NeuroImage 89 (2014) 244–255

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Dissociable roles of default-mode regions during episodic encoding

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ARTICLE INFO

Article history:
Accepted 30 November 2013
Available online 6 December 2013

Keywords:
Default-mode network
Task-unrelated thoughts
Mind-wandering
Episodic memory encoding
Encoding strategy

ABSTRACT

We investigated the role of distinct regions of the default-mode network (DMN) during memory encoding with fMRI. Subjects encoded words using either a strategy that emphasized self-referential (pleasantness) processing, or one that emphasized semantic (man-made/natural) processing. During encoding subjects were intermittently presented with thought probes to evaluate if they were concentrated and on-task or exhibiting task-unrelated thoughts (TUT). After the scanning session subjects performed a source retrieval task to determine which of two judgments they performed for each word at encoding. Source retrieval accuracy was higher for words encoded with the pleasantness vs. the man-made/natural task and there was a trend for higher performance for words preceding on-task vs. TUT reports. fMRI results show that left anterior medial PFC and left angular gyrus activity was greater during successful vs. unsuccessful encoding during both encoding tasks. Greater activity in left anterior cingulate and bilateral lateral temporal cortex was related successful vs. unsuccessful encoding only in the pleasantness task. In contrast, posterior cingulate, right anterior cingulate and right temporoparietal junction were activated to a greater extent in unsuccessful vs. successful encoding across tasks. Finally, activation in posterior cingulate and bilateral dorsolateral prefrontal cortex was related to TUT across tasks; moreover, we observed a conjunction in posterior cingulate between encoding failure and TUT. We conclude that DMN regions play dissociable roles during memory formation, and that their association with subsequent memory may depend on the manner in which information is encoded and retrieved.

Introduction

The default-mode network (DMN) refers to a set of regions including medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), inferior parietal lobes (IPL), and lateral temporal cortex (LTC) (Buckner et al., 2008). A formal characterization of this network came from task-based meta-analyses which found that these regions were activated to a greater extent during passive resting-state conditions compared to a variety of externally-driven and cognitively demanding tasks, such as visual search and episodic memory retrieval (Nyberg et al., 1996; Shulman et al., 1997). More recently, similar task-related reductions in activity in DMN regions has been reported during episodic encoding studies (e.g., Daselaar et al., 2004). Furthermore, a recent meta-analysis indicated that increased activation in all major DMN regions during episodic encoding, including ventral medial PFC, PCC, bilateral IPL and LTC is predictive of retrieval failure (Kim, 2010). It has been suggested that since successful encoding requires externally-directed attention, activation in DMN regions should be suppressed, reflecting down-regulation of task-unrelated thoughts (TUT) (Daselaar et al., 2009; Shrager et al., 2008), defined here as thoughts that are not relevant to encoding items. This suggestion is consistent with behavioral evidence indicating that the frequency of TUT at encoding is negatively correlated with retrieval performance in young adults (Maillet and Rajah, 2013; Seibert and Ellis, 1991); and is also compatible with evidence that DMN regions are involved in TUT at rest and during some cognitive tasks such as the sustained attention to response task (Andrews-Hanna et al., 2010a; Christoff et al., 2009; Stawarczyk et al., 2011). However, to our knowledge, the hypothesis that activation in DMN regions during episodic encoding reflects TUT has never been directly tested.

Furthermore, although the majority of the literature indicates that activation in DMN regions is suppressed during successful episodic encoding, these studies have mostly used semantic encoding tasks, such as judging whether words are man-made/natural (Kim, 2010). Such tasks are known to deactivate DMN regions (e.g., Lustig et al., 2003). In contrast, increased activation in some DMN regions has been observed during successful encoding when the encoding task emphasized subjective evaluation of stimuli in relation to oneself. For example, successful encoding using both pleasantness judgments, or judging whether adjectives are descriptive of oneself have both been associated with activation in mPFC (e.g., Leshikar and Duarte, 2012; Macrae et al., 2004; Maillet and Rajah, 2011; Shrager et al., 2008; Zierhut et al., 2010) and at least one study using pleasantness judgments has also reported correct subsequent memory effects in IPL (Schott et al., 2011). Moreover, encoding using such self-referential strategies results in better memory compared to semantic and perceptual

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1053-8119/$ – see front matter.
http://dx.doi.org/10.1016/j.neuroimage.2013.11.050

encoding tasks (e.g., Leshikar and Duarte, 2012; Maillet and Rajah, 2013). It has been suggested that this increase in memory is due to the superior organizational and elaborative processes associated with encoding information in relation to the self (Rogers et al., 1977; Symons and Johnson, 1997). In contrast, in another fMRI study where subjects encoded words using a pleasantness judgment, it was found that activation in left mPFC predicted retrieval success; but, activation in right mPFC, PCC/precuneus, and bilateral temporoparietal junction predicted retrieval failure (Shrager et al., 2008). Taken together, these studies suggest that when self-referential encoding strategies are used, a subset of DMN regions may be involved in encoding success, while a distinct set of regions may be involved in encoding failure, perhaps due to TUT.

These results are consistent with evidence that the DMN can be fractionated into distinct subsystems, only some of which are preferentially recruited during self-referential processing. For example, Andrews-Hanna et al. (2010b) reported that a dorsal medial PFC subsystem, which included regions such as dorsal medial PFC, LTC, temporal pole and temporoparietal junction was preferentially activated when people made self-relevant decisions. In addition, Andrews-Hanna et al. (2010b) identified a distinct subsystem, which included retrosplenial cortex and IPL, that was preferentially engaged when individuals constructed mental scenes based on memory. More recently, Qin and Northoff (2011) performed a quantitative meta-analysis indicating that in contrast to other DMN regions, only the ventral anterior cingulate (ACC) was preferentially recruited during self-referential decisions. In another meta-analysis, Kim (2012) reported evidence that a subsystem including anterior medial PFC and posterior cingulate mainly supports self-referential processes, while regions including IPL and LTC were involved in memory retrieval. Thus, although there is some inconsistency, these results converge to suggest a particularly important role of mPFC in self-referential processes, which is in agreement with studies indicating that this region is involved in encoding success when items are encoded in relation to the self.

These prior studies also suggest that other DMN regions, including PCC, IPL and LTC, are involved in encoding failure regardless of whether the encoding task is self-referential or semantic because the cognitive processes subserved by these regions are recruited to a greater extent during TUT relative to encoding items using these strategies. Previous studies suggest that the content of TUT during the performance of a cognitive task in an fMRI scanner is varied and may include: mind-wandering (e.g. thoughts about the past or the future), distractions involving monitoring of the internal or external environment (e.g. thinking about how hungry one is, thinking about scanner noise etc.), and task-related interferences (e.g. thoughts related to the appraisal of the current task) (Stawarczyk et al., 2011). These thoughts may recruit cognitive processes that have been associated with PCC, LTC and IPL such as, scene construction (Hassabis et al., 2007), memory retrieval (Kim, 2012; Wagner et al., 2005), internally focused attention (Buckner et al., 2008), prospection (Addis et al., 2007), and monitoring of internal/external milieus (Raichle et al., 2001).

The current study was designed to investigate the role of distinct DMN regions during encoding of word stimuli. We used fMRI to examine regional activity while subjects performed self-referential (pleasantness) and semantic (man-made/natural judgment) encoding of verbal stimuli. We pseudo-randomly inserted thought probes throughout the encoding task that asked subjects to provide self-reports of their current mental state (Christoff et al., 2009; Stawarczyk et al., 2011). During thought probes, subjects reported whether they were focused on task, or whether they were exhibiting TUT (i.e. mind-wandering, task-related interferences or distractions) (Stawarczyk et al., 2011). Ten minutes after fMRI scanning, subjects performed a source memory retrieval task for encoded stimuli.

The first goal of this study was to directly test the hypothesis that due to its involvement in self-referential processes, mPFC would be activated to a greater extent in successful vs. unsuccessful encoding of verbal items when a pleasantness but not when a man-made/natural encoding strategy is used. Also, based on findings that retrosplenial cortex/PCC, IPL and LTC may be recruited during in processes such as construction of mental scenes (Andrews-Hanna et al., 2010b; Hassabis et al., 2007) and/or memory retrieval (Kim, 2012; Wagner et al., 2005), and that these regions have been involved in encoding failure even when a self-referential task is used (Shrager et al., 2008), we predicted that these regions would be activated to a greater extent in unsuccessful vs. successful encoding of word stimuli independently of the task. In addition, we tested the hypothesis that the DMN regions activated in unsuccessful vs. successful encoding would also be activated to a greater extent when subjects were off-task (exhibiting TUT) vs. on-task. To identify the neural correlates of TUT during episodic memory encoding, we contrasted the activation in encoding trials preceding TUT (off-task) reports with the activation in encoding trials preceding on-task reports. Reaction times for the events preceding thoughts probes were used as an objective measure for whether the TUT episode, whose occurrence was measured during the thought probe, extended to the preceding encoding event. Specifically, we predicted that if this was the case, encoding trials in which TUT occurred would be associated with longer reaction times vs. those where no TUT occurred.

Methods

Subjects

Twenty-one, right-handed, healthy adults (age range 18–30, mean age = 23.33, 12 women) participated in the study. Participants reported no history of psychiatric illness, neurological disorders, or substance abuse and were healthy at time of testing. Participants had a minimum of high school education (mean education = 16.35 year). Volunteers were recruited with advertisements on university websites in the city of Montreal. All participants signed a consent form approved by the ethics boards of the Douglas Mental Health University Institute.

Behavioral methods

Participants visited the Douglas Mental Health University Institute on two separate occasions. In the first session, they completed a series of neuropsychological tasks including the Montreal Cognitive Assessment Scale (Nasreddine et al., 2005) (cut-off > 25) and the Beck Depression Inventory (Beck, 1987; Beck et al., 1961) (cut off < 10). They also completed the Edinburgh inventory (Oldfield, 1971), and were all right-handed according to this test. Finally, participants performed a practice version of the fMRI task in a mock MRI scanner, which familiarized them with the memory task and thought classification prior to the fMRI session (session two).

Participants returned for a second session to perform an episodic memory task for words, while undergoing fMRI scanning. The MRI session consisted of an anatomical scan (5 min) and 4 fMRI encoding runs (each 10 min 20 s). Thus, in total, the encoding portion of the experiment lasted approximately 41 min. The stimuli used in the memory task were 414 French nouns of 3–11 letters, taken from Desrochers and Thompson (2009) and the OMNILEX database (http://www.omnilex.uottawa.ca/scrServices.asp). The experiment was carried out in French, given that Montreal is a primarily French-speaking city. In total, 414 nouns were used: 276 served as encoding words, while the other 138 were used as distractors at retrieval. Half of the words were used in the pleasantness task, while the other half was used in the man-made/natural task. The words were not switched across the pleasantness and man-made/natural task for different subjects. However, T-tests indicated that words used in pleasantness encoding, man-made/natural encoding and words used as distractors in the retrieval task were matched for number of letters (mean with standard deviation: 6.46 (1.82), 6.68 (1.67) and 6.60 (1.74) respectively), number of syllables (mean with standard deviation: 2.05 (0.68), 2.02 (0.72)