



Review

Neural bases of prospective memory: A meta-analysis and the “Attention to Delayed Intention” (AtoDI) model



Giorgia Cona^{a,*}, Cristina Scarpazza^b, Giuseppe Sartori^{a,e}, Morris Moscovitch^{c,d},
Patrizia Silvia Bisiacchi^{a,e}

^a Department of General Psychology, University of Padua, Via Venezia 8, 35131 Padua, Italy

^b Department of Psychosis Studies, King's College Health Partners, King's College London, De Crespigny Park, SE5 8AF London, UK

^c Department of Psychology, University of Toronto, 100 St. George Street, Toronto, ON M5S 3G3, Canada

^d Rotman Research Institute, Baycrest Centre, 3560 Bathurst Street, Toronto M6A 2E1, Canada

^e Department of General Psychology, Center for Cognitive Neuroscience, University of Padua, Padua, Italy

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ABSTRACT

Remembering to realize delayed intentions is a multi-phase process, labelled as prospective memory (PM), and involves a plurality of neural networks. The present study utilized the activation likelihood estimation method of meta-analysis to provide a complete overview of the brain regions that are consistently activated in each PM phase. We formulated the ‘Attention to Delayed Intention’ (AtoDI) model to explain the neural dissociation found between intention maintenance and retrieval phases. The dorsal frontoparietal network is involved mainly in the maintenance phase and seems to mediate the strategic monitoring processes, such as the allocation of top-down attention both towards external stimuli, to monitor for the occurrence of the PM cues, and to internal memory contents, to maintain the intention active in memory. The ventral frontoparietal network is recruited in the retrieval phase and might subserve the bottom-up attention captured externally by the PM cues and, internally, by the intention stored in memory. Together with other brain regions (i.e., insula and posterior cingulate cortex), the ventral frontoparietal network would support the spontaneous retrieval processes. The functional contribution of the anterior prefrontal cortex is discussed extensively for each PM phase.

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* Corresponding author. Tel.: +39 049 8276248; fax: +39 049 8276600.

E-mail addresses: giorgia.cona@unipd.it (G. Cona), cristina.scarpazza@gmail.com (C. Scarpazza), giuseppe.sartori@unipd.it (G. Sartori), momos@psych.utoronto.ca (M. Moscovitch), patrizia.bisiacchi@unipd.it (P.S. Bisiacchi).

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1. Introduction

"It's a poor sort of memory that only works backwards" wrote Lewis Carroll. Indeed, in order to manage their daily life successfully, individuals are usually required to remember to execute intentions at the appropriate time in the future. Remembering to take medication at noon or to refuel the car on the gas station are two examples of this function, called prospective memory (PM), and clarify how this is indispensable for an independent life (Brandimonte et al., 1996). Kliegel and Martin (2003) showed that 50–80% of everyday memory problems involve difficulties with appropriate realization of delayed intentions (Terry, 1988).

1.1. Cognitive architecture of PM

PM entails multiple phases (Kliegel et al., 2002). In every PM activity, individuals have to encode the intention, maintain it over some period of time, and retrieve and execute it at the right moment. Moreover, PM is a multi-componential ability. According to the multiprocess framework, PM is supported by many distinct processes, classically clustered under the terms *strategic monitoring* and *spontaneous retrieval* (McDaniel and Einstein, 2007). Strategic monitoring refers to the set of top-down memory and attentional processes required, respectively, to maintain the intention active in mind and to monitor the environment for detecting the PM cues (i.e., the stimuli associated with the intention to execute) (Gynn, 2003; Smith, 2003). For example, if you form the intention to refill your tank, you are likely to maintain this intention while driving and to monitor the street looking for a gas station. Spontaneous retrieval can also mediate PM and it relies more on bottom-up processes (McDaniel and Einstein, 2007; Scullin et al., 2013). In certain situations, indeed, the PM cue spontaneously triggers retrieval of the intention, which appears to 'pop into mind' (McDaniel and Einstein, 2007; Moscovitch, 1994). For example, if a gas station appears right in front of you, this could spontaneously trigger in you the intention to refill the tank. According to McDaniel and Einstein, multiple processes contribute to spontaneous retrieval (McDaniel and Einstein, 2000, 2007). These are (1) a reflexive associative process, in which processing of the PM cue triggers a bottom-up retrieval of the intention once a link between

the PM cue and the intention has been encoded and maintained in long-term memory (Moscovitch, 1994); (2) a discrepancy plus search process, in which detecting the discrepancy of PM cue relative to other stimuli in that context elicits a search of memory for the origin of such discrepancy; (3) and an alert process, in which salient and distinctive stimuli capture attention and stimulate deeper processing of the significance of the PM cue. The extent to which individuals rely on strategic monitoring or spontaneous retrieval to accomplish PM intentions seems to depend on a multitude of factors, such as the focality, valence and salience of the PM cues, the cognitive load and the importance of the ongoing and the PM tasks, as well as individual factors (Einstein et al., 2005; Cona et al., 2015; McDaniel and Einstein, 2000; Scullin et al., 2013). More specifically, when the PM cue is nonfocal (i.e., processing of the PM cue is independent from that of the ongoing stimuli) or nonsalient, or when the PM task is particularly relevant and demanding, then the individuals tend to recruit strategic monitoring. By contrast, when the PM cue is focal (i.e., processing of the ongoing stimuli implies processing of the PM cue), or salient, or when the ongoing task is very demanding and absorbing so that there are not enough resources for strategic monitoring, then individuals tend to rely more on spontaneous processes (Einstein et al., 2005; McDaniel and Einstein, 2000). Interestingly, Scullin and collaborators (2013) have recently proposed an updating of this view, labelled 'The Dynamic Multiprocess Framework', according to which strategic monitoring and spontaneous retrieval could be both recruited in the same PM task, but at different times and/or in distinct contexts.

The neural correlates of PM have been gradually delineated over the past fifteen years by neuroimaging studies. Nevertheless, these studies provide, to date, scattered results. Thus, the current study aimed to identify the brain regions that are consistently activated in PM processes and to differentiate the neurocognitive processes underlying each PM phase by means of a neuroimaging meta-analysis technique.

1.2. The role of aPFC regions in PM

The majority of the studies focused on the role of the anterior prefrontal cortex (aPFC, Brodmann's area 10), which is reported to play a crucial role in maintaining intention (e.g., Burgess et al., 2001,

2003; den Ouden et al., 2005; Gilbert et al., 2009; Momennejad and Haynes, 2012; Okuda et al., 1998; see Burgess et al., 2011 for a review). More specifically, it has been typically found that, as compared with “uncontaminated” ongoing task conditions (in which the ongoing task was performed alone), PM conditions are associated with increased activity in lateral aPFC (BA 10) and decreased activity in medial aPFC (BA 10). Burgess et al. (2005, 2007) have explained these results by proposing that lateral aPFC mediates attending to internal representations, i.e., stimulus-independent (SI) processes, such as delayed intentions for future actions. By contrast, medial aPFC is important for attending to external perceptual information, so that it mediates stimulus-oriented (SO) processes (see also Gilbert et al., 2005, 2006a,b). Medial and lateral aPFC regions are considered to comprise a mechanism underpinning the balance of attention between the external ongoing stimuli and the internally represented PM intention. This ‘gateway’ mechanism seems to be central to maintaining intentions in PM tasks (‘the Gateway Hypothesis’, Burgess et al., 2007). Therefore, one aim of the meta-analysis was to test the Gateway Hypothesis to determine whether the pattern of lateral aPFC activation coupled with medial aPFC deactivation in the maintenance phase is consistent across the PM studies.

Despite the large number of studies focusing on the aPFC, however, there are still several unresolved issues concerning what is the role of the aPFC in the other PM phases (i.e., in the phase of encoding and retrieving intentions) and whether the aPFC itself represents the content of specific intentions, or plays a more general “content-free” role in supporting PM. Recent studies using multivoxel pattern analysis (MVPA) to decode intentions from patterns of brain activity were designed to answer this question (Gilbert, 2011; Haynes et al., 2007; Momennejad and Haynes, 2012, 2013). While the study by Gilbert showed that the aPFC was recruited only in maintenance phase and did not decode the content of the intentions, other studies found that the aPFC is involved not only in maintaining, but also in encoding and retrieving the intentions (Momennejad and Haynes, 2013) and that distinct aPFC regions may represent distinct kinds of intentions (Haynes et al., 2007; Momennejad and Haynes, 2012). Hence, the present meta-analysis was helpful in determining whether the aPFC is involved only in the maintenance phase, being associated with strategic monitoring (Barban et al., 2014; Beck et al., 2014; McDaniel et al., 2013), or whether it is recruited also in the encoding and/or retrieval phases.

1.3. The role of frontoparietal networks in PM

Recently, some investigators have proposed that the frontoparietal networks may play a key role in PM processes as well (e.g., Bisiacchi et al., 2011; Kalpouzos et al., 2010; McDaniel et al., 2013). In particular, the dorsal frontoparietal control network, including precuneus and DLPFC, seems to mediate strategic monitoring, whereas the ventral frontoparietal and the temporoparietal networks are associated mainly with the capture of attention by PM cue and with intention retrieval (Beck et al., 2014; Kalpouzos et al., 2010; McDaniel et al., 2013). In the present article, we proposed a new model – the Attention to Delayed Intention (AtoDI) model – that could account for the dissociation between the dorsal and ventral frontoparietal networks found among the distinct PM phases. Though admittedly speculative, the model helps organize the current literature and suggests a possible role of such networks in PM. The model is derived from the combination of two prominent models: the ‘dual attention’ (Corbetta and Shulman, 2002) and the Attention to Memory (AtoM) models (Cabeza et al., 2008; Ciaramelli et al., 2010). These models posit that dorsal and ventral frontoparietal networks mediate, respectively, the top-down and the bottom-up attention, which are directed to environmental stimuli (according to the ‘dual attention’ view) and to memory

contents (according to the AtoM model). The neural dissociation within frontoparietal networks seems to mirror the distinction proposed by the multiprocess framework between strategic monitoring and spontaneous retrieval (Einstein et al., 2005; McDaniel and Einstein, 2000; Scullin et al., 2013). Thus, if the dorsal frontoparietal network subserves the top-down allocation of attentional to perceptual and memory contents, it would be recruited mainly in the maintenance phase for strategic monitoring. On the other hand, if the ventral frontoparietal network mediates bottom-up attentional and memory processes, it would be activated in the retrieval phase for supporting spontaneous retrieval (McDaniel and Einstein, 2007; Scullin et al., 2013). The AtoDI model is also driven by more recent studies, which began to explore the functional dissociation within frontoparietal networks, revealing a relation between activations in regions belonging to dorsal frontoparietal network and strategic monitoring and between activations in ventral frontoparietal regions and spontaneous retrieval (Barban et al., 2014; Beck et al., 2014; McDaniel et al., 2013; Oksanen et al., 2014).

1.4. Other brain regions involved in PM

Coupled with frontoparietal networks, other brain structures and networks cooperate to accomplish PM tasks. Studies exploring brain activations associated with the detection of the PM cue and the retrieval of the associated intention have shown transient activations in anterior cingulate cortex (ACC), posterior cingulate cortex (PCC), temporal cortex and insula (e.g., Beck et al., 2014; Gilbert et al., 2012; Gonneaud et al., 2014; Hashimoto et al., 2011; Oksanen et al., 2014; Rusted et al., 2011; Simons et al., 2006). Some of these regions were also found to be recruited during encoding of the intention (e.g., Gilbert et al., 2012; Poppenk et al., 2010). Nevertheless, the specific functional significance of such regions in relation to the distinct PM phases is not yet well specified (Burgess et al., 2011).

1.5. The current study

At present, we have a rather fragmented view of the brain regions recruited in the PM phases, leaving the reader without a whole picture of the neurocognitive mechanisms involved in prospective remembering. The present meta-analysis is meant to provide an overview of the neural mechanisms that lead from encoding of an intention to the execution of it, exploring more deeply the functional contribution of brain regions other than aPFC to PM. Thus, we isolated three distinct phases: encoding of intention, maintenance of intention, and retrieval of intention. Since different types of PM tasks have been employed, a meta-analysis is useful in factoring out statistical idiosyncrasies in individual neuroimaging studies to arrive at a consensus as to which PM processes cut across tasks. In this regard, this meta-analysis is the first to attempt to identify the ‘core’ brain regions consistently involved in the distinct PM processing phases, regardless of the nature of stimuli and tasks.

For an objective assessment of interstudy concordance, we used the Activation Likelihood Estimation (ALE) approach (Eickhoff et al., 2009; Laird et al., 2005; Turkeltaub et al., 2002) which has considerable advantages over other meta-analytic methods. The key advantage of ALE is that it has a neurobiologically and mathematically stringent concept based on probabilistic inference about activation coordinates. Instead of trying to model the activation map or even effect sizes, ALE coherently only deals with activation coordinates, which are represented in a probabilistic fashion to account for spatial uncertainty. The ALE approach represents the most widely used method for a quantitative integration of neuroimaging findings.

Finally, we proposed the AtoDI model, which, though speculative, seeks to account for the functional role of the brain regions involved in each PM phase. Particular attention is paid to the dissociation between dorsal and ventral frontoparietal regions, and to how the neural findings can be integrated with behavioural theories, exemplified by the multiprocess framework.

2. Methods

2.1. Study selection

To identify appropriate articles for the prospective memory meta-analysis, several online electronic databases (e.g. Psycinfo, Medline, PubMed) were searched using various combinations of relevant search terms: “prospective memory”, “delayed intention”, “future intention”, “time-based”, “event-based”, “neuroimaging”, “fMRI”, “PET”, “functional magnetic resonance imaging”, “positron emission tomography”. Moreover, further studies were found by means of the “related articles” function of the PubMed database and by tracing the references from review articles and the identified papers. The meta-analysis included both event-based and time-based PM studies, in which the PM cues were, respectively, particular events (e.g., to press the spacebar when a particular number occurs on the screen) or moments (e.g., to press the spacebar every 30 s).

The following inclusion criteria were used to select articles for the present meta-analysis:

1. Only articles that utilized PET or fMRI methodology were considered. We did not restrict the study selection to a certain imaging technique to maximize statistical power. Electrophysiological (e.g., electroencephalography, magnetoencephalography, skin conductance response [SCR]), transcranial magnetic stimulation (TMS) and behavioural-only studies were excluded. Both blocked and event-related studies were allowed.
2. Only articles with experiments that performed a whole brain analysis were included: i.e. articles performing only ROI analysis were excluded.
3. Only articles with experiments that yielded a clear contrast representing locations of greater activation/deactivation for PM conditions as compared with control conditions were included. Control conditions typically consist of ongoing tasks performed alone (e.g., same-different judgments, N-back tasks), thus that are ‘uncontaminated’ by the PM instruction, or ongoing trials not containing the PM cue.
4. Only articles that reported areas of peak activation in a standardized coordinate space (e.g., Talairach and Tournoux, 1988, or MNI) were considered. Other articles (e.g., only reported Brodmann areas [BAs] or only showed contrast maps) were excluded. Tailarach coordinates had been reported into MNI space before performing the meta-analysis using a linear transformation (Laird et al., 2010; Lancaster et al., 2007).
5. Only peer-reviewed articles reporting novel data involving a sample size of at least 5 participants were included.

Based on these criteria, 24 studies were found to be eligible for inclusion into the meta-analysis (cf. Table 1). Together, these studies reported 456 activation foci obtained from 39 individual experiments (with a “study” referring to a paper, and “experiment” referring to an individual contrast reported in this paper) representing regions of significantly greater activation in the PM task as compared with the control task, as well as 112 deactivation foci obtained from 15 individual experiments.

2.2. ALE consistency analysis

The peaks of activation were used to generate an Activation Likelihood Estimation (ALE) map, using the revised ALE algorithm for coordinate-based meta-analysis of neuroimaging results (Turkeltaub et al., 2012). This approach aims to identify areas with a convergence of reported coordinates across experiments that is higher than expected from a random spatial association. The exact procedure was largely explained elsewhere (Eickhoff et al., 2009, 2012; Turkeltaub et al., 2012). Briefly, this algorithm treats activated foci of brain regions as three dimensional Gaussian probability distributions centred at the given coordinates instead of points (Eickhoff et al., 2009; Laird et al., 2005). The algorithm incorporates the size of the probability distributions by considering the sample size of each study. This is an important parameter to take into account given that smaller effect size can potentially be associated with studies having larger sample size (Eickhoff et al., 2009; Turkeltaub et al., 2012). Moreover, the algorithm utilizes the random-effect rather than the fixed-effect inference. It does so by testing the above chance clustering between experiments/contrasts rather than the above-chance clustering between foci. Inference is then sought regarding regions where the likelihood of activation being reported in a particular set of experiments is higher than expected by chance, i.e., where there is a non-random convergence. Importantly, this inference is performed against an appropriate null-hypothesis reflecting random spatial association. The p -value of the ALE score was given by the proportion of equal or higher values obtained under the null distribution, which reflects a random spatial association among foci. For consistency, the resulting non-parametric p values were then assessed at a false discovery rate (FDR) corrected threshold of $p < 0.05$ on cluster level and transformed into Z scores for display (Laird et al., 2005). Moreover, an extent threshold of $k > 50$ voxels was applied to the results. GingerALE 2.3 software (<http://www.brainmap.org/ale/>) was used for the analysis.

2.3. ALE discriminability analyses

A further advantage of ALE methods is that the individual ALE maps can then be directly compared statistically. We conducted a discriminability analysis to understand if there are statistical differences in the direct comparison between maintenance and retrieval of intention. The theoretical reason why this comparison has been performed is that the majority of the studies speculated about the neural underpinnings of maintenance and retrieval, while only few studies investigated the neural basis of encoding. Thus, we could provide reliable interpretations about the neural dissociation (e.g., in the frontal and parietal regions) mainly between the maintenance and retrieval, while the functional meaning of the activations that distinguished the encoding was more difficult to clarify and hypothesize.

Statistical differences between two ALE maps were tested by first performing separate ALE meta-analyses for both the maintenance and retrieval phases. The experiments contributing to either analysis were then pooled and randomly divided into two groups of the same size as the sets of contrasted experiments (Eickhoff et al., 2011). Voxelwise ALE scores of these two randomly assembled groups were subtracted from each other and recorded. Repeating this process 10,000 times yielded an empirical null distribution of ALE-score differences between the two conditions. Based on this permutation procedure, the map of true differences was then thresholded at a posterior probability of $p > 0.99$ for a true difference between the two samples ($p < 0.01$ uncorrected). In addition, a cluster extent threshold of $k > 50$ was applied to eliminate minor, presumably incidental, findings.

Table 1
Studies included in PM meta-analysis.

First author	Year	Number of subjects	Contrast	Foci (n)	PM meta-analysis		Specific PM processes			Gateway Hypothesis (maintaining)	
					A	D	E	M	R	A	D
Okuda	1998	6	Maintenance	7	x			x		x	
Burgess	2001	8	Maintenance	10	x			x		x	
			Decreased activity in maintenance	2		x					x
			Retrieval	1	x				x		
			Decreased activity in retrieval	1		x					
Burgess	2003	9	Maintenance	1	x			x		x	
			Decreased activity in maintenance	2		x					x
Den Oden	2005	11	Maintenance	3	x			x		x	
			Switching between PM and ongoing activity	1	x						
Simons	2006	16	Maintenance	2	x			x		x	
			Retrieval (stimulus high identification demand)	16	x				x		
			Retrieval (stimulus with high retrieval demand)	29	x				x		
			Decreased activity in retrieval (stimulus with high identification demand)	11		x					
			Decreased activity in retrieval (stimulus with high retrieval demand)	10		x					
Eschen	2007	10	Encoding	6	x		x				
Okuda	2007 EX1	10	Maintenance (event-related)	10	x			x		x	
			Decreased activity in maintenance (event-related)	3		x					x
	2007 EX2	12	Maintenance of intention (time-related)	6	x			x		x	
			Decreased activity in maintenance (time-related)	5		x					x
Gilbert	2009	16	Maintenance	13	x			x		x	
			Retrieval (self initiated cue)	14	x				x		
			Retrieval (external cue)	6	x				x		
Kalpourzos	2010	14	Maintenance	24	x			x		x	
			Decreased activity in maintenance	10		x					x
			Retrieval	26	x				x		
			Switching between PM and ongoing activity	18	x						
Poppenk	2010	13	Encoding	5	x		x				
			Encoding	8	x		x				
			Decreased activity in encoding	9		x					
Benoit	2011	16	Maintenance	7	x			x		x	
			Decreased activity in maintenance	7		x					x
			Switching between PM and ongoing activity	4	x						
Gilbert	2011	32	Encoding	7	x		x				
			Maintenance	5	x			x		x	
			Retrieval	5	x				x		
Rea	2011	13	Retrieval (neutral stimulus)	25	x				x		
			Retrieval (emotional stimulus)	33	x				x		
Rusted	2011	8	Retrieval	7	x				x		
			Decreased activity in retrieval	2		x					
Gilbert	2012	32	Encoding	3	x		x				
			Decreased activity in encoding	1		x					
			Maintenance	5	x			x		x	
			Decreased activity in maintenance	3		x					x
			Retrieval	7	x				x		
			Decreased activity in retrieval	1		x					
Hashimoto	2011	16	Maintenance	17	x			x		x	
			Decreased activity in maintenance	16		x					x
			Retrieval with cue	22	x				x		
			Retrieval	28	x				x		
			Decreased activity in retrieval	7		x					

Table 1 (Continued)

First author	Year	Number of subjects	Contrast	Foci (n)	PM meta-analysis				Specific PM processes				Gateway Hypothesis (maintaining)	
					A	D	E	M	R	A	D			
Okuda	2011	16	Maintenance	8	x				x			x		
			Decreased activity in maintenance	13										x
McDaniel	2013	15	Switching between PM and ongoing activity	7	x									
			Retrieval (focal PM)	10	x								x	
Barban	2014	16	Retrieval (nonfocal PM)	9	x								x	
			Retrieval	19	x									x
Beck	2014	47	Decreased activity in Retrieval	2									x	
			Retrieval	24	x									x
Gonneaud	2014	20	Maintenance (time + event)	9	x									
			Decreased activity in Maintaining (time + event)	5										x
Halahalli	2014	18	Maintenance	17	x								x	
			Retrieval	7	x									x
Oksanen	2014	24	Maintenance	7	x								x	
			Retrieval	10	x									x
Wang	2014	22	Decreased activity in Retrieval	2									x	

A, activation; D, deactivation; E, encoding of intention; M, maintenance of intention; R, retrieval of intention.

3. Results

3.1. PM processes: all activations and deactivations

The activation meta-analysis of all PM studies included 456 foci from 39 experiments (see Table S1 and Fig. S1, Supplementary Material). A large number of brain regions were identified as consistently activated across all studies and can be grouped in five main regions:

1. prefrontal regions, including lateral aPFC (BA10), DLPFC (BA 9, 46), mid-ventrolateral prefrontal cortex (BA 45, 47);
2. frontal regions, including bilateral medial premotor cortex (BA 6) and left frontal eye fields (FEF; BA 8);
3. cingulate regions (BA 31, 32, 33, 22, 23, 24) and insular regions (BA 13);
4. bilateral parietal regions, including superior (BA 7, 19) and inferior parietal lobule (BA 40), and angular gyrus (BA 39);
5. temporal regions, including right middle temporal gyrus (BA 21).

Additionally, there were other foci of activation located in occipital regions (BA 19, 3, 2), and in thalamus, putamen, caudate nucleus and cerebellum regions.

The deactivation meta-analysis of all PM studies included 112 foci from 15 experiments (Table S1 and Fig. S1). Brain areas that were deactivated in PM tasks were located mainly in medial aPFC (BA 10, 9) and also near both the anterior cingulate cortex (ACC; BA 24, 32, 33) and posterior cingulate cortex (PCC; BA 29, 30, 23), in the left insular cortex (BA 13) and in the left superior parietal lobule (BA 7).

3.2. Activations related to specific PM phases

A list of all activations separated for each PM phase is provided in Table 2.

3.2.1. Encoding of intention

The encoding meta-analysis included 29 foci from 5 experiments. Encoding was associated with activations in left lateral aPFC (BA 10) and left inferior parietal lobule (BA 40), in left postcentral gyrus (BA 2) and in PCC regions (BA 23). Occipital regions were also activated (BA 18, 19) as well as several subcortical regions (i.e., caudate, thalamus).

3.2.2. Maintenance of intention

The maintenance meta-analysis included 134 foci from 16 experiments. Figs. 1 and 2 illustrate the regions activated during the maintenance phase. Maintaining an intention was found to be associated with activations in lateral regions of aPFC (BA 10). Among frontal regions, multiple loci of activation were identified in the right DLPFC (BA 9), in the pre-supplementary motor area (pre-SMA, BA 6) and in the FEF (BA 8). Among parietal regions, superior parietal lobule and precuneus (BA 7,19) were found consistently activated. To a lesser extent, also some regions near supramarginal gyrus (BA 40) were activated.

3.2.3. Retrieval of intention

The retrieval meta-analysis included 308 foci from 19 experiments. The analysis showed again a broad system of prefrontal, premotor, and posterior parietal activation (Fig. 2). The analysis revealed activation in many prefrontal and frontal areas, including mid-ventrolateral prefrontal regions (BA 45, 47), lateral aPFC areas (BA 10) as well as FEF (BA 8), premotor area and SMA (BA 6). Notably, large foci of activations were found in inferior parietal lobule and supramarginal gyrus (BA 40), especially in the left hemisphere. Also the dorsal and ventral parts of the ACC (BA 32/24) and

Table 2
Foci of activation separated for the distinct PM phases.

Cluster size	Brain regions	Brodmann areas	MNI coordinates			ALE extrema value
			x	y	z	
<i>Encoding of intention</i>						
408	Postcentral gyrus	2	−56	−26	42	0.011
152	Thalamus	−	16	−28	−2	0.009
152	Cuneus	19	−30	−76	34	0.009
96	Middle occipital gyrus	18	36	−84	2	0.008
96	Middle frontal gyrus	10	−30	41	25	0.008
96	Inferior parietal lobule	40	−46	−48	46	0.008
80	Caudate	−	−18	17	4	0.008
80	Caudate	−	18	20	7	0.008
80	Posterior cingulate cortex	23	0	−28	25	0.008
80	Superior occipital gyrus	19	36	−70	30	0.008
<i>Maintenance of intention</i>						
2176	Precuneus	7	0	−60	54	0.012
	Precuneus	7	−2	−62	48	0.012
	Precuneus	7	−6	−74	52	0.011
896	Middle frontal gyrus	10	34	42	26	0.015
	Middle frontal gyrus	9	36	38	34	0.011
856	Precuneus	19	−22	−72	38	0.014
	Cuneus	19	−30	−76	34	0.010
728	Superior parietal lobule	7	−26	−56	66	0.016
688	Middle frontal gyrus	10	−32	48	14	0.014
680	Inferior parietal lobule	40	−46	−34	52	0.015
648	Inferior parietal lobule	40	48	−42	42	0.012
368	Superior frontal gyrus	6	0	20	50	0.012
312	Red nucleus	−	0	−22	−4	0.010
312	Medial frontal gyrus	6	−8	0	60	0.010
288	Middle frontal gyrus	8	−38	30	40	0.010
272	Precentral gyrus	6	−32	−4	64	0.010
240	Precuneus	7	18	−64	60	0.010
112	Precuneus	19	−42	−74	44	0.008
80	Superior occipital gyrus	19	36	−70	32	0.009
56	Precuneus	19	36	−66	42	0.009
56	Precuneus	7	34	−46	42	0.009
<i>Retrieval of intention</i>						
3072	Inferior parietal lobule	40	−40	−40	58	0.022
	Inferior parietal lobule	40	−48	−36	40	0.021
	Inferior parietal lobule	40	−52	−34	50	0.011
3032	Inferior frontal gyrus	47	52	22	−8	0.031
	Inferior frontal gyrus	45	46	24	−2	0.014
2832	Clastrum	−	−32	18	−6	0.032
960	Middle frontal gyrus	10	−38	56	2	0.019
944	Supramarginal	40	56	−52	38	0.015
	Inferior parietal lobule	40	66	−34	38	0.014
904	Medial frontal gyrus	6	−2	22	44	0.016
	Medial frontal gyrus	6	8	20	47	0.019
864	Culmen (Cerebellum)	−	22	−52	−22	0.023
696	Middle frontal gyrus	6	−24	4	54	0.010
768	Caudate	−	16	6	8	0.017
664	Inferior parietal lobule	40	44	−42	50	0.016
	Inferior parietal lobule	40	52	−36	48	0.010
544	Thalamus	−	−6	−12	−2	0.014
504	Middle frontal gyrus	8	38	28	44	0.018
416	Superior occipital gyrus	19	36	−70	32	0.015
400	Anterior cingulate gyrus	32	−2	36	24	0.013
	Anterior cingulate gyrus	32	−6	30	30	0.012
384	Middle temporal gyrus	21	62	−38	−6	0.014
360	Middle frontal gyrus	10	−34	50	18	0.015
304	Precentral gyrus	9	−56	6	38	0.013
248	Posterior cingulate gyrus	23	2	−24	30	0.015
248	Precuneus	19	40	−66	−46	0.013
248	Middle frontal gyrus	6	30	−4	64	0.014
240	Cuneus	7	8	−68	38	0.012
232	Insula	−	56	−18	20	0.014
216	Precentral gyrus	9	44	12	40	0.013
192	Insula	−	50	14	10	0.013
192	Posterior cingulate gyrus	31	8	−42	36	0.013
192	Supramarginal gyrus	40	−58	−46	38	0.013
184	Superior frontal gyrus	10	28	54	−12	0.013
176	Anterior cingulate cortex	32	−20	40	20	0.012
168	Precentral gyrus	9	−40	2	28	0.013
160	Postcentral gyrus	3	32	−28	62	0.012
144	Superior frontal gyrus	10	42	56	10	0.011
144	Postcentral gyrus	3	−28	−32	50	0.012

Table 2 (Continued)

Cluster size	Brain regions	Brodmann areas	MNI coordinates			ALE extrema value
			x	y	z	
120	Thalamus	–	10	–14	6	0.012
96	Cingulate gyrus	32	12	30	32	0.011
96	Postcentral gyrus	2	60	–20	44	0.011
80	Middle frontal gyrus	8	–40	28	44	0.011
72	Putamen	–	–14	4	4	0.011
72	Anterior cingulate cortex	24	–2	40	2	0.010
72	Caudate	–	–12	8	14	0.010
64	Globus pallidus	–	10	4	–6	0.010
56	Precentral gyrus	44	–48	10	10	0.010

$P_{FDR} < 0.05, k > 50$.

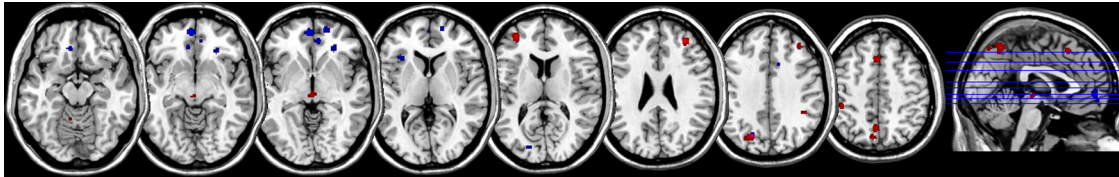


Fig. 1. Activations (red) and deactivations (blue) in intention maintenance phase: the Gateway Hypothesis. Maintaining an intention is associated with increase of activation within lateral aPFC regions (lateral BA 10) and with a decrease of activation within medial aPFC regions (medial BA 10). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

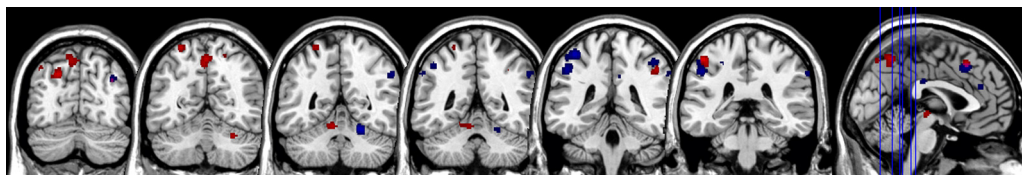


Fig. 2. Activations in maintenance (red) and retrieval phase (blue). Maintenance is mainly associated with activation within dorsal frontal and parietal regions, such as the DLPFC and the precuneus. Retrieval is mainly associated with activation with ventral frontal and parietal regions, such as the vPFC, insula and the inferior parietal lobule. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

PCC (BA 31/23) were found to be consistently activated. Foci of activations were shown in the insula (BA 13) and in the right middle temporal gyrus (BA 21).

We decided to contrast the activations pattern between maintenance and retrieval phases in order to find possible neural dissociations between them (see Table 3 and Fig. S2). The precuneus (BA 7) showed increased activation during maintenance phase compared to retrieval phase. By contrast, increased signal in the retrieval phase versus maintenance phase was shown mainly in the insula (BA 13), in the ventral PFC (BA 45, 47), and in the inferior parietal regions (BA 40) (see Table 3).

3.3. Testing the Gateway Hypothesis: activations and deactivations during maintenance phase

In order to test the Gateway Hypothesis, we conducted an analysis to define the loci of activation and deactivation specifically during the maintenance phase (see Fig. 1 and Table 4).

As previously described in Section 2.2, maintaining an intention was consistently associated with enhanced activation in lateral regions of aPFC (BA 10) and in dorsal frontal and parietal regions (see Section 2.2 for more details).

The deactivation meta-analysis in maintenance phase was conducted on 66 foci from 9 experiments. The deactivation pattern included some regions of medial aPFC (BA 10), of dorsal ACC (BA 32) and ventral PCC (BA 23). Some regions located in the insula (BA 13), in the parietal (BA 7) and occipital lobes (BA 19, 17) were shown deactivated (Table 4, Fig. 1).

4. Discussion

There is increasing interest in the neural mechanisms that underpin prospective remembering. Although PM is a multi-componential function, the single imaging studies were focused on detecting activations associated with only one, or some, of the PM processing phases. Furthermore, the majority of the studies gave greatest attention to the role of the aPFC in PM because of its close link to Gateway Hypothesis (Burgess et al., 2007, 2011), leaving the functional significance of the other regions still poorly explored. Therefore, we aimed at identifying the neural regions that are consistently involved in each PM phase to have an overview of the neural mechanisms that lead from encoding of an intention to its execution. We isolated three processing phases underlying PM – encoding, maintaining and retrieving the intention – and we identified the brain areas that were found to be consistently activated in each PM phase across the experiments. For each brain structure we begin by discussing results concerning the maintenance and retrieval phases, and then we proceeded discussing the results on encoding. Though counterintuitive, we chose this order because (1) the majority of studies focused on maintenance and retrieval phases, making the results from our meta-analysis more reliable on these phases, and (2) the role of the areas involved in these phases has been more clearly defined so they can provide a better starting point for the discussion.

Furthermore, we investigated the functional role of the aPFC, with particular reference to the Gateway Hypothesis, and explored the neural dissociation between ventral and dorsal frontoparietal networks.

Table 3
Contrasts between activations in maintenance and retrieval phases.

Cluster size (mm ³)	Brain regions	Brodmann areas	MNI coordinates			ALE extrema value
			x	y	z	
<i>Maintenance > retrieval</i>						
1072	Precuneus	7	1	−59	56	0.033
	Precuneus	7	−8	−68	57	0.029
<i>Retrieval > maintenance</i>						
2600	Inferior frontal gyrus	47	−37	18	−10	0.037
	Clastrum	−	−30	17	−6	0.034
	Clastrum	−	−35	12	−2	0.032
1992	Insula	−	38	24	−6	0.037
	Clastrum	−	38	16	−6	0.034
	Insula	−	42	22	−6	0.032
	Insula	−	40	20	−2	0.031
	Putamen	−	26	22	−4	0.030
	Insula	−	32	20	−12	0.029
	Putamen	−	26	22	−8	0.029
352	Inferior parietal lobule	40	65	−31	37	0.034
	Supramarginal gyrus	40	60	−44	38	0.024
96	Postcentral gyrus	1	61	−20	43	0.035

$P_{\text{uncorrected}} < 0.001, k > 50$.

Table 4
Testing the Gateway Hypothesis: activations and deactivations in maintenance phase.

Cluster size (mm ³)	Brain regions	Brodmann areas	MNI coordinates			ALE extrema value
			x	y	z	
<i>Increase of activation</i>						
2176	Precuneus	7	0	−60	54	0.012
	Precuneus	7	−2	−62	48	0.012
	Precuneus	7	−6	−74	52	0.011
896	Middle frontal gyrus	9	34	42	26	0.015
	Middle frontal gyrus	9	36	38	34	0.011
856	Precuneus	19	−22	−72	38	0.014
	Cuneus	19	−30	−76	34	0.010
728	Superior parietal lobule	7	−26	−56	66	0.016
688	Middle frontal gyrus	10	−32	48	14	0.014
680	Inferior parietal lobule	40	−46	−34	52	0.015
648	Inferior parietal lobule	40	48	−42	42	0.012
368	Superior frontal gyrus	6	0	20	50	0.012
312	Red nucleus	−	0	−22	−4	0.010
312	Medial frontal gyrus	6	−8	0	60	0.010
288	Middle frontal gyrus	8	−38	30	40	0.010
272	Precentral gyrus	6	−32	−4	64	0.010
240	Precuneus	7	18	−64	60	0.010
112	Precuneus	19	−42	−74	44	0.008
80	Superior occipital gyrus	19	36	−70	32	0.009
56	Precuneus	19	36	−66	42	0.009
<i>Decrease of activation</i>						
968	Medial frontal gyrus	10	−4	54	−6	0.015
	Medial frontal gyrus	10	2	58	−12	0.008
712	Medial frontal gyrus	10	16	56	−2	0.013
	Medial frontal gyrus	10	14	60	8	0.007
536	Precuneus	7	−20	−70	40	0.008
	Cuneus	19	−20	−82	38	0.008
384	Anterior cingulate cortex	32	8	44	−2	0.012
336	Insula	−	−32	22	6	0.007
312	Anterior cingulate cortex	32	−8	34	−12	0.010
192	Middle temporal gyrus	21	−60	−6	10	0.009
144	Precentral gyrus	44	−50	4	8	0.009
96	Cuneus	17	−18	−86	12	0.008
80	Posterior cingulate cortex	29	6	−52	6	0.008
64	Anterior cingulate gyrus	32	12	16	36	0.008
56	Superior temporal gyrus	22	−54	−10	−6	0.008
56	Middle temporal gyrus	39	−44	−68	30	0.008

$P_{\text{FDR}} < 0.05, k > 50$.

Finally, we proposed a new model, the AtoDI model, to account for the neural activation patterns found in the distinct PM phases, and to provide a cohesive, although admittedly speculative, description of the functional role of the brain regions involved, integrating our interpretations with the predictions postulated by the multiprocess framework (McDaniel and Einstein, 2007).

4.1. The role of aPFC regions in PM

The present meta-analysis confirmed that intention maintenance was consistently associated with lateral BA 10 activation coupled with medial BA10 deactivation (Fig. 1). This finding supports the Gateway Hypothesis, according to which the aPFC is involved in the biasing of attention between external stimuli (e.g., detecting the PM cue amid ongoing stimuli) and internal thought processes (i.e., maintaining the intention in mind) (Burgess et al., 2007, 2011). More specifically, medial aPFC would be engaged in supporting SO attending whereas lateral aPFC would mediate SI attending (Burgess et al., 2007). A recent study tested this hypothesis directly within the PM context, by manipulating the salience of the PM cue and the memory load of PM task (Barban et al., 2014). The findings corroborated the Gateway Hypothesis, revealing that the medial aPFC showed enhanced activity for highly salient PM cues, which stress SO attending, whereas the lateral aPFC showed increased activity especially for high memory load, which emphasizes SI attending. As such, the pattern of activation/deactivation within aPFC regions would allow individuals both to maintain the intentions actively in mind when they are simultaneously engaged in an ongoing task, and to monitor for the presence of the PM cue in the environment (e.g., Burgess et al., 2001, 2003; den Ouden et al., 2005; Gilbert et al., 2009; Okuda et al., 2011; Reynolds et al., 2009; Simons et al., 2006). This result is also in line with electrophysiological studies that showed sustained modulations of the event-related potentials (ERPs) over prefrontal sites associated with strategic monitoring processes (e.g., Cona et al., 2012a,b; Knight et al., 2010; West et al., 2011).

Nevertheless, the Gateway Hypothesis did not clearly specify the functional role of the aPFC in the other PM phases. Moreover, it is still unclear whether the aPFC represents information regarding the content of future intentions. A number of MVPA studies on delayed intentions suggested indeed that the medial and lateral aPFC regions play a key role in encoding the specific content of the intentions (Haynes et al., 2007; Momennejad and Haynes, 2012, 2013; but see Gilbert, 2011). More specifically, distinct aPFC regions encode specific information about intentions (e.g., the ‘what’ and ‘when’ components of delayed intentions) and are involved during distinct phases of PM (Momennejad and Haynes, 2012). The present meta-analysis seems to support this role for the aPFC by revealing that the involvement of the aPFC regions was not restricted to the maintenance of intention but was involved also in the encoding and retrieval phases. This would lead to the suggestion that the aPFC may have a role not only in maintaining intentions, but also in encoding the content of intentions. Moreover, in agreement with the findings by Momennejad and Haynes’ study (2012), the ventrolateral aPFC regions were found to be involved especially in the retrieval phase so, as proposed by the authors, they might represent the ‘what’ content of the intentions, which needs to be retrieved in this phase.

Even though a MVPA study did not find aPFC involvement in the encoding phase (Gilbert, 2011), considering the evidence provided by other MVPA studies regarding the functional role that the aPFC has in encoding the content of intentions, it was not surprising to have observed activation of aPFC regions also in the encoding phase (Haynes et al., 2007; Momennejad and Haynes, 2012, 2013). In particular, we found activation of the left aPFC. This finding is consistent with the study by Poppenk et al. (2010) who showed

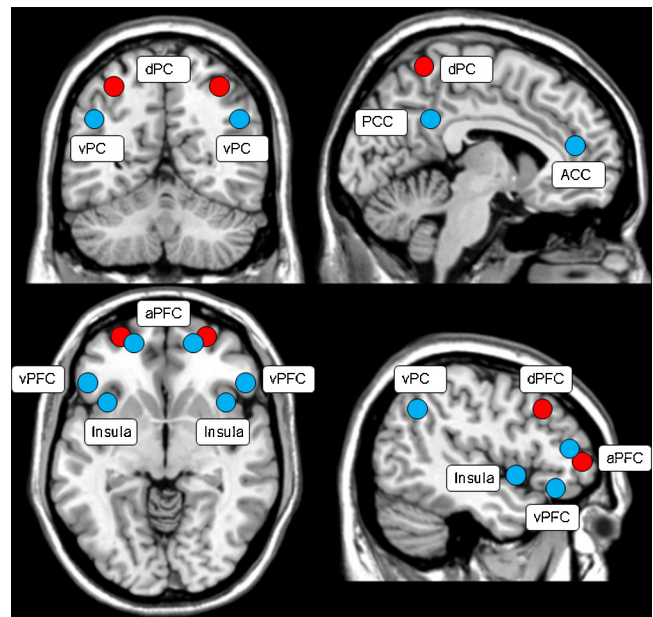


Fig. 3. Neural dissociation between maintenance and retrieval phases. Red dots represent centre of mass for activity related to intention maintenance. Blue dots represent centre of mass for activity related to intention retrieval. *Note:* dPC, dorsal parietal cortex; vPC, ventral parietal cortex; PCC, posterior cingulate cortex; ACC, anterior cingulate cortex; aPFC, anterior prefrontal cortex; vPFC, ventral prefrontal cortex; dIPFC, dorsolateral prefrontal cortex. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

that activity in the lateral aPFC regions of the left hemisphere was predictive of the subsequent success in accomplishing PM intention. Other studies also demonstrated that left aPFC is associated with the generation of future events (Addis et al., 2007) and with episodic memory encoding (Habib et al., 2003; Kapur et al., 1994). Driven by the present result, we suggest that PFC regions might subservise the organization of input and output in order to create a representation of the intention and, as proposed by previous studies, an association between the PM cue and the to-be-performed action (McDaniel and Einstein, 2000; Moscovitch, 1994).

4.2. Dissociation between dorsal and ventral frontoparietal networks in PM processes

In the present study, we found a dissociation within the frontoparietal networks when considering maintenance and retrieval phases (see Figs. 2 and 3). More specifically, concerning the parietal regions, maintaining intention was associated with more activation in dorsal parietal cortex (dPC) regions, such as the superior parietal lobule and precuneus regions (BA 7, 19) (Fig. 2). Retrieval of intentions was instead related to activity in ventral parietal cortex (vPC) regions, especially in the inferior parietal lobule and supramarginal gyrus (BA 40) (Fig. 2). Furthermore, when contrasting the pattern of activation between these two phases, increased activity in the precuneus (BA 7) was shown during maintenance relative to retrieval phases (Fig. S2). By contrast, increased activity in the inferior parietal lobule (BA 40) was found in the retrieval phase compared to maintenance phase (Fig. S2). To explain these results, it is useful to introduce two prominent models, developed in the context of two different cognitive domains, which are relevant for our concerns. In the attention domain, the ‘dual-attention’ model posited that dorsal and ventral parietal regions are components of two separate, yet interacting, frontoparietal attentional systems (Corbetta and Shulman, 2002). The superior attentional system, which involves dPC regions and dorsal frontal regions, is considered to mediate the allocation of top-down and goal-directed attention

to relevant stimuli of the environment. The inferior attentional system, which involves vPC regions together with ventral frontal regions, is thought to mediate the bottom-up capture of attention by the environmental stimuli (Corbetta and Shulman, 2002). Later, this dissociation was extended to the episodic memory domain by the AtoM model (Cabeza et al., 2008; Ciaramelli et al., 2010). According to this model, activity in dPC would be associated with maintenance of retrieval goals and mediates top-down and goal-directed attention to memory contents. On the other hand, vPC activity would support the bottom-up capture of attention by memory contents when a match is detected between information that was studied and retrieved. The functional dissociation found in the present study seems to be consistent with the above-presented models. During the maintenance phase, indeed, strategic monitoring is usually¹ engaged to allocate top-down attention to the ongoing stimuli for checking the PM cue occurrence and to direct attention towards the intention so as to keep it actively in mind and refreshed (Guynn, 2003; Smith and Bayen, 2004; Scullin et al., 2013). These processes resemble, respectively, the allocation of top-down attention towards both the environment (Corbetta and Shulman, 2002) and the goal states maintained in memory (Cabeza et al., 2008; Ciaramelli et al., 2010). Consistent with these models, and in agreement with recent neuroimaging studies on PM, we proposed that such strategic monitoring processes would be mediated mainly by dPC regions (Beck et al., 2014; Barban et al., 2014; McDaniel et al., 2013). In the retrieval phase, bottom-up attention is captured externally by the PM cue, which reflexively triggers the allocation of attention towards its representation stored in memory, as well as towards its associated intention (McDaniel and Scullin, 2010; Moscovitch 1994; Scullin et al., 2013). These processes underlying spontaneous retrieval qualitatively parallel the processes described by the ‘dual-attention’ view and the ‘AtoM’ model, and might be mediated by vPC activity, as proposed by recent studies in PM field (Beck et al., 2014; Barban et al., 2014; McDaniel et al., 2013; Rusted et al., 2011). More specifically, in line with the AtoM model, the vPC would be engaged in bottom-up allocating attention towards internally generated representations of PM cue and intention (Cabeza, 2008; Cabeza et al., 2012; Ciaramelli et al., 2010; Rusted et al., 2011; Wagner et al., 2005). This result is also supported by a TMS study, which showed that stimulation of the left inferior parietal lobule interfered selectively with the retrieval of intention (slowing down the execution of the intended action) whereas did not affect the maintenance (Bisiacchi et al., 2011).

As such, prospective remembering seems to be a bridge between the attentional and memory domains, given that it requires to balance the attentional resources between the external stimuli and the intention-related contents stored in memory. One might wonder whether there is an overlap or a separation between parietal regions involved in the allocation of attention to external PM stimuli and to internal intention-related contents. Nevertheless, since this meta-analysis found large activations within parietal regions, it is difficult to answer this question, which is still a matter of debate also in other fields of cognitive neuroscience (cf. Cabeza et al., 2011; Sestieri et al., 2010).

A dorsal-ventral dissociation was found also within frontal regions. In fact, we found that the maintenance phase was associated with activation mainly of dorsal frontal regions, including the DLPFC (BA 9), the pre-SMA (BA 6) and the FEF (BA 8), whereas the retrieval phase was associated with activation of ventrolateral prefrontal regions (BA 45, 47), which would elicit the bottom-up

activation of intention representation in memory (Momennejad and Haynes, 2012). These observations also corroborate the findings of recent PM studies that borrowed the explanations provided by dual-attention and the AtoM models and proposed that strategic monitoring processes are accomplished mainly by dorsal frontoparietal regions (Beck et al., 2014; Gonneaud et al., 2014; McDaniel et al., 2013; Oksanen et al., 2014). More specifically, dorsal frontal regions would generate and maintain endogenous information based on current goals (i.e., intention in the case of PM task) and would send out top-down signals that modulate the processing of relevant stimulus features in sensory cortex (e.g., Beck et al., 2014; Corbetta et al., 2000, 2008; McDaniel et al., 2013). In line with this, a TMS study found that the stimulation of the right DLPFC impaired maintaining of PM intentions (Bisiacchi et al., 2011). Finally, a study by Lau and collaborators (2004) found that, when individuals attended to their intentions, there was an increased activity in the right dorsal prefrontal regions, in the left intraparietal cortex and in pre-SMA. Thus they suggested that such areas are involved in the attention to intentions.

In the encoding phase, we found activation in some frontal (BA 10) and vPC regions (BA 40). The evidence of an involvement of vPC in both the retrieval and encoding phases corroborated the findings by Gilbert’s study (2012), which showed voxelwise similarity in activity patterns of the parietal lobule between encoding and retrieval phases, and demonstrated that such a similarity was greater for successful than unsuccessful PM cues. We extended the AtoM hypothesis for the role of the vPC to the encoding phase, suggesting that the vPC would support the allocation of attention both externally, to process the to-be-encoded PM cue, and internally, to form the intention, likely in cooperation with the left PFC areas, which would represent its content. However, given the small number of studies on PM encoding, this proposal remains speculative and warrants further investigation.

To summarize, we propose that parietal regions are responsible for the allocation of attention towards the external stimuli and to the content of intentions, represented by frontal regions. When the PM cue is not present in the environment, as in the maintenance phase, and if it is not easy to detect, the attentional operations need to be top-down managed and would involve mainly the dorsal frontoparietal regions (Fig. 3). When the PM cue occurs in the environment, and it is easy to detect, it would boost a bottom-up capture of attention, mediated by ventral parietal regions, which would then be redirected internally towards the intention content, provided by lateral and ventrolateral frontal regions (Fig. 3).

4.3. Other brain regions involved in PM

The current meta-analysis revealed the consistent involvement of the cingulate and insular cortices in PM processes. The cingulate cortex is a structurally and functionally heterogeneous area, and is subdivided in the anterior cingulate cortex (ACC) and the posterior cingulate cortex (PCC), which belong to distinct networks and subserve distinct processes.

ACC typically co-activates with lateral PFC regions and with posterior parietal cortex, forming the so-called “Cognitive Control Network” (Burgess et al., 2001; Cabeza et al., 2003; Coull et al., 1996; Duncan and Owen, 2000; Gilbert et al., 2010; Margulies et al., 2007; Miller and Cohen, 2001). Broadly, the ACC (BA 24/32) is considered to be responsible for detecting conflict when a stimulus activates two competing processes. Such conflict signal leads to an enhancement of the top-down control in the DLPFC that is required for the maintenance of task goals (e.g., Barch et al., 2001; Botvinick et al., 2001, 2004; Shenhav et al., 2013). The present meta-analysis showed ACC activation in the retrieval phase. This seems to support the functional significance for ACC as related to conflict monitoring and cognitive control. Indeed, when the PM cue

¹ We state ‘usually’ because these controlled and strategic processes are not required in all PM circumstances as intentions might also be retrieved spontaneously (see Einstein and McDaniel, 2005).

occurs in the environment, individuals might activate both PM- and ongoing-related instructions, thus they would need to orchestrate and coordinate such competing goals. As also proposed by recent studies on PM (Halahalli et al., 2014; Okuda et al., 2011), ACC might signal the competition between PM and ongoing task rules to lateral PFC regions, which, based on this signal, would exert top-down control over the other regions supporting adjustment of attention between ongoing- and PM-related rules and responses.

The PCC is the core region of the Default Network, a system of brain areas that are involved when the mind is not engaged in goal-directed tasks (Buckner et al., 2008; Raichle et al., 2001). The PCC has high structural connectivity to many brain regions (Hagmann et al., 2008), including those in the frontoparietal Cognitive Control Network (Leech et al., 2011, 2012; Smallwood et al., 2012). One interpretation of the role of PCC is that it subserves internally directed thoughts (Buckner et al., 2008), such as memory recollection and autobiographical memory retrieval (Svoboda et al., 2006). It has been also proposed that PCC is implied in the regulation of the focus of attention between external and internal information (Hampson et al., 2006; Gilbert et al., 2007; Pearson et al., 2011). Indeed the PCC was shown to interplay with frontoparietal networks to manage the balance between externally and internally directed cognition. In the current study we found increased activity in the PCC (BA 23, 31), specifically during the encoding and retrieval phase. Among the PM phases, these are the most related to retrospective memory. Both require attention to be shifted from external stimuli towards internal thoughts, respectively, to encode the intention or to retrieve it from memory. We proposed that the PCC might cooperate with parietal regions to shift attention from the external PM cue to the internal to-be-encoded or to-be-retrieved intention. This hypothesis is also based on recent evidence from the PM field, suggesting a role for the PCC in processing intentions (e.g., Beck et al., 2014; den Ouden et al., 2005).

A brain structure that was found to be co-activated consistently with the cingulate cortices is the insula (e.g., Leech and Sharp, 2014; Menon and Uddin, 2010; Seeley et al., 2007). Together with the ACC, the insula forms the “Salience Network”, which is thought to serve the detection of the most relevant (internal or external) stimuli in order to guide thoughts and behaviour (Seeley et al., 2007). In line with this view, in the present meta-analysis, the retrieval phase was associated with increased activity in the insular regions. It is noteworthy that the insula was shown to be one of the most strongly activated regions in the retrieval phase (when contrasted with the maintenance phase) (see Table 3 and Fig. S2 in Supplementary Material). This finding suggests that the insula might function in the bottom-up detection of PM cues. When the PM cue occurs in the environment, the insula would provide a selective processing amplification of such a relevant and salient event, and would trigger an alert signal to the ACC and to the PCC (Leech and Sharp, 2014; Menon and Uddin, 2010). Given its connections with cingulate regions, the insula functions as an interface between large-scale brain networks, such as the Cognitive Control Network and the Default Network, and has a role in coordinating between attentional control signals and the internally oriented processing (Deen et al., 2011; Uddin et al., 2014). Such an interpretation has been extended to the PM context by Halahalli and collaborators (2014). The authors proposed, however, that the anterior insula is uniquely involved in endogenous-cue PM tasks requiring incremental updating of working memory. The evidence of insula activity from our meta-analysis, which included studies using both exogenous- and endogenous-cue PM tasks, seems to contradict this statement, confirming instead the critical role of this region for detecting the presence of relevant stimuli, as the PM cues, and accordingly informing the connected regions about the presence of such information in the external environment or internal thoughts.

It is somehow surprising that we did not find consistent activations in medial temporal lobe (MTL) regions, such as hippocampal and parahippocampal areas, given their well-established role in retrospective memory (see Moscovitch et al., 2005 for a review). The involvement of such regions in PM is indeed still controversial, with some studies reporting activations in these areas (e.g., Okuda et al., 1998; Beck et al., 2014) and others not (e.g., McDaniel et al., 2013). Since MTL regions are considered to underpin spontaneous retrieval of intentions, they are recruited only in particular tasks, as in focal tasks (Beck et al., 2014; Gordon et al., 2011). This would explain the lack of consistent MTL activation in our meta-analysis, which included many studies using nonfocal PM tasks. Another possibility is that MTL areas are relatively small, such that the criterion used to identify only a reliable pattern of activations (i.e., number of voxels > 50) might have excluded these areas. Alternatively, it is possible that the hippocampus is not needed to maintain PM cues, and retrieve information, on these laboratory-based PM tasks, any more than it is needed to maintain ‘experimental set’ in any memory task.

4.4. Putting the pieces of PM puzzle together: the ‘Attention to Delayed Intention’ (AtoDI) model

To conclude, we would like to suggest an integrated interpretation of the current results. This has to be considered only an initial attempt to provide a comprehensive overview of the functional contribution of the brain structures involved in the distinct PM phases, and a hypothesis of their interactions. Hence, we propose the “Attention to Delayed Intention” (AtoDI) model on the role of distinct networks, and especially of frontoparietal networks, in prospective remembering. Though AtoDI is speculative and relies in some cases on reverse inference, as such models do, we, nonetheless, believe it is a useful, testable model for integrating the material and guiding future research. This model is meant to be a combination and an extension of the ‘dual-attention’ (Corbetta and Shulman, 2002) and the AtoM (Ciaramelli et al., 2010) models. Based on the studies reviewed in this study, Fig. 4 illustrates the specific brain areas that are involved in the three PM phases.

In the encoding phase (Fig. 4, upper diagram), the perception of the to-be-encoded PM cue would trigger a bottom-up capture of attention, mediated by the activity in vPC, which seems to be responsible for the allocation of attention not only towards such external stimulus but also towards its representation in memory and its associated intention (Corbetta and Shulman, 2002; Ciaramelli et al., 2010). Moreover, the shift of attention from the external PM cue to the internal corresponding content in memory might be mediated by the PCC (Gilbert et al., 2007; Pearson et al., 2011). The information about intention would be provided by the left aPFC, which was suggested to encode the content of the intention itself (Momennejad and Haynes, 2012, 2013). Finally, somatosensory areas located in the postcentral gyrus would contribute to the encoding of the actions for later execution (Eschen et al., 2007).

In the maintenance phase (Fig. 4, middle diagram), individuals are engaged in an ongoing activity while simultaneously they have to keep the PM intention in mind and, in some circumstances, to actively monitor for the PM cue occurring amid ongoing stimuli. The balance between processing of ongoing-related and PM-related information would be mediated by deactivation of medial aPFC regions (associated with SO processing) and activation of lateral aPFC regions (associated with SI processing), as proposed by the Gateway Hypothesis (Burgess et al., 2007). The aPFC is connected to the dorsal frontoparietal network, which would exert top-down and goal-directed attention internally, to actively maintain the PM intention and, based on this PM goal, externally, to monitor for the presence of the corresponding PM cue (see also Fig. 3). This set of

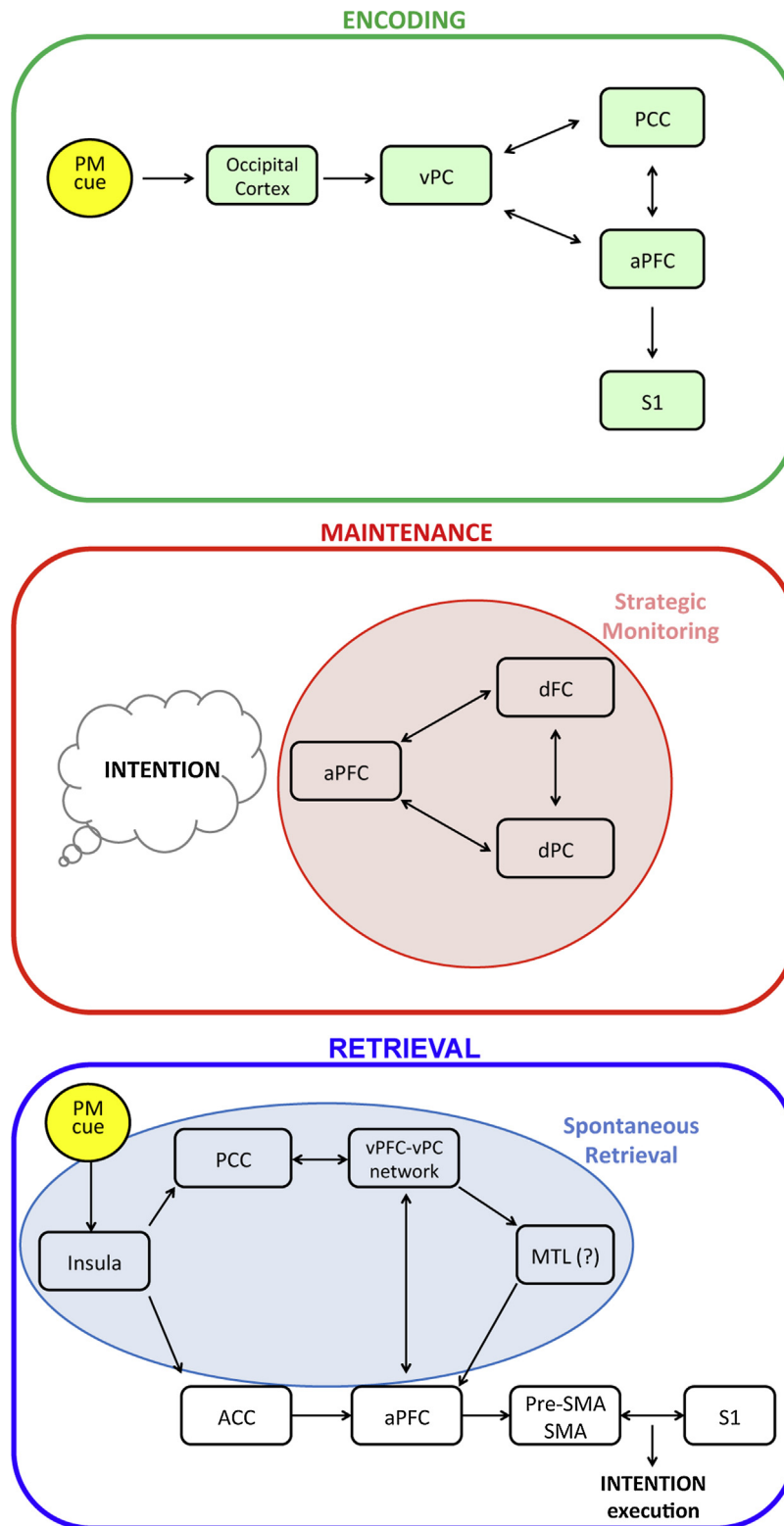


Fig. 4. Graphic illustration of the Attention to Delayed Intention (AtoDI) model for the phases of encoding, maintenance and retrieval of intention. *Note:* dPC, dorsal parietal cortex; vPC, ventral parietal cortex; PCC, posterior cingulate cortex; ACC, anterior cingulate cortex; aPFC, anterior prefrontal cortex; vPFC, ventral prefrontal cortex; dFC, dorsal frontal cortex; SMA, supplementary motor area; S1, primary somatosensory area; MTL, medial temporal lobe.

processes, underpinned by the dorsofrontal network, would constitute strategic monitoring (Beck et al., 2014), as will be explained in Section 4.5.

In the retrieval phase (Fig. 4, lower diagram), when the PM cue occurs, the presence of this relevant stimulus would be detected by the insula, which is connected to both the anterior and the posterior

cingulate cortices. The ACC might be responsible for the detection of the conflict between the activation of two distinct task goals – the goal for the ongoing task and the goal for the PM task – and would inform the lateral aPFC regions, which would regulate processing of ongoing information in favour of PM-related information. The PCC, together with ventral frontoparietal regions, would

support the bottom-up attention processes captured externally by the PM cue, and shifted internally, towards the internal representation of the PM cue and the intention stored in memory. Finally, the pre-SMA and SMA, in conjunction with the somatosensory regions providing the information processed during the encoding phase, would implement the corresponding action. Thus, the intention scheme would be translated from a more abstract level to a more concrete and action-related level by means of the passage of information processing from anterior to more posterior frontal regions (Momennejad and Haynes, 2013). Nevertheless, there is still a debate about which brain regions represent the content of intentions, with some studies showing that such a role is played mainly by the aPFC (e.g., Haynes et al., 2007; Momennejad and Haynes, 2012, 2013), and others showing that it is played by posterior brain regions (Gilbert, 2011). The AtoDI model cannot rule out certainly either of these two alternatives. One of the most plausible hypotheses, however, is that the neural locus of intention encoding might depend on the nature of the intention and the type of the task, as suggested by all the above-mentioned studies. Furthermore, because it is still not clear what is the role of the MTL regions in PM, as described in Section 4.3, we added a “question mark” on the MTL box in the diagram we presented (Fig. 4).

Given the sparse evidence provided by the existing literature on this topic so far, it is important to highlight the speculative nature of the interpretations developed in the AtoDI model, which should be treated with caution. The AtoDI model should instead be meant as a good starting point to encourage future studies to directly test the hypotheses formulated in this model.

4.5. The AtoDI model as the neural counterpart of the multiprocess framework

The neural mechanisms predicted by the AtoDI model appear to be suitable candidate for mediating the cognitive processes proposed by the multiprocess framework (McDaniel and Einstein, 2007). In this regard, strategic monitoring would be supported by the dorsal frontoparietal network, which is involved in the allocation of top-down monitoring attentional resources to the environment (i.e., target checking process), as well as the allocation of memory resources to maintain the intention active in mind (i.e., retrieval mode) (see also Beck et al., 2014, for a similar interpretation). Moreover, according to the multiprocess framework, a number of different processes seem to contribute to spontaneous retrieval. One of these is the discrepancy plus search process, where noticing a discrepancy in the processing fluency of the PM cue relative to other stimuli in the context leads to a search of memory for the corresponding trace that origins this discrepancy. According to our model, such process would be mediated by the ventral frontoparietal network that, in cooperation with the PCC, underpins and shifts the bottom-up attention from the external PM cue towards the internal memory, to search for corresponding stored trace. Moreover, spontaneous retrieval relies on an alert process occurring with relevant or distinctive PM cues, which stimulate further processing of their significance. The insula seems to be the best candidate for supporting the alert process, given its key role in detecting salient stimuli in the environment. Finally, spontaneous retrieval is based on a reflexive associative process, in which processing of the PM cue reflexively leads to retrieval of the linked intention (Moscovitch, 1994). The association between PM cue and intention is encoded by the cooperation between vPC regions and the lateral aPFC regions. In the retrieval phase, this association leads to a reflexive retrieval of the intention when the PM cue occurs. Thus, the vPC regions and the lateral aPFC regions would be re-activated. This is in line with a recent hypothesis stating that successful realization of intended action may be related to re-statement of encoding context at the time of retrieval (Gilbert et al.,

2012). The MTL regions might contribute to activate reflexively the intention as well. Nevertheless, as described in the previous paragraph, we did not find a consistent activation in these areas.

The multiprocess framework states that the relative contribution of strategic monitoring and spontaneous retrieval processes depends on a multitude of factors including, for example, focality and salience of the PM cue, load and emphasis of the PM and ongoing tasks, and individual differences (McDaniel and Einstein, 2000; Einstein et al., 2005; Scullin et al., 2013).

McDaniel et al.'s study (2013) explored the neural underpinnings of focal and nonfocal tasks, providing results that might support the AtoDI model. Indeed, the authors found that two distinct routes subserved prospective remembering.

One route involves transient activity in vPC and ventral brain regions (as insula and cingulate cortex) and it was suggested to mediate bottom-up processes, such as the capture of attention by the PM cue detection and spontaneous retrieval. This route was evidenced during the retrieval phase, especially when a focal cue occurred.

The other route involves activity mainly in dorsal network areas, such as DLPFC, FEF and superior parietal lobe, and is interpreted to be engaged in top-down monitoring processes. This route involves a sustained activation pattern during the maintenance phase and was active only for nonfocal PM cues, which typically require top-down attentional and memory processes to be recognized as PM cues (Cona et al., 2014; Scullin et al., 2010).

The effects of salience of PM cue on the neural mechanisms remain less clear since the only neuroimaging study that directly explored its influence focused on the role of aPFC regions (Barban et al., 2014; see Section 4.1). On the basis of the AtoDI model and the Multiprocess view, we predict that PM tasks with salient cues, boosting spontaneous retrieval, would be mediated mainly by transient activation in insula and ventral frontoparietal network and would be less likely to implicate the recruitment of dorsal frontoparietal regions in the maintenance phase. Notably, since insula belongs to the salience network, which is related to detection of salient events and bottom-up capture of attention, it might be particularly sensitive to salience of the PM cue. Our prediction seems to be supported by the findings by Simons and collaborators (2006), who showed greater activation in the anterior insula (BA13/47) when the PM cue was easy to identify relative to when it was not. On the other hand, nonsalient and less distinctive PM cues, implying a higher involvement of strategic monitoring to be detected, would lead to sustained activation of dorsal frontoparietal regions throughout the task.

The extent to which strategic monitoring is recruited depends also on the load of both the PM and ongoing tasks. Based on the AtoDI model, we hypothesize that increasing the load of PM task (placing higher demands on intention retrieval and/or on cue identification) would result in greater recruitment of regions in dorsal frontoparietal and cognitive control networks, since it would imply an increase of attentional and controlled resources (Simons et al., 2006). This hypothesis is also driven by electrophysiological data, which showed that the addition of a prospective memory load was associated with sustained activity over the occipital-parietal and frontal regions (West et al., 2006). A similar pattern of dorsal frontoparietal recruitment might be expected also when the emphasis given to the PM task is high. Nevertheless, it needs to take into account the cognitive demands required to accomplish the ongoing task. Indeed, if the ongoing task is highly demanding, it would prevent individuals to be fully engaged in strategic monitoring, with the result that dorsal frontoparietal and cognitive control regions would be less involved. In line with our prediction, Momennejad and Haynes (2013) found that dorsal frontal and parietal regions were recruited to accomplish PM intentions specifically when the ongoing task load was low. By contrast, when the ongoing task

load is high, individuals might be more likely to rely upon spontaneous processes (West et al., 2006) and, in turn, upon the reactive transient activity of insula/ventral frontoparietal network.

Inter-individual differences in monitoring were also observed (Einstein et al., 2005). It was recently shown that some individuals tend to engage strategic monitoring even when it is not strictly necessary for the PM task, and this was found to be associated with sustained modulations of the ERPs over frontal and parietal regions (Cona et al., 2014). In this regard, we expect high-monitoring individuals to rely mainly upon sustained activity of dorsal frontoparietal network during the maintenance phase, whereas low-monitoring individuals would rely mainly upon transient activity in ventral frontoparietal network and ventral brain regions (e.g., insula) at retrieval.

It is important to underline, however, that at this point the predictions derived from the AtoDI model are still speculative, and need to be tested by future studies.

4.6. Missing pieces of PM puzzle: limitations and future directions

The present study sought to provide a complete overview of the neural networks involved in the distinct PM phases. Nevertheless, because of the low number of studies that focused on encoding phase, conclusions about the functional contribution of the brain areas activated during this PM phase had to be qualified.

Recent interest and debate in the PM field concerns the role of multiple factors, such as focality, valence and salience of the PM cue, or task load, on modulating the neurocognitive mechanisms in PM tasks (e.g., Barban et al., 2014; Cona et al., 2014, 2015; McDaniel et al., 2013; Momennejad and Haynes, 2013). In the present study we did not manipulate directly these factors to explore their impact on brain mechanisms. Thus, future studies might be useful to better clarify this issue. Likewise, it is plausible to suppose that time-based and event-based PM tasks share some neurocognitive mechanisms but differ for others, as revealed by several studies (Cona et al., 2012a; Gonneaud et al., 2014). Nevertheless, the small number of imaging studies on time-based PM tasks did not allow us to perform a reliable comparison between the two types of PM tasks.

In proposing the AtoDI model, we tried to provide an account of the functional meaning of the brain regions that are involved in each PM phase, and a hypothesis of their interactions to accomplish delayed intentions. Some of the speculations embedded in the model, and the predictions derived from it, are based on the results of studies that have explored other cognitive domains. Thus, a more direct investigation of the role of such brain areas in PM processes is needed. Moreover, further studies of connectivity are required to better define how these regions are connected, and to specify the direction of their interaction.

Another limitation is that we could not include all the existing neuroimaging studies on PM. Indeed, some of them (e.g., Reynolds et al., 2009) gave preference in their analysis to a priori ROIs by using more lenient threshold for these regions, which would tend to increase the representation of these regions in the ALE analysis, thereby biasing the results. This is the reason that these studies were not included, and this necessarily limited the number of studies that were included in the present meta-analysis. A further potential limitation includes publication biases such as the file-drawer problem (tendency for null findings not to be published), which is unavoidable. However, even if such studies were available, ALE methods would not permit studies with null results to be included. The ALE methods also make some simplifying assumptions that may affect the relative influence of individual activations and individual studies. All the activation maxima above the significance threshold adopted in a particular study are given equivalent weight in the analysis, so that variations in activation intensity are not be accounted for. Likewise, studies with greater number

of activation maxima will contribute more to the ALE map than studies with fewer maxima.

These limitations aside, the present review and meta-analysis, and the AtoDI model we proposed, offer the first integrative explanation of the neural mechanisms recruited for prospective remembering. In fact, the AtoDI model sheds new light on the functional contribution of brain structures other than the aPFC and provides a more complete description of the multiple networks involved in the distinct PM phases. It is noteworthy that the AtoDI model might have possible translational clinical applications in patients with PM problems. It could also be considered an initial step for the study of premeditation and intention, with possible applications in forensic practice as well.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.neubiorev.2015.02.007>.

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