantly, the anterior PFC has been found to play a role in several other processes including cognitive branching (Koechlin et al., 1999) and relational integration (Kroger et al., 2002), and it has been suggested that the general function of the anterior PFC is to integrate information from two or more separate cognitive operations (Ramnani and Owen, 2004). This seems plausible given the distinct anatomical features of this area that include high dendritic spine density and larger number of dendritic spines per cell coupled with lower cell body density, which together suggests that the computational properties of this region, compared to other cortical areas, involves integration of its inputs (Jacobs et al., 2001). Furthermore, the anterior prefrontal cortex is also the only prefrontal region that has mainly reciprocal connections to supramodal cortex inside and outside the PFC (Ramnani and Owen, 2004).

It is therefore possible that personal future thinking engages this region more strongly as it entails integration of a wider range of information than personal past thinking. Indeed, it has been shown that this region is most strongly activated when participants make self-referential evaluative judgments of statements based on their subjective preferences (e.g., I enjoy going to New Year's parties), and only secondarily activated in an episodic memory retrieval condition (e.g., I spent New Year's 2000 at home), both relative to a semantic retrieval condition (e.g., December 31st is New Year's Eve) (Zysset et al., 2002). While both the episodic and evaluative conditions were self-referential, the evaluative condition additionally involved assimilating a wider spectrum of information (e.g., extended personal history, personal preferences) to be able to make the subjective judgment.

Furthermore, higher activation of this area in non-personal future thinking compared to non-personal past thinking further bolsters the integration hypothesis because non-personal future thinking in itself involves accessing, manipulating and consequently integrating more information than semantic past thinking. However, the amount of associative information that is called upon during non-personal thinking is inherently more limited when compared to personal or episodic thinking due to the defining feature of semantic memory, namely that the specifics of the learning event cannot be recalled (Suddendorf and Corballis, 2007). The involvement of the anterior mPFC in the current paradigm may therefore reflect greater integration demands over and above the self-referential facets of episodic or personal thinking, which perhaps inherently entails the automatic access and integration of a wide range of information. Indeed, recent studies have shown activations in the anterior mPFC not only when recalling real events relative to fictitious events (Hassabis et al., 2007a), but also when reading contexts containing real (famous) people compared to contexts about fictional characters (Abraham et al., 2008a). These findings perhaps reflect higher degree of information integration in such real contexts which are associated with a broader and richer repertoire of information compared to imaginary contexts.

It is, however, critical not to confuse the distinction made between visualizing real versus imaginary/fictional situations (Abraham et al., 2008a; Hassabis et al., 2007b) with thinking about real past and the imaginary future. In both situations, we postulate that what is vital is not whether the information is externally determined to be "real" or "imaginary". It is rather the type and amount of associated information to given concepts which are retrieved and integrated that plays a role in whether or not the anterior mPFC is recruited. This is why it was postulated in a previous study that spontaneously elicited retrieval and integration of more information was associated with the presence of "real" entities (Abraham et al., 2008a) and in the current study the same is associated with processing "imaginary" contexts as both lead to more information being retrieved, sampled and integrated. This accounts for not only why personal future thinking more strongly activated this region than personal past thinking, but also why non-personal future thinking activated this region more strongly than non-personal past thinking.

3.6. *Parietal lobe contributions to past and future thinking*

What was particularly interesting about the medial parietal activations in the present study was that there was a dissociation between the dorsal PCC (dPCC), showing highest activations during personal future thinking, and the RSC/vPCC, that was highly activated during personal past thinking (Fig. 3). The dorsal–ventral distinction of the PCC referred to here is based on the classification by Vogt et al. (2006). In contrast, the precuneus/PCC (BA 31) was comparably activated by both personal thinking conditions. These posterior medial regions have been widely reported to be involved in episodic memory retrieval and self-referential processing (Cavanna and Trimble, 2006; Vogt et al., 2006). What our findings suggest are subtle differences within this region such that the RSC/vPCC areas are involved when accessing concrete past personal events (personal past thinking), whereas dPCC areas are involved during more divergent or open-ended retrieval of personal memories (personal future thinking).

While the dPCC receives projections from the lateral posterior parietal cortex and interacts with other structures within the cingulate cortex, the vPCC receives input from the superior and middle temporal gyri and interacts chiefly with only one region in the cingulate cortex, namely the subgenual ACC (Vogt et al., 2006). This subgenual ACC region, which is said to play a role during emotional and motivational processes (Vogt et al., 2006), was also found to be selectively activated during episodic past thinking in the current study, just like the RSC/ventral PCC.

The lateral parietal activations found in the study are also noteworthy because they reveal dissociations in terms of structure and lateralization accompanying different functional aspects of declarative memory systems (Fig. 4). While previous studies have shown different parts of the lateral inferior parietal lobe to be differentially affected by subtle facets of episodic memory retrieval (Wagner et al., 2005), our results indicate more global content-related effects. Personal past and future thinking were found to unequivocally engage ventral regions in the bilateral inferior parietal cortices including and surrounding the temporo-parietal junction (TPJ). Dorsal aspects of the lateral inferior parietal cortices, in contrast, showed lateralization effects such that the left lateral parietal cortex was specifically engaged when retrieving memories of the past to give an objective yes/no answer (personal past and non-personal past), whereas regions in the right hemisphere were engaged when retrieving memories to provide subjective answers to open-ended questions concerning hypothetical personal and world events in the future (personal future and non-personal future). These findings add wholly novel dimensions to the differential roles played by various parts of the lateral posterior parietal cortex as well as the medial parietal cortex when thinking about the future (divergent/open-ended) or the past (convergent/close-ended) in personal (episodic) versus non-personal (semantic) terms.

3.7. *Relating current findings to existing theoretical frameworks*

Prominent ideas concerning the overarching function of the network of regions is that the network is responsive when a situation necessitates self-projection (Buckner and Carroll, 2007), mental scene construction (Hassabis et al., 2007a; Hassabis and Maguire, 2007), constructive simulation (Schacter and Addis, 2007; Schacter et al., 2007) or proactive associative processing (Bar, 2007; Bar et al., 2007). We allude to the commonalities and differences between the condition-specific activations associated with the different regions in our study to make ad-hoc speculations about how these may relate to the different theories.

Ventral regions in the bilateral inferior parietal cortices were selectively responsive when thinking about one's personal past or future, and given the role of these regions in visuospatial perspective taking and bodily self-processing (Abraham et al., 2008b; Blanke and Arzy, 2005), it is likely that these regions are more involved in processes relevant to self-projection and scene construction (Buckner and Carroll, 2007; Hassabis and Maguire, 2007). As more dorsal regions of the inferior parietal cortex were differentially responsive as a function of past thinking (LH: left hemisphere) and future thinking (RH: right hemisphere), it appears that the latter RH region is more pertinent for proactive associative processing (Bar, 2007) whereas the former LH region perhaps reflects retrieval success, as has been reported in other studies (Wagner et al., 2005). Similar distinctions may also be in place in the medial parietal cortex, which was linked specifically to personal past and future thinking. Here it appears that, within the context of self-projection and scene construction (Buckner and Carroll, 2007; Hassabis and Maguire, 2007), ventral PCC/RSC regions code for retrieval success and is associated with a convergent retrieval mode whereas dorsal PCC regions may be involved in constructive simulation and is associated with divergent retrieval modes (Schacter and Addis, 2007). Finally, regions in frontal lobe appear to be responsive to processes relevant for proactive associative processing and constructive simulation (Bar, 2007; Schacter and Addis, 2007).

3.8. *Caveats and conclusions*

The objective of the current study was to gain novel insights into the functions of the many brain regions that are commonly involved in future versus past thinking by including both semantic and episodic conceptual domains in the research focus. The patterns of brain activity in various regions that reflected commonalities, differences and interactions between the variables have indeed led to the achievement of this aim. In particular, functional dissociations between areas in the prefrontal cortex, namely the dorsal mPFC, SFG and anterior mPFC, allowed us to distinguish between areas involved in the constructive relative to the self-referential and integrative aspects of prospective and retrospective thought. Dissociations within the medial parietal cortex and the lateral parietal cortex pointed to localization and lateralization differentiations based on the divergent (future) or convergent (past) nature of the retrieval process within and across episodic (personal) and semantic (non-personal) domains. The functional dissociations within the medial parietal cortex were between the dorsal posterior cingulate cortex and the ventral posterior cingulate/retrosplenial cortices, whereas those in the lateral parietal cortex, were between the left and right inferior parietal cortex as well as the more dorsal and ventral parts of the inferior parietal cortex.

The overall findings of this study are in line with the bulk of the imaging literature on episodic prospection (or future thinking) and memory (Addis et al., 2007; Botzung et al., 2008; Okuda et al., 2003; Szpunar et al., 2007), which suggests that a common “core system” comprising of the medial prefrontal cortex, lateral inferior parietal cortex, medial parietal cortex and medial temporal lobe structures, are activated during episodic past and future thinking (Schacter et al., 2007). This is especially notable because the design and methodology adopted in this study differed considerably from that of previous studies, where (a) the trial lengths were much longer ensuring that subjects had enough time to generate vivid imagery concerning an episodic event (Addis et al., 2007; Szpunar et al., 2007), and (b) either online, pre-scan or post-scan rating measures were used (Addis et al., 2007; Botzung et al., 2008; Szpunar et al., 2007), mostly to gain phenomenological indices of the subject's imagery experience. The adoption of the present design was primarily motivated by the inclusion of the semantic or non-personal thinking conditions, so the various task demands for the personal and non-personal thinking conditions needed to be made comparable. Also, a shorter trial length makes it possible to have more trials per condition and thereby increase the statistical power, which was necessary to tap possibly subtle effects. The downside to this was that because we could not have subjects report trial-by-trial ratings concerning their phenomenological experiences, the possibility that personal or episodic thinking automatically triggered more vivid visual imagery, for instance, than non-personal or semantic thinking, cannot be excluded. So other factors apart from self-referential processing that are typically associated with episodic thinking may have also played some role in orchestrating these differences. This would however mean that it is necessary to reassess the relationship between temporal duration and vividness of imagery in the construction and retrieval of memories.

A further shortcoming of the current paradigm was that the control task was only convergent in nature and was therefore perhaps a more fitting control task for the past thinking conditions (where there was an objective answer) than the future thinking conditions (which were more subjective). Devising a comparable open-ended control task that does not tap episodic or semantic processes is, however, quite challenging. But it will be one that needs to be undertaken for future studies in this research area.

That the general findings of the field were corroborated using a qualitatively different speeded experimental design, as employed in this study, attests to the strength of the phenomena in question. Moreover, differences in experimental design may explain some specific discrepant findings between the studies. For instance, while we found that the anterior mPFC (BA 10) was more strongly activated in the personal future condition relative to the personal past condition, just as in the Addis et al. (2007) study, the right hippocampus was found to be more stronger engaged during personal past than personal future thinking, contrary to what was found in the Addis et al. (2007) study. Employing different experimental designs to assess various aspects of future thinking and memory allows one to distinguish between brain regions that are stably activated across experimental designs from those that are influenced by component processes that are design-specific.

In summary then, the results of the present study have as such confirmed many of the reported findings in the literature and uncovered several novel facets of brain function that are highly pertinent not only to the discussion on prospection and memory, but also for understanding processes that are generally relevant for human imagination (Abraham et al., 2008a; Hassabis et al., 2007a,b).

4. Experimental procedures

4.1. *Participants*

After excluding two participants due to severe imaging movement artifacts, the final sample included 20 right-handed healthy volunteers (10 female; mean age: 26; age range: 22–30) with normal or corrected-to-normal visual acuity. All participants were native German speakers with no history of neurological or psychiatric illness. None were taking medication at the time of measurement and all gave informed consent before participation. The experimental standards were approved by the local ethics committee of the University of Leipzig in Germany.

4.2. *Experimental design*

A 2×2 factorial design was employed varying the type of context (personal or non-personal) and the time period (past or future). The experimental conditions together with a control condition (40 trials per condition), a resting control baseline condition (22 trials) were presented in a randomized trial design. With a trial length of 8 s and total of 222 trials, the experimental session lasted 29.6 min. The participants performed a 5-minute practice session on a laptop prior to the fMRI session.

4.3. *Stimuli*

The stimulus parameters as well as the timing of trial events were determined on the basis of behavioral pilot studies. The experimental material consisted of written sentences in German (font size: 26), which were presented in the centerfield of a screen (resolution: 800×600) spanning three lines. The number of words for statements ranged between 10 and 11 words. The statements for the past thinking conditions referred to world events (non-personal past) or personal events (personal past) in the past that were not true of the present. The statements for the future thinking conditions referred to hypothetical world events (non-personal future) or hypothetical personal events (personal past) that were set in the future. While the statements for the past thinking conditions (personal past, non-personal past) could be answered with an objective yes/no response, this was not true for the future thinking conditions (personal future, non-personal future). The term “objective” here refers to yes-or-no answers that can be given based on one’s knowledge, be it of events that took place in one’s own personal past (episodic past) or in the historical past of the world (semantic past). In the case of the future conditions, there can only be a “subjective” yes-or-no response because such events have yet to take place. Here, the subjects agree or disagree with the statements depending on whether their estimation of the likelihood that the given hypothetical personal events (personal future) or world events (non-personal future) could take place in the future. Examples of each sentence type are given in Fig. 1.

For stimuli in the non-personal future condition, care was taken to avoid topics that were currently receiving a lot of press, like global warming or the Iraq war, to avoid potential confounding effects that could arise when asking participants about issues where there was a high likelihood of having a well-thought out personal opinion. After the testing session, participants were also asked to indicate if any of the personal future statements involved events that were either invalid for them or had already taken place in the past. For instance, a participant who did not own a TV would be unable to answer the question “Are you likely to get rid of your TV within the next 10 years?” Of all the participants, 11 reported that 1 or 2 of the personal future statements were invalid for them. So these trials were excluded from the analyses.

During the course of the experiment, the left button press was always used to indicate “yes” response or agreement and the right button press always signalled a “no” response or disagreement. In line with these response codes, statements concerning the coding of response keys were presented in the control condition. The control condition statements were devised to be either correct (e.g., Is it false that the left key is the “NO” answer key?) or incorrect (e.g., Is it false that the right key is the “NO” answer key?). Just as in the case of the experimental conditions, subjects here had to indicate whether they agreed or disagreed with the accuracy of the statement.

4.4. *Procedure*

Across all conditions, each trial began with a fixation cross (duration: 500 ms) which was followed by the presentation of single sentence for 3500 ms to which the participant was required to respond (Fig. 1). Participants were able to respond any time from the presentation of the scenario up to 1 s after the presentation. Subjects were instructed to read the sentence and were to respond by agreeing or disagreeing with the statement. The response (yes or no) was made by pressing the appropriate response key (index or middle finger). Variable jitter times were inserted at the beginning of each trial (0–1500 ms) and after the stimulus event and response phase (1500–3000 ms) to enhance the temporal resolution of the blood oxygenation level-dependent (BOLD) signal. The jitter durations were in fact longer and more varied during the course of the experiment because the average reaction times across conditions ranged between 2.8 and 3.2 s (see Results section). For the baseline rest trials, a blank screen was presented for the duration of the trial.

4.5. *MRI scanning procedure*

The imaging was carried out on a 3 T Bruker (Ettlingen, Germany) Medspec 30/100 system, which was equipped with the standard birdcage head coil. Participants were placed on the scanner bed in a supine position with their right index and middle fingers positioned on the appropriate response buttons of a 2-button response box. The participants' hands were carefully stabilized and form-fitting cushions were used to prevent head, arm and hand movements. Earplugs were also provided to the participants so that scanner noise would be attenuated. The sentences were presented via an LCD projector on a back-projection screen mounted in the bore of the magnet behind the participant's head. Participants viewed the screen through a mirror placed directly in front of their eyes.

24 axial slices (19.2 cm field of view; 64×64 pixel matrix; 4 mm thickness; 1 mm spacing; in-plane resolution of 3×3 mm) parallel to bicommissural line (AC–PC) covering the whole brain were acquired using a single-shot gradient echo-planar imaging (EPI) sequence (TR=2000 ms; TE=30 ms; flip angle=90°; acquisition bandwidth=100 kHz) sensitive to blood oxygenation level-dependent contrast. Prior to the functional imaging, 24 anatomical T1-weighted MDEFT images (Lohmann et al., 2001) (data matrix=256×256; TR=1300 ms; TI=650 ms TE=10 ms) with the same spatial orientation as the functional data were acquired.

4.6. *fMRI data analysis*

The fMRI data were processed using the LIPSIA software package (Lohmann et al., 2001), which contains tools for preprocessing, registration, statistical evaluation and visualization of fMRI data. Functional data were first motion-corrected using a matching metric based on linear correlation. To correct for the temporal offset between the slices acquired in one scan, a cubic-spline-interpolation was applied. Low-frequency signal changes and baseline drifts were removed using a highpass filter with a cut-off frequency of 1/120 Hz. Spatial smoothing was performed with a Gaussian filter of 5.65 mm FWHM.

To align the functional data slices onto a three-dimensional stereotactic coordinate reference system, a rigid linear registration was performed with 6 degrees of freedom (3 rotational, 3 translational). The rotational and translational parameters were acquired on the basis of the MDEFT (Norris, 2000; Ugurbil et al., 1993) slices to achieve an optimal match between these slices and the individual three-dimensional reference data set. This high-resolution three-dimensional reference data set was acquired for each subject during a previous scanning session. The MDEFT volume data set with 160 slices and 1 mm slice thickness was standardized to the Talairach stereotactic space (Talairach and Tournoux, 1988). These rotational and translational parameters were subsequently normalized in that they were transformed by linear scaling to a Talairach standard size. The normalized parameters were then used to transform the functional slices using trilinear interpolation so that the resulting functional slices were aligned with the stereotactic coordinate system, thus generating output data with a spatial resolution of 3×3×3 mm (27 mm^3).

The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston et al., 1995; Worsley and Friston, 1995). The design matrix used for modelling the data consisted of onset vectors for the correct trials of each of the conditions, with additional vectors for baseline rest trials as well as response periods which included trial-by-trial RT as a parameter. The design matrix was generated with a box-car function, convolved with the hemodynamic response function. Brain activations were analyzed in an event-related design, time-locked to the presentation of the sentence of all presented trials. The analyzed event was the presented scenario. The model equation, including the observation data, the design matrix, and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to account for the temporal autocorrelation (Worsley and Friston, 1995). In the following, contrast images or beta value estimates of the raw-score differences between specified conditions were generated for each participant. As all individual functional data sets were aligned to the same stereotactic reference space, the single-subject contrast images were entered into a second-level random-effects analysis for each of the contrasts. One-sample *t*-tests were employed for the group analyses across the contrast images of all subjects which indicated whether the observed differences between conditions were significantly distinct from zero. *t* values were then transformed into Z scores.

A conjunction analysis was performed from the one-sample t-tests, where the output is a Z-map that corresponds to a logical 'AND' of all input images (Nichols et al., 2005). All the direct contrasts were thresholded on a single voxel level at $Z > 3.09$ prior to the conjunction analysis. All reported activations passed a minimum whole-brain False Discovery Rate (FDR) (Benjamini and Hochberg, 1995; Genovese et al., 2002) threshold of at least $P < 0.05$ and a minimum cluster size of 8 voxels (216 mm^3).

Inclusive masked analyses were carried out from the corrected one-sample *t*-tests. In each inclusive mask analysis, the statistic parametric map of the random-effects analysis of the experimental condition A-versus-control condition direct contrast was used as an inclusive mask in the random-effects analysis of the experimental condition A-versus-experimental condition B direct contrast. The findings that result from an inclusive masked analysis indicate which of the brain areas that were significantly activated for experimental condition A relative to a control condition C were also significantly activated for experimental condition A relative to experimental condition B.

For the percentage signal change (PSC) analyses of the BOLD response, the mean PSC over the analyzed event was extracted from the peak voxel within significantly activated brain areas for the experimental conditions and the resting baseline. The mean PSC of a peak voxel for each condition was calculated in relation to the mean signal intensity of that voxel across time steps. All graphs display the mean and standard error of the mean PSC or all conditions and the zero point in the graphs represents the resting baseline.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.brainres.2008.07.084.

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