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The default network and processing of personally relevant information: Converging evidence from task-related modulations and functional connectivity

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ABSTRACT

Despite a growing interest in the default network (DN), its composition and function are not fully known. Here we examined whether the DN, as a whole, is specifically active during a task involving judgments about the self, or whether this engagement extends to judgments about a close other. We also aimed to provide converging evidence of DN involvement from across-task functional connectivity, and resting-state functional connectivity analyses, to provide a more comprehensive delineation of this network. Using functional MRI we measured brain activity in young adults during tasks and rest, and utilized a multivariate method to assess task-related changes as well as functional connectivity. An overlapping set of regions showed increased activity for judgments about the self, and about a close other, and strong functional connectivity with the posterior cingulate, a critical node of the DN. These areas included ventromedial prefrontal cortex, posterior parietal cortex, and medial temporal regions, all thought to be part of the DN. Several additional regions, such as the left inferior frontal gyrus and bilateral caudate, also showed the same pattern of activity and connectivity. These results provide evidence that the default network, as an integrated whole, supports internally oriented cognition involving information that is personally relevant, but not limited specifically to the self. They also suggest that the DN may be somewhat more extensive than currently thought.

1. Introduction

The default network (DN) is a topic of much research in recent years (Buckner, Andrews-Hanna, & Schacter, 2008; Greicius, Krasnow, Reiss, & Menon, 2003; Gusnard, Akbudak, Shulman, & Raichle, 2001; Raichle et al., 2001; Shulman et al., 1997). This network of brain areas is active when one is engaged in internally-driven thought and decreases when there is a switch into a condition in which an external task-based focus is required (Gusnard et al., 2001; Raichle et al., 2001; Shulman et al., 1997). Despite growing literature, the composition of the network (which brain areas participate in it) and its functional connectivity (how these areas interact) are still not fully known. Currently, a set of regions has been reported in several studies (Buckner et al., 2008; Fox et al., 2005; Toro, Fox, & Paus, 2008) that is generally considered to represent the nodes of the DN: these are the superior frontal cortex, medial prefrontal cortex (including ventromedial prefrontal cortex (VMPFC) and more dorsal regions), inferior temporal cortex, lateral parietal cortex, posterior cingulate/retrosplenial cortex, and the hippocampal formation. Some studies (e.g., Fransson & Marrelec, 2008; Grady et al., 2010; Greicius et al., 2003; Greicius, Supekar, Menon, & Dougherty, 2009) have shown evidence of functional connectivity (FC) among these putative DN regions, mostly concentrating on major nodes, such as the posterior cingulate cortex (PCC). The DN may reflect a fundamental organizational property of the brain, as it develops early in childhood (Fair et al., 2008; Fransson et al., 2007), is preserved during sleep and anesthesia (Boly et al., 2008), and can be identified in chimpanzees (Rilling et al., 2007). In addition, some progress has been made in outlining DN structure through white matter tractography (Greicius et al., 2009), and default mode activity has been successfully simulated using information on structural connections from the non-human primate literature (Ghosh, Rho, McIntosh, Kotter, & Jirsa, 2008). Thus, despite some discrepancy in the reported nodes of the network, there is growing evidence that the DN consists of a group of anatomically and functionally connected regions that together may subserve a fundamental cognitive state.

Exactly what this cognitive state might be is still unclear. However, current evidence (Buckner & Carroll, 2007; Buckner et al., 2008; Gusnard et al., 2001; Johnson et al., 2002; Mason et al.,

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2007; Uddin, Iacoboni, Lange, & Keenan, 2007; Weissman, Roberts, Visscher, & Woldorff, 2006) indicates a role for self-referential processing, which can be engaged during a variety of cognitive tasks, including autobiographical memory retrieval, thinking about the future, and judgments about how well descriptions, such as "honest", apply to one's self. Studies exploring the neuronal correlates of the self (Fossati et al., 2003; Gusnard et al., 2001; Johnson et al., 2002; Kelley et al., 2002; Northoff & Bermpohl, 2004; Uddin et al., 2007) indicate that at least some areas currently believed to be part of the DN, primarily medial prefrontal cortex, exhibit increased activity during tasks requiring self-referential processing. These studies suggest that the DN supports internally generated processes that depend on, or are related to, representations of the self. However there are no studies to date showing that the DN, as an integrated whole, supports self-referential processing specifically.

The goal of our study was to address this question of whether the DN is involved in self referential processing, and to do this by both activating and deactivating the network during tasks, and by assessing its functional connectivity during these tasks and during rest. Most studies have attempted to derive the DN either through analyses of the resting state or task-related modulations (Buckner et al., 2008; Damoiseaux et al., 2006; Fox et al., 2005; Greicius et al., 2003; Mason et al., 2007; McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003; Raichle et al., 2001; Shulman et al., 1997; Toro et al., 2008), but not both. We aimed to provide a more comprehensive assessment of the role of the DN in self related processing and also of the composition of the DN by combining, within one study, activating and deactivating conditions, in addition to rest. One previous study (Harrison et al., 2008) used a similar approach, but utilized quite different and complex tasks for activating and deactivating the DN. We sought to constrain the processing engaged by our participants by requiring them to carry out a relatively simple self-reference task, i.e., judging whether trait descriptors characterized themselves. In addition, some have suggested that making decisions about a close other is thought to involve self-related cognitive processing (Ames, Jenkins, Banaji, & Mitchell, 2008; Buckner & Carroll, 2007; Kelley et al., 2002) and is reported by some to activate the same brain regions that are active for self-reference, including some DN regions (Ames et al., 2008; Ochsner et al., 2005). However, making judgments about another person, even if someone close to you, undoubtedly involves other processes in addition to any thoughts about the self that might occur. So examining the utilization of the DN in both self and other judgments could be a way of determining if this network supports self-reference specifically, or a wider range of personally relevant information. Therefore, we also included a task involving judgments about a close other, to assess whether the DN is engaged to a greater degree in processing information about the self, which would suggest a role in self reference *per se*, or equally engaged for self and close other, which would indicate a broader role.

For comparison to the internal tasks, we used two externally-driven tasks that would be expected to reduce activity in the DN (a sensorimotor control task and a vowel detection task). For these tasks we also used trait descriptors to ensure similar input and output characteristics, varying only the specific task demands. Our analysis also differed in an important way from previous studies because we opted not to specify *a priori* the brain areas that make up the DN, as other studies have done (e.g., Harrison et al., 2008). Rather than restricting the analysis to only a pre-selected set of regions, we used an approach that examined activity across the entire brain, so that a common set of regions across task and rest conditions could be identified, in an attempt to be inclusive rather than exclusive. We were then able to compare this set of regions to those of the putative DN in the literature. Data from a separate resting-state run also were obtained. The analysis consisted of contrasting task to baseline, as well as FC analyses of both task and resting state runs, to provide converging evidence regarding the areas involved in the DN. Moreover, we used a multivariate analysis combined with resampling statistics, an approach more sensitive and statistically powerful than the conventional univariate GLM approach to identifying task-related activations or deactivations (Fletcher et al., 1996; Lukic, Wernick, & Strother, 2002; McIntosh & Lobaugh, 2004; Nichols & Holmes, 2002). We expected to find a set of brain regions, consistent with the putative DN, to exhibit the highest level of activity during the self-relevant condition, less activity during the other condition and resting baseline, and the lowest activity during the external conditions. In addition, using a commonly accepted node of the DN, the posterior cingulate as a seed, we expected to find strong functional connectivity among DN regions across the task conditions, as well as during the resting-state run. This would provide converging evidence that the set of brain regions active when individuals perform relatively simple tasks that require them to process information relevant to themselves is the same set of regions that are functionally interconnected and known as the DN. In addition, the overlap of regions with task modulations, functional connectivity during the tasks and functional connectivity at rest would contribute to our knowledge of the composition of the DN.

2. Methods

2.1. Participants

Twenty healthy right-handed subjects (age M = 23.7 years, SD = 3; 10 males) participated in this study after providing informed consent. The ethics committee of Baycrest Centre approved this experiment.

2.2. Tasks

The eight task-runs were composed of 17 blocks of 20 s each, alternating between task and a resting baseline. Each task block contained five trials of the same task type. Trials included a fixation screen shown for 1 s, followed by a task screen shown for 3 s. The task screen included a personality-trait word, a cue word (representing the task) and two response options. In the pre-scan briefing, we instructed subjects that rapid responses are not required, but to respond within the 3-s time frame. We selected 320 personality-trait words from a widely-used source (Anderson, 1968). Word order within the session was randomized, and no word was repeated.

We used four task types: self-reference, other-reference, vowel identification, and motor. In the Self task (cue: "You?") subjects needed to decide whether the word represents them or not, in the Other task ("Other?") subjects needed to decide whether the word represents a person they know well, and in the Vowel task ("Vowel?") subjects needed to identify whether the third letter from the end of the word was a vowel. The possible answers for these three tasks were "yes" or "no". In the Motor task ("Button:") subjects needed to press button 1 or 2, depending on a number shown on the screen. The responses, and the timing, were recorded.

2.3. Image acquisition and preprocessing

We used a Siemens Trio 3T scanner. Anatomical scans were acquired with a 3D MP-RAGE sequence (TR = 2 s, TE = 2.63 ms, FOV = 25.6 cm^2, 256 × 256 matrix, 160 slices of 1 mm thickness). Functional runs were acquired with an EPI sequence (170 volumes, TR = 2 s, TE = 30 ms, flip angle = 70°, FOV = 20 cm^2, 64 × 64 matrix, 30 slices of 5 mm thickness, no gap). Pulse and respiration were measured during scanning.

The scanning session included a high-resolution structural scan, followed by 10 functional runs, each lasting 5:40 min. The first and last runs were resting-state runs, where subjects were instructed to lie still with their eyes closed, relax, and clear their minds, but to not avoid any thoughts that may spontaneously arise. Following scanning, subjects were asked if they fell asleep during the resting runs.

Preprocessing was performed with AFNI (Cox, 1996) and consisted of physiological motion correction (Glover, Li, & Ress, 2000), slice-timing correction for the resting run, rigid-body motion correction, concatenation of the 8 task runs, spatial normalization to the MNI template (TT_avg152T1, resampling our data to 2 mm × 2 mm × 2 mm), and smoothing (full-width half-maximum, 6 mm).

2.4. Data analysis

Image analysis was performed with partial least squares, or PLS (McIntosh & Lobaugh, 2004; McIntosh, Bookstein, Haxby, & Grady, 1996), a multivariate analysis approach that robustly identifies spatiotemporal patterns related to varying tasks (task-PLS) or correlated to neuronal activity (seed-PLS). Because the decomposition of the data matrix is done in a single analytic step, no correction for multiple