

FROM PROSPECTION TO PROSPECTIVE MEMORY: CONSTRUCTING, ENCODING, AND REMEMBERING FUTURE PLANS

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Recent studies have documented cognitive and neural processes related to human abilities for prospection and prospective memory. In this review article, I discuss functional neuroimaging findings on these two inter-related neurocognitive processes in humans, which are both thought to develop in relation to episodic memory. Prospection is the ability to construct ideas about possible future events, whereas prospective memory involves the formation and encoding of personal behavioural plans that are then maintained and retrieved at a planned time (or condition) during other ongoing activities. A growing body of neuroimaging studies investigating human prospection has consistently identified a core brain network consisting of medial regions of the frontal, temporal, and parietal lobes. The medial prefrontal cortex has also been identified to play a significant role for executive processes in prospective memory. Further investigations will be needed to disambiguate the contributions of the medial temporal lobe in constructing, encoding, and remembering future plans.

Key words: prospection, prospective memory, future plans, medial temporal lobe, medial frontal lobe, Brodmann area 10

Thinking prospectively about possible future events is a fundamental cognitive ability that is necessary to construct appropriate behavioural plans to act in the future. Recent theories in the field of cognitive and evolutionary psychology have proposed that this kind of prospective ability largely depends on episodic memory or an ability to mentally travel across different time points (Suddendorf & Corballis, 2007). Thus, episodic memory not only stores past experiences but also has an adaptive role for providing necessary information to construct ideas or plans for the future. Indeed, an increasing number of recent studies have demonstrated that overlapping brain systems are responsible for episodic memories and thinking about the future (for review, please see Schacter, Addis, & Buckner, 2007, 2008). The notion that thinking back to the past and forward into the future may rely on a common cerebral mechanism can go back to an empirical claim raised from observations in patients with amnesic syndrome (e.g., Tulving, 1983). However, direct experimental evidence for shared brain networks

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involved in recalling past experiences and imagining the future was first demonstrated in a study that examined direct comparisons of brain activity using neuroimaging methods (Okuda et al., 2003). Many researchers have now consistently replicated the common brain activations across these two domains, which typically involve medial aspects of cerebral hemispheres, including the medial frontal, medial temporal, and medial parietal lobes. Moreover, this kind of research is now growing into applied fields that link the prospective abilities to emotional (D'Argembeau, Xue, Lu, Van der Linden, & Bechara, 2008; Sharot, Riccardi, Raio, & Phelps, 2007) and social (Benoit, Gilbert, & Burgess, 2011; Peters & Büchel, 2010) domains.

Although such a rapid, successful development of the studies on the human ability to think about the future is amazing and exciting, future-oriented activities in our daily life are not limited to just imagining possible future events. We also formulate, maintain, and remember a number of personal behavioural plans that are to be realised at some time in the future, and these executive memory processes have been termed "prospective memory" (Brandimonte, Einstein, & McDaniel, 1996; Dalla Barba, 1989; Meacham & Singer, 1977). Interestingly, prospective memory has been investigated independently from the recent development of the field of future thinking. Studies of cerebral mechanisms of prospective memory have initially been motivated by clinical observations of abnormal planning behaviour by brain-damaged patients, especially those with frontal lobe lesions (e.g., Shallice & Burgess, 1991), but details of brain activations were experimentally revealed by a subsequent neuroimaging investigation in normal subjects (Okuda et al., 1998). Similar to the case of future thinking, numbers of follow-up studies (Burgess, Quayle, & Frith, 2001; Burgess, Scott, & Frith, 2003; Gilbert, Gollwitzer, Cohen, Oettingen, & Burgess, 2009; Hashimoto, Umeda, & Kojima, 2011; Okuda, et al., 2007; Okuda, Gilbert, Burgess, Frith, & Simons, 2011; Simons, Scholvinick, Gilbert, Frith, & Burgess, 2006) have reliably replicated an original finding of the involvement of the anterior part of the prefrontal cortices encompassing Brodmann area (BA) 10 in the maintenance, coordination, and retrieval of future behavioural plans in prospective memory (for a recent review, please see Burgess, Gonen-Yaacovi, & Volle, 2011).

In the present review article, I summarise recent advances in functional neuroimaging findings pertaining to the two topics of the future-oriented human abilities briefly mentioned above. Thinking about the future and prospective memory should be closely related with each other, but they have not been extensively examined and discussed together in the same framework. This may be because the two topics have been investigated independently by different research communities. In addition, research regarding thinking about the future is relatively new and still rapidly developing. However, the brain regions revealed in each study topic have converged into a focal network that consists of a small number of brain regions, some of which appear to overlap across the two topics. Therefore, as an initial attempt to construct a unified framework covering these two future-oriented cognitions in humans, it will be useful to discuss the commonalities and distinctions between the cerebral networks suggested in the two topics. I introduce studies about brain activation related to thinking about future events, or "prospection", and then I introduce studies related to prospective memory. I also compare

the findings from the two topics in an attempt to uncover basic brain functions supporting these future-oriented cognitive abilities in humans.

PROSPECTION

The term “prospection” is used to refer to the act of thinking about possible future events (Buckner & Carroll, 2007), but some researchers attribute a more general and extensive meaning to this term that covers a wide range of future-oriented cognition and behaviour (Suddendorf & Corballis, 2007). For example, Suddendorf and Corballis (2007) distinguished procedural, semantic, and episodic prospection to apply the well-known taxonomy of the memory system to corresponding future-oriented cognitions. In their framework, “episodic prospection” is the most appropriate term for the present topic, but I use the simple term “prospection” in the present review. Prospection has also been expressed using a variety of phrases, such as “imagining the future” (Addis, Wong, & Schacter, 2007), “envisioning the future” (Szpunar, Watson, & McDermott, 2007), “foresight” (Suddendorf & Corballis, 2007), “episodic simulation of future events” (Schacter, Addis, & Buckner, 2008), “episodic future thinking” (Atance & O’Neill 2001), and “mental time travel into the future” (Suddendorf & Corballis, 2007). However, these phrases commonly refer to a process of mentally constructing vivid images about events that might happen at some point in the future. Therefore, in the present paper, I use these phrases without distinction when referring to thinking about future events.

Although a great deal of effort has been put forth to clarify brain activations related to episodic memory processes using functional neuroimaging, researchers have paid little attention to the mechanisms related to future prospection. Nevertheless, observations in patients with focal brain damage [e.g., the famous case of Phineas Gage (Harlow, 1999; Damasio, Grabowski, Frank, Galaburda, & Damasio, 1994), who experienced selective loss of anterior medial prefrontal regions by an unexpected accident during work for railway construction] have clearly shown that the ability to mentally construct ideas about the future could be based on the functioning of restricted areas of the brain. Moreover, neuroimaging studies using the free recall paradigm have successfully identified brain activations related to thinking about autobiographical memories of one’s past (Maguire, 2001; Tsukiura et al., 2002). Motivated by these lines of evidence, Okuda et al. (2003) performed a simple but challenging experiment that directly compared brain activations while participants freely talked about particular events of different time periods in the future and the past.

Specifically, the participants in the Okuda et al. study were presented with a keyword on a monitor in front of them and were asked to construct and orally express their own ideas in relation to the keyword for one minute. During this process, the participants’ brain activities (regional cerebral blood flow, rCBF) were measured by positron emission tomography (PET). The participants took part in 4 experimental tasks and a control task in which different keywords were displayed according to the purpose of each task. The 4 experimental tasks were designed as a 2 × 2 combination of temporal direction (future/

past) and temporal distance (far/near) about which the participants expressed their ideas. The keywords for each task were “during the next few years” (a far future task), “during the next few days” (a near future task), “during the last few days” (a near past task), and “during the last few years” (a far past task). For the control task, three keywords (“car”, “money”, and “surprise”) were presented for 20 s each, and the participants were asked to explain the semantic meaning of the keywords without referring to any specific event information in the past or the future. By contrasting the rCBF images during the experimental tasks with the images from the control task, brain activation related to sensori-motor processes (watch a keyword and make mouth/tongue movements for verbal output) could be cancelled out, whereas activation specifically related to recalling or constructing event information for each time period of the past and future was revealed. Moreover, the factorial design of the experimental tasks enabled Okuda et al. to examine characteristic effects of temporal direction and distance on brain activity in each region.

The results of the experiment revealed interesting patterns of brain activation that clearly showed a shared brain network for recalling past episodes and reporting ideas about the future. Compared with the control task, both the future and the past tasks (average of the far and near conditions) showed significant increases in rCBF in multiple regions of the medial frontal, medial temporal, and medial parietal lobes, and these regions considerably overlapped across the future and past tasks. Moreover, when rCBF changes in segregated activation clusters identified in each region were analysed in detail according to the 2-way factorial design, the activity of each cluster was found to exhibit characteristic modulation that was dependent on the temporal direction and distance. For example, the clusters in the most anterior part of the medial frontal cortex showed effects of both “future” and “far” (the highest rCBF during the far future task), and most (4 out of 5) clusters in the medial temporal lobe, including the hippocampus and the parahippocampal cortices, exhibited greater or equivalent rCBF values for the future task than the past task.

Okuda and colleagues’ findings indicated that remembering past episodes and constructing ideas about the future were primarily based on the workings of a common neural network that consisted of the medial aspects of cerebral hemispheres; however, subregions of the network had slightly different roles depending on the time periods for which the events were concerned (future or past and far or near). Although the medial temporal lobe is known to be involved in retrieving episodic memories, the results suggested that the medial temporal lobe structures may also play an active role in constructing ideas about the future. Taken together, the results of Okuda and colleagues’ experiment have led to the hypothesis that the construction of ideas about the future may require retrieval of information about past experiences, which could adaptively be recombined or reorganised to make up meaningful scenarios in the future. Thus, Okuda et al. (2003) speculated that the anterior part of the medial prefrontal region may work to orient one’s attention towards distant future events, and meaningful ideas about the future may be organised from episodic information retrieved through the medial temporal and parietal structures.

Stimulated by this demonstration of common brain activation across episodic

memory retrieval and future thinking, a number of studies have attempted to elucidate further details of the activation patterns during prospection. Addis et al. (2007) presented concrete nouns (e.g., "flower") to their subjects and asked them to remember past experiences or imagine possible future events associated with the presented item. They strictly controlled for the phenomenological quality of the future and past events so that details, emotionality, personal significance, and field/observer perspectives of the remembered or imagined events should not differ across the future and past conditions. By using event-related functional magnetic resonance imaging (fMRI), they dissociated brain activity patterns during event construction (search for autobiographical event tags) and elaboration (subsequent retrieval/imagination of supplementary details). Under such a well-controlled experimental setting, a common activation in the medial frontal, temporal, and parietal network was observed, particularly during the event elaboration, which might be considered a consequence of greater demand for reorganisation of pieces of event information into a coherent scenario during the event elaboration for both the future and the past.

Szpunar et al. (2007) have also reported evidence for a common engagement of the medial network, especially in remembering and envisioning self-relevant, autobiographical events in the past and future. They asked subjects to remember or envision personally relevant specific events (e.g., episodes from one's birthday) and to imagine that a well-known person (e.g., Bill Clinton, the US president at the time of the study) would experience such episodes. The medial network was significantly more activated in the personal past/future conditions than in the Bill Clinton condition, which led Szpunar et al. to conclude that self-relevance and temporal dissociation from the present would be critical factors to explain the activity in the medial network.

More recent studies have extended the research about prospection into more applied fields that have attempted to examine the functional specialisation of the medial network in relation to emotional valuation processes. For example, Sharot et al. (2007) examined the emotional modulation of activity in the medial network and reported that positive emotion attached to imagined future events promotes greater activation in the medial regions. They asked subjects to imagine emotionally positive (e.g., pass an exam or win the lottery) or negative (e.g., lost love or traffic accident) events in the future or past and found significant modulation of activation in the anterior medial frontal regions by positive emotion (greater activation for positive events compared with negative events), particularly in the future condition. A similar activity pattern was also observed in the amygdala, which is one of the medial temporal structures that are known to be involved in processing of emotional aspects of environmental stimuli. Moreover, functional connectivity analyses have revealed a greater correlation of the activation in the anterior medial frontal and amygdala regions in the future positive condition than in the future negative condition. In addition, the activity in the medial frontal region has been shown to be correlated with scores of a questionnaire that measured the optimism trait in individual subjects. Further examination by D'Argembeau et al. (2008) revealed that the enhanced activity of the anterior medial frontal region by imagining future positive events was observed only for a distant, less predictable period in the future (beyond a year), whereas

positive future events with a short delay of a predictable range (several weeks) activated the basal ganglia (a part of the brain's reward-prediction network) rather than the medial frontal region. Taken together, these lines of emerging evidence tentatively suggest a scheme where the anterior region of the medial frontal lobe might act for controlling organisation processes of retrieved episodic information towards a desirable image of one's own future in the long term, possibly by interacting with the other core regions of the medial network that may support the retrieval and recombination of pieces of episodic information.

Regarding the role of the medial temporal structures in the prospection processes, the discovery of a common brain network for episodic memory retrieval and the construction of ideas about the future has reminded researchers to reconsider ability of future imagining in patients with amnesic syndrome, who have been regarded as having a selective loss of episodic memory about past events. Indeed, Hassabis, Kumaran, Vann, and Maguire (2007) have demonstrated striking evidence that amnesic patients with bilateral medial temporal damage have deficits in imagining new experiences in addition to their impairment in remembering past episodes. Hassabis et al. tested whether a group of patients with amnesia associated with bilateral hippocampal damage could construct new imagined experiences in response to short verbal cues that outlined a range of simple commonplace scenarios. They found that a composite score that measured the overall richness of imagined experiences in the patients was significantly lower than the scores in matched control subjects. Importantly, the deficit was not restricted to personally relevant possible future events (e.g., a possible Christmas event) but was common to a wide variety of commonplace scenarios to which any distinctive temporal factors were not necessarily attached (e.g., standing in the main hall of a museum). Instead, the patients' impairments were apparent in placing fragmented images into one coherent spatial context. Based on these results, Hassabis et al. concluded that the medial temporal structures have an *essential function in the integration of fragmented images of event information into a unified spatial representation regardless of whether it is a past memory or a future scenario.*

The deficits of imagining future events paralleled to episodic memory disturbance in medial temporal amnesia have further been confirmed by a recent study (Race, Keane, & Verfaellie, 2011) that showed that the amounts of information retrieved from past experiences were positively correlated with the information of imagined future events in patients with medial temporal lobe damage. However, another study by Squire et al. (2010) reported that patients with more focal damage to the hippocampus showed a normal ability to construct ideas about the future but had a selective impairment for retrieving recent memories within several years. Thus, there is still controversy regarding which structure in the medial temporal lobe is essential for future simulation, and further theorising and experimental evaluations are necessary.

PROSPECTIVE MEMORY

In contrast to the processes of prospection that contribute to the construction of ideas about possible future events, prospective memory specifically deals with one's own behavioural plans that should be realised at a certain time point (or a condition) in the future. Prospective memory is typically understood as a form of everyday memory activity, such as remembering a plan to post a letter when noticing a postbox on the way home. This kind of memory activity for behavioural plans in the future should involve multiple processes over a certain length of time (i.e., the formation and encoding of a future behavioural plan, maintaining the plan, and retrieval and performance of the plan at the intended timing or condition) (Brandimonte et al., 1996). In addition, the retention interval during which the plan is maintained is typically filled with other ongoing activities unrelated to the plan, which precludes conscious and continuous rehearsal of the existence of the plan (Burgess et al., 2003). For example, we do not always keep our attention focused on the plan of posting a letter during the daytime when we usually have a lot of other ongoing activities unrelated to the plan. This nature of intermittent attention to the future plan also demands that finding the time or condition for remembering the plan should be self-initiated during ongoing activities. Indeed, we need to voluntarily remember that we had a plan to post a letter when noticing the postbox without any explicit cues from others.

Because of the complicated memory structure of prospective memory that can extend for relatively long periods of time in our daily lives, there are methodological difficulties involved with examining the underlying processes and factors of prospective memory. However, a proposal of an in-laboratory task paradigm by Einstein and McDaniel (1990) has created a method to conduct controlled experiments that could effectively simulate prospective memory processes with experimental manipulation of task parameters. Their paradigm consists of two task components: an ongoing task in which subjects are continuously engaged and a prospective action that should be performed at a specific condition (called a "retrieval condition") embedded in the ongoing task stimuli at a very low frequency. In the first demonstration of the task, for example, subjects were told to participate in research focusing on the short-term memory ability for words, but the subjects were also asked to remember and perform a specific action (press a space bar) when a specific target word ("rake") appeared during the short-term memory task (immediate recall of a set of visually presented words). The target word (i.e., retrieval condition) was presented three times during 42 trials of the short-term memory task (ongoing task), and the subjects' performances of pressing the space bar (prospective action) were monitored. By developing various versions of the prospective memory task paradigm, Einstein and McDaniel have revealed a wide range of evidence about the psychological nature of the maintenance and retrieval of prospective memory (e.g., effects of aging, load of ongoing tasks, stimulus saliency effects, and an interplay between the ongoing task and the prospective action) (for a conceptual review, please see McDaniel & Einstein, 2000).

Based on the success of psychological studies using the in-laboratory prospective

memory task paradigm, Okuda et al. (1998) attempted to identify brain regions involved in prospective memory processes by conducting a PET experiment with tasks arranged according to the original study by Einstein and McDaniel (1990). Okuda et al. asked subjects to engage in an ongoing task of word repetition (orally repeating a set of five words presented auditorily) and to tap with their left hand when one of 10 target words was repeated. The subjects heard and encoded the target words several minutes before the prospective memory task, and three randomly selected target words were embedded in 10 trials (5 words in each trial). The PET scan was conducted during two minutes of this prospective memory task (performance of the prospective action while being engaged in the ongoing task) and also during a control task that required the ongoing task alone with 10 target words held in mind (subjects were told that there was no demand for the prospective action and that the target words would not appear in the control task). Therefore, comparing the rCBF images during the prospective memory task with those of the control task would reveal brain regions specifically related to maintaining and remembering the plan to perform the prospective action when the retrieval condition occurred during the ongoing task.

As a result, significant rCBF increases were found in highly localised frontal and medial temporal regions during the prospective memory task compared with the control task. The frontal activation was found in bilateral lateral and medial prefrontal cortices, including a region in the anterior prefrontal cortex corresponding to BA 10. These data not only confirmed the involvement of the frontal lobes and the medial temporal lobe in prospective memory processes for the first time but also provided a novel insight about frontal processes involved in prospective memory. Although some of the frontal activations were easily explained by known functions, such as working memory load for dorsolateral prefrontal activations and switching attention in the anterior cingulate cortex, functional activation of the most anterior part of the prefrontal cortex (BA 10) has been less extensively reported. Okuda et al. (1998) attributed the BA 10 activation to the maintenance of an intention to remember and perform future plans while being engaged in other ongoing activities, a process that is critical to prospective memory and may be regarded as a separable function from working memory or attention control in general.

Subsequently, researchers have started to replicate this original finding of the anterior prefrontal activation during prospective memory tasks. Burgess et al. (2001) have examined whether the prefrontal activation was related to maintenance or retrieval of the intention to perform prospective actions. In a study by Okuda et al. (1998), PET scans did not have enough temporal resolution to dissociate activations during the ongoing task period and those at the retrieval condition; thus, the study could not definitively determine whether the observed activation was related to the maintenance process or the retrieval process. Burgess et al. (2001) also used PET, but they scanned brain activity during a period just before the appearance of the first target stimulus, which eliminated the possibility of the inclusion of the retrieval process in their results. Moreover, they utilised the cognitive conjunction method (Price & Friston, 1997), which employed 4 different (2 verbal and 2 visuospatial) tasks to examine the brain regions pertinent to the core processes of prospective memory regardless of the type of stimuli or ongoing tasks.

Interestingly, Burgess et al. found strong bilateral activation in the lateral anterior prefrontal cortices situated in BA 10 during the maintenance of the plan to perform the prospective action in all 4 of the different types of tasks. Burgess et al. have further advanced their study to show another set of findings related to activity patterns of the lateral and medial BA 10 (Burgess et al., 2003). With the use of PET and the conjunction design, Burgess et al. demonstrated decreased activation of the medial part of the anterior prefrontal cortex during the maintenance period, in addition to increased activation of the lateral part of the anterior prefrontal cortex.

The similar pattern of lateral-medial dissociation in the anterior prefrontal activation has consistently been replicated in other studies (e.g., Okuda et al., 2007; Simons et al., 2006). For example, Okuda et al. (2007) examined the effects of two different types of retrieval conditions (event-based and time-based conditions) on brain activation during prospective memory tasks and found an interesting pattern of the lateral-medial dissociation depending on the type of the retrieval condition. Existing neuroimaging studies have only focused on remembering to perform a prospective action based on an event cue (event-based prospective memory), but many of the plans in our daily life are often dependent on the time during which the plan is to be realised (time-based prospective memory: e.g., to make a phone call to a friend at 3 p.m. in the afternoon). Importantly, Okuda et al. (2007) have developed a time-based prospective memory task in which a clock was presented in addition to ongoing task stimuli to provide information about the time since the start of the task. For the time-based prospective memory performance, Okuda et al. asked subjects to press a specific button each minute with the aid of the clock information during ongoing tasks lasting 3 min (conjunction design of a word task requiring syllable judgement and a shape task requiring mental rotation). In an event-based prospective memory task, the subjects were required to perform the prospective action when a specific target stimulus (the word “guitar” for the word task and an exact square for the shape task) appeared at approximately each minute of the 3 min task period. Brain activation related to the maintenance of the plans was measured by PET during a period of 30 s just before the third instance of the prospective action in both the time-based and the event-based prospective memory tasks. Activities during the control tasks that required the ongoing task alone were also measured. Comparison of the event-based prospective memory tasks with the control tasks revealed rCBF increases in lateral regions of the anterior prefrontal cortices and rCBF decreases in the medial prefrontal regions, which replicated the previous findings by Burgess et al. (2003). Interestingly, activation during the time-based prospective memory task showed the same pattern as the control task (i.e., rCBF increases in the medial regions and rCBF decreases in the lateral regions). These complementary patterns in the lateral and medial regions, which were dependent on the event-based, time-based, and ongoing-alone conditions, were robustly observed regardless of the type of the ongoing task (word/shape) or the clock face (analogue/digital), even in another time-based condition in which the clock was not presented and the subjects had to make the prospective action based on their own estimation of the passage of time.

Based on these series of neuroimaging results indicating complementary functions of

the lateral and medial prefrontal regions as well as related findings from patients with frontal lobe lesions, Burgess et al. proposed the gateway hypothesis (Burgess, Dumontheil, & Gilbert, 2007; Burgess, Gilbert, Dumontheil, & Simons, 2005; Burgess, Gilbert, Okuda, & Simons, 2006), which suggests that the activity balance between the lateral and medial prefrontal regions may help coordinating the attention orientation between ongoing cognition and the intention for plans to be performed in the future. The roles for regulating attention towards one's future act might be particularly suggestive to interpret seemingly controversial findings of the common activations of the medial prefrontal regions during the time-based prospective memory task and the ongoing-alone task. A remarkable commonality between the two tasks is the predictability of the task to be performed in the future. Indeed, the subjects should have a clear and definite idea about what they would do in the future in both tasks because they were able to mentally simulate the performance of the prospective action with the aid of the clock or self-estimation of time in the time-based prospective memory task. In addition, subjects only have one task to perform during the ongoing-alone task. In contrast, a mental simulation of performance of the prospective action was less available in the event-based prospective memory task in which the timing of the appearance of the target stimulus was unpredictable. Importantly, the idea of the function for attentional coordination towards one's future act in the medial prefrontal cortices is in good harmony with the robust activations in the anterior medial frontal lobes during prospection.

To further investigate this issue, Okuda et al. (2011) recently conducted an fMRI study in which attention coordination between current performance and future action plans could be systematically varied within the continuous performance of a single prospective memory task. In the Okuda et al. study, intervals of ongoing task trials that contained target stimuli for a prospective action were systematically manipulated in a periodic cycle of expanding (4, 8, 12, 16, and 20) and contracting (20, 16, 12, 8, and 4) intervals of target trials. Based on the assumption that the degree of anticipatory attention towards prospective memory performance would vary depending on the history of previous experiences of the prospective action, attention towards remembering to perform the prospective action would be enhanced in the expanding period because the target stimuli for the prospective action appeared later than expected from the previous target interval. In addition, attention towards the ongoing task performance would be diminished in the expanding period. As expected, this expanding-contracting cycle of the target trials resulted in significant modulation of subjects' behaviours without awareness of the periodic cycle of the targets. Indeed, remembering to perform the prospective action to target stimuli was more successful and faster in the expanding target interval period (at the cost of lower and slower performance of the ongoing task), whereas an opposite direction of this trade-off effect was observed in the contracting target interval period. In accordance with these behavioural results, event-related analyses of fMRI data identified similar trade-off effects in activation of the anterior medial prefrontal cortices (i.e., activation elevation at the target trials and deactivation at the ongoing trials in the expanding period compared with the contracting period). Thus, the behavioural and fMRI results in the Okuda et al. study clearly revealed a medial prefrontal function for automatic

coordination of attentional resources between current task performance and future action plans that is dependent on the history of past experiences.

DISCUSSION

There has been a rapid explosion and solid advancement in the fields of functional neuroimaging of prospection and prospective memory in recent years. Converging evidence in each field has suggested the existence of core brain networks that underlie future-oriented abilities, which are also thought to be related to episodic memory processes. Indeed, prospection is mediated by a core network of the medial frontal, medial temporal, and medial parietal lobes, which also support retrieval of autobiographical event information from episodic memories. The performance of prospective memory involves complementary workings of the medial and lateral prefrontal cortices, especially in the anterior portions encompassing BA 10. The medial prefrontal region overlaps with the region in the core network for prospection and autobiographical memory, and lateral prefrontal activation has also been widely reported during episodic memory retrieval (Grady, 1999). Thus, it appears that prospection and prospective memory are based on partially overlapping brain systems that are also involved in episodic memory processes.

Among the candidate brain regions in the core networks for prospection and prospective memory, the available data suggest that the medial prefrontal region may have the most consistent and convergent function for attention orientation to support the two forms of future-oriented cognition. A review of the studies concerning prospection has suggested that the medial frontal region supports engaging one's attention towards distant time periods in the future to efficiently construct ideas using retrieved episodic information. Moreover, findings from the prospective memory literature consistently suggest a role for attention coordination towards the performance of one's own future behaviour, which may occur automatically during other ongoing activities. Therefore, the general function of the medial prefrontal region could be summarised as an executive control process of attention towards future behaviour regardless of current situations or tasks. To further extend this idea, Buckner and Carroll (2007) have proposed a more comprehensive model in which the core network of the medial regions acts for projecting oneself into other times, places, and agents that should be based on a stimulus-independent mental representation that may be reconstructed from episodic information in the past (Okuda, 2007). However, the possibility of finer functional differentiation within the anterior prefrontal cortices should also be noted (please see Gilbert et al., 2006 for a comprehensive meta-analysis). Indeed, the activation clusters in the medial prefrontal regions that were revealed in the studies regarding prospection and prospective memory processes are situated in a partially overlapping manner with a slight deviation along the anterior-posterior axis: peak MNI coordinates (x, y, z in mm) were -2, 68, -6 and 4, 62, -18 for future prospection (Okuda et al., 2003), -2, 66, 4 and 8, 46, 4 for time-based prospective memory (Okuda et al., 2007), and -15, 36, -3 and 18, 42, -6 for attention

coordination towards future plans (Okuda et al., 2011).

In contrast to the plausible account for the medial frontal function, the contributions of the medial temporal and the medial parietal lobes in prospection and prospective memory remain less clear. In particular, the exact roles of the hippocampus and other medial temporal structures in prospection have been a controversial issue. Neuroimaging studies have consistently shown activation in the medial temporal lobes during prospection, whereas patient studies have reported mixed evidence of impaired (Hassabis et al., 2007; Race et al., 2011) and intact (Squire et al., 2010) abilities for constructing a new idea that has not been experienced in the past. To address this controversy, studies (Addis & Schacter, 2012; Martin, Schacter, Corballis, & Addis, 2011) have recently proposed that the medial temporal activations during the imagining of future events may reflect the encoding of imagined events into episodic memory rather than the construction of the future ideas per se. Therefore, further functional subdivisions in the medial temporal lobe structures should be sought by future studies that dissociate possible processes involved in prospection, such as the retrieval of episodic information, the recombination of episodic elements into a coherent future scenario, and the encoding of the constructed idea into the episodic memory system.

Studies to determine the roles of the medial temporal structures in prospective memory processes are lacking. The activation in the medial temporal region (the left parahippocampal gyrus) found in the first study by Okuda et al. (1998) has rarely been replicated in subsequent studies. One possible reason for this discrepancy might be differences in memory load across studies. In the Okuda et al. study (1998), subjects had to memorise 10 target words for the retrieval condition, which probably required a long-term memory system beyond a short-term memory buffer. Moreover, the episodic nature of the retrieval condition should have been enhanced because the subjects had learned each target word as a single episode before each PET scan. In contrast, other studies used a kind of categorical criteria, such as words representing any animal name (Burgess et al., 2001) or diagonal line patterns made by three dots (Okuda et al., 2011), instead of using episodic criteria as the retrieval condition. The perceptual-semantic nature of the retrieval condition in the other studies may be less demanding on the episodic memory system, which could result in the lack of significant activation in the medial temporal lobes. Future studies will be needed to experimentally validate the possibility of the relation between episodic memory demands for the retrieval condition and the medial temporal activations in prospective memory tasks.

Another important point is the lack of studies concerning formation and encoding processes of future plans in prospective memory literatures. The encoding of future plans in prospective memory definitely requires the initial formation of future plans, which should be based on the construction of possible scenarios that might happen in the future (i.e., prospection). Importantly, the encoding of ideas about the future might involve the functioning of medial temporal structures. Related to this idea, a recent study by Poppenk, Moscovitch, McIntosh, Ozelik, and Craik (2010) demonstrated that activities in the medial temporal structure (the right parahippocampal gyrus) and the lateral region of the anterior prefrontal cortex during the encoding of visual scene stimuli with intentions to

perform a personal act in the future predicted later performance of judgement about whether the scene had been encoded with the future intention. Based on this result, Poppenk et al. argued that the right parahippocampal cortex and the lateral prefrontal cortex have a critical role for the successful encoding of the intention to act in the future. However, this interpretation seems problematic because their test for the retrieval of intention did not involve the actual performance of the encoded action plans. Indeed, Poppenk et al. only examined source judgement about retrospective memory as to whether the visual scenes were encoded with the task of forming action plans.

To address the issue regarding contributions of the medial temporal lobes in the encoding of future plans in prospective memory, Okuda, Suzuki, and Fujii (in press) tried to identify encoding-related brain activations during the formation of future action plans that could predict a later ability to remember the plans using the formal prospective memory task paradigm. Okuda et al. asked subjects to form action plans of joystick movements (leftward, rightward, upward, or downward) to pictures of manmade objects or natural scenes (animals and flowers) during which brain activities were measured by fMRI. The subjects then participated in an ongoing task of manmade/natural judgement of successively presented picture stimuli that contained the specific pictures to which they had formed action plans of joystick movements at approximately every 30 trials. The subjects' ability to move the joystick to the target pictures during the ongoing task was monitored and classified into 3 categories: a correct movement as they planned, an incorrect movement as they did not plan, and a failure to make any joystick movement. Activities in several regions, including the medial temporal and ventromedial prefrontal (subcallosal) regions, during the formation of future action plans could differentiate later performances of remembering the plans. Moreover, correlations of activity in the ventromedial prefrontal area with activity in the medial temporal and visual sensory areas were significantly modulated depending on the subsequent ability to remember the plans. Therefore, in addition to identifying activation patterns in each functional region, the results indicated the importance of examining the significance of functional correlations among a network of regions during the formation of robust memory for future plans (please see also Martin et al., 2011 for a similar discussion).

In conclusion, the present paper reviewed recent advances of functional neuroimaging studies on prospection and prospective memory and discussed commonalities and controversy about functional networks involved in these two future-oriented abilities in humans. It is now well established that the retrieval of autobiographical event memories and the ability to think of possible future events are mediated by a common core network including the medial regions of the frontal, temporal, and parietal lobes. The medial prefrontal regions encompassing BA 10 have been identified to play a role in orienting attention towards one's future behaviour, which links the basic function for executive processes involved in prospective memory to that of prospection. Contributions of the medial temporal structures to constructing, encoding, and remembering future plans, as well as the functional connectivity across the core regions, should be clarified in more detail by further studies.

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