When less is more: TPJ and default network deactivation during encoding predicts working memory performance

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ABSTRACT

Previous work has shown that temporo-parietal junction (TPJ), part of a ventral attention network for stimulus-driven reorienting, deactivates during effortful cognitive engagement, along with the default mode network (DMN). TPJ deactivation has been reported both during working memory (WM) and rapid visual search, ostensibly to prevent reorienting to irrelevant objects. We tested whether the magnitude of this deactivation during WM encoding is predictive of subsequent WM performance. Using slow event-related fMRI and a delayed WM task in which distracter stimuli were presented during the maintenance phase, we found that greater TPJ and DMN deactivation during the encoding phase predicted better WM performance. TPJ and DMN, however, also showed several functional dissociations: (1) TPJ exhibited a different task-evoked pattern than DMN, responding to distracters sharing task-relevant features, but not to other types of distracters; and (2) TPJ showed strong functional connectivity with the DMN at encoding but not during distracter presentation. These results provide further evidence for the functional importance of TPJ suppression and indicate that TPJ and DMN deactivation is especially critical during WM trace formation. In addition, the functional connectivity results suggest that TPJ, while not part of the DMN during the resting state, may flexibly "couple" with this network depending on task demands.

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Introduction

Recent studies have defined two broadly distributed but functionally distinct cortical networks involved in allocation of attentional resources: the dorsal and the ventral attention systems (Corbetta et al., 2002, 2008). One key region of the ventral attention system is the right temporo-parietal junction (TPJ), situated at the intersection of the posterior end of the superior temporal sulcus and the inferior parietal lobule. Previous work has suggested that TPJ is involved in re-orienting attention to the external environment when behaviorally important stimuli are encountered (Arrington et al., 2000; Corbetta et al., 2000; Downar et al., 2001; Indovina and Macaluso, 2007; Macaluso et al., 2002; Marois et al., 2000; Serences et al., 2005) and that it is maximally responsive to behavioral relevance of stimuli rather than their sensory salience (Indovina and Macaluso, 2007; Kincade et al., 2005). For instance, previous work showed that TPJ is most responsive when an unexpected environmental stimulus is encountered (Downar et al., 2000, 2001, 2002) that matches the features of the current task (Serences et al., 2005). While reorienting to behaviorally important stimuli is critical for an animal's survival, reorienting to

irrelevant stimuli may interfere with ongoing task performance. Therefore, during effortful cognitive engagement (e.g., encoding novel information into working memory) it may be advantageous to impose an attentional filter that restricts TPJ activation, protecting the ongoing focus of attention from distraction (Shulman et al., 2003, 2007; Todd et al., 2005).

In line with the idea that TPJ deactivation may be necessary at times, previous work has shown that TPJ is deactivated when cognitive demands are imposed (e.g. WM or difficult perceptual search) and the dorsal attention system is engaged (Shulman et al., 2003; Todd et al., 2005). Shulman and colleagues (2003) showed that TPJ was deactivated in a rapid-visual search paradigm (RSVP) prior to target onset when subjects monitored a stream of letters for a target digit, and that the mean magnitude of deactivation was greater on trials in which the subsequent target was detected than on trials in which it was missed (Shulman et al., 2007). They postulated that the magnitude of TPJ deactivation reflected the degree of "filtering" of irrelevant information, which ensured that attentional resources were directed towards task-relevant candidate targets (Shulman et al., 2007). Related results have been reported in the context of working memory (WM) tasks. Todd and colleagues (2005) demonstrated TPJ suppression during delayed WM and that the magnitude of TPJ suppression increased at higher WM loads, leading them to postulate TPJ suppression as a mechanism for protecting the contents of WM.

Because TPJ is responsive to information potentially relevant to the task, it may be particularly important to suppress TPJ activity during WM encoding, when re-orienting might interfere with establishing a novel memory trace. However, previous work on TPJ suppression during WM has not explicitly examined whether the amount of suppression, especially during WM trace formation, is related to behavioral performance, similar to the relationship between suppression and performance that has been observed during rapid visual search (Shulman et al., 2007).

While TPJ is deactivated during certain phases of a task, a well-defined system of regions known as the default mode network (DMN) is deactivated under a broader range of conditions (Buckner et al., 2005; Mazoyer et al., 2001; McKiernan et al., 2003; Raichle et al., 2001; Ralchle and Snyder, 2007; Shulman et al., 1997) and shows highly correlated activity in the resting state (Fox et al., 2005; Greicius et al., 2003). Importantly, unlike TPJ, the DMN is not activated by behaviorally relevant stimuli and functional connectivity studies indicate that TPJ *is not* correlated with the DMN in the resting state (Fox et al., 2005). Because the relationship between TPJ and task-negative/default regions is uncertain, we investigated the degree to which TPJ and DMN regions showed similar properties during WM performance. To our knowledge, only one study has investigated the relationship between the DMN and WM performance (Hampson et al., 2006). However, this study examined across-subject variability in performance as a function of connectivity strength in only *two* default network nodes and did not test whether DMN deactivation is predictive of WM performance within subjects.

Additionally, while TPJ and DMN regions are not functionally coupled in the resting state (Fox et al., 2005), their activity may be correlated during active WM function. One interesting possibility is that the relationship between TPJ and DMN regions changes as different cognitive demands emerge. Therefore, we explored the relationship between TPJ and the DMN during the encoding and maintenance phases of a WM task.

In summary, the current study addressed three main goals: (1) to examine whether the degree of TPJ deactivation during encoding is predictive of subsequent WM performance; (2) to examine whether there are other regions in which suppression during encoding predicts subsequent WM performance and whether these regions overlap with the DMN; and (3) to characterize the relationship between TPJ and the DMN across different phases of WM.

Materials and methods

Subjects

21 neurologically intact right-handed, healthy adults (8 male and 13 female, mean age = 24.95) were recruited from the Washington University community by the Psychology Department subject coordinator. All subjects completed and signed an informed consent approved by the Washington University Institutional Review Board and were paid $25 an hour for their participation.

Materials

Subjects performed a Sternberg-type delayed WM task, which was modeled after the task employed by Dolcos and colleagues (Dolcos et al., 2008; Dolcos and McCarthy, 2006; Sternberg, 1969) (see Fig. 1). The task contained two levels of working memory load (2 or 3 complex geometric shapes) and one of three potential distracter types presented during the maintenance period of the WM task: (1) a task-related geometric shape, which was expected to maximally engage TPJ (Serences et al., 2005); (2) a visually complex neutral image; and (3) an emotional image which was highly distracting and salient, but not task-related. A portion of the trials did not contain distraction (total of 30 blank trials randomized across the experiment, 15 at each WM load), but these trials were not the focus of the current study. Trial types were presented randomly to ensure that subjects had no ability to predict the nature of upcoming distraction and could not resort to a consistent filtering strategy for any of the distracter types. Lastly, we opted for a single instead of multiple distracters to examine whether previously published effects generalize when even less distraction is present.

The memory sets and task-related distracters consisted of complex geometric shapes (Attneave and Arnoult, 1956), which were generated using a Matlab algorithm (Collin and McMullen, 2002).
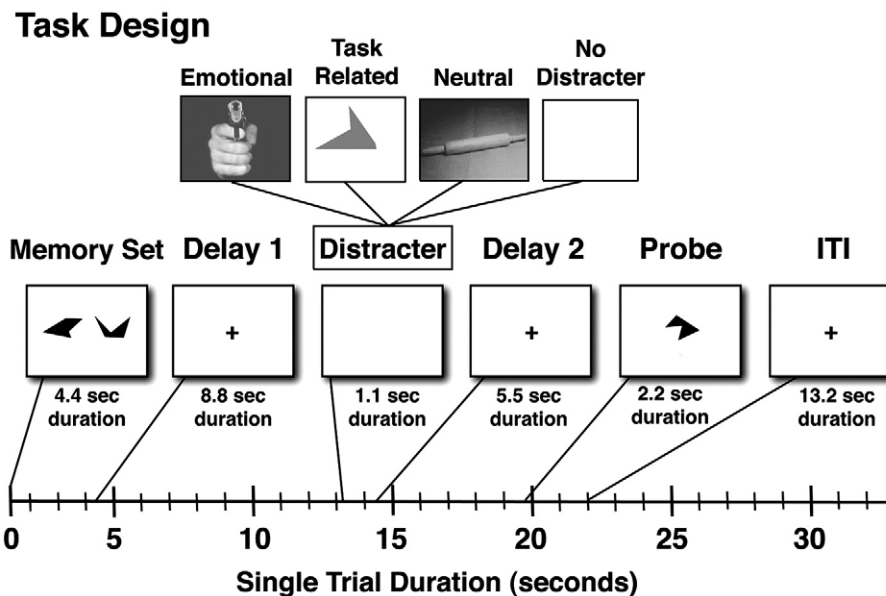

Fig. 1. Task design. A schematic representation of a single trial is shown along with different components and their onsets marked along the timeline. Each box represents a trial component with the duration marked bellow. First, subjects were presented with a set of complex geometric shapes, which they were instructed to memorize, followed by a delay. Next, during the middle phase of the trial subjects saw either: (1) an emotional distracter; (2) a task-related geometric shape distracter of a different color distinguishing it from the probe; (3) a neutral distracter; or (4) no distraction. This was followed by another delay. Finally, subjects were shown a probe for which they indicated using a button response if it was part of the memorized set or not.