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A dual-subsystem model of the brain's default network: Self-referential processing, memory retrieval processes, and autobiographical memory retrieval

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ABSTRACT

Most internally oriented mental activities are known to strongly activate the default network, which includes remembering the past, future thinking and social cognition, and are heavily self-referential, and demanding of memory retrieval processes. Based on these observations and building on related findings from the literature, the present article proposed a simple, dual-subsystem model of the default network. The ability of the model to estimate brain activity during autobiographical memory (AM) retrieval and related reference conditions was then tested by performing a quantitative meta-analysis of relevant literature. The model divided the default network into two subsystems. The first, called the 'cortical midline subsystem (CMS)', was comprised of the anteromedial prefrontal cortex and posterior cingulate cortex, and primarily mediates self-referential processing. The other, termed the 'parieto-temporal subsystem (PTS)', included the inferior parietal lobule, medial temporal lobe and lateral temporal cortex, and mainly supports memory retrieval processes. The meta-analysis of AM retrieval contrasts yielded a double dissociation that was consistent with this model. First, CMS regions associated more with an AM > laboratory-based memory (LM) contrast than with an AM > rest contrast, confirming that these regions play more critical roles in self-referential processing than memory retrieval processes. Second, all three PTS regions showed a greater association with an AM > rest contrast than with an AM > LM contrast, confirming that their role in memory retrieval processes is greater than in self-referential processing. Although the present model is limited in scope, both in terms of anatomical and functional specifications, it integrates diverse processes such as self-referential processing, episodic and semantic memory and subsystem interface, and provides useful heuristics that can guide further research on fractionation of the default network.

Introduction

Purpose of the study

The default network is a current topic of great interest in neuroscience and related disciplines (Buckner et al., 2008; Raichle, 2010). Originally, researchers defined the default network as the set of regions showing greater activity during the passive resting state than during attention-demanding cognitive tasks (Raichle et al., 2001). The association of this network with internally oriented mental activities including past remembering (Kim, 2010; Svoboda et al., 2006), future thinking (Addis et al., 2007; Spreng et al., 2009), social cognition (Mar, 2011; Schilbach et al., 2008), mental imagery (Hassabis et al., 2007), and mind wandering (Christoff et al., 2009; Mason et al., 2007) is now firmly established. Furthermore, the network activity has a high predictive value for observing performance errors during externally oriented cognitive tasks including perception (Boly et al., 2007), selective attention (Weissman et al., 2006) and memory encoding (Kim, 2011). A current challenge in the field is to unravel the network's organizational architecture and delineate differential contributions of the componential regions to the overall internally directed mental experience.

Most internal mental activities known to strongly activate the default network draw heavily on self-referential processing and require memory retrieval processes. Based on these observations and related findings in the literature, a simple, dual-subsystem model of the default network is proposed in the present article. A quantitative meta-analysis of relevant literature was performed to test the ability of the model to estimate brain activity during autobiographical memory (AM) retrieval and related reference conditions. The intention for proposing this simple default network model was not to account for all, or even most, of the related findings in the literature. Rather, this study had the more modest aim of addressing a few of the most representative findings such as those confirmed in recent meta-analyses of self-referential processing (Northoff et al., 2006; Northoff et al., 2011;

Abbreviations: AG, angular gyrus; ALE, activation likelihood estimation; AM, autobiographical memory; AmPFC, anteromedial prefrontal cortex; CMS, cortical midline subsystem; HF, hippocampal formation; IPL, inferior parietal lobule; LM, laboratory-based memory; LTC, lateral temporal cortex; MTL, medial temporal lobe; NM, nonmemory; PCC, posterior cingulate cortex; PTS, parieto-temporal subsystem; SM, semantic memory; TPJ, temporo-parietal junction.

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Qin and Northoff, 2011; van der Meer et al., 2010), AM retrieval (McDermott et al., 2009; Spreng et al., 2009; Svoboda et al., 2006), laboratory-based memory (LM) retrieval (Ciaramelli et al., 2008; Hutchinson et al., 2009; Kim, 2010; Kim, in press; Skinner and Fernandes, 2007; Spaniol et al., 2009; Vilberg and Rugg, 2008), semantic memory (Binder et al., 2009) and other functions (Decety and Lamm, 2007; Kim, 2011; Mar, 2011; Schilbach et al., 2008). This approach provided an initial, tentative model which helps address the current paucity of an explicit model for the anatomical/functional default network fractionation. Below, the dual-subsystem model and its rationale are first described, and then the implications of the model relative to AM retrieval and related reference conditions are discussed.

A dual-subsystem model of the default network

All neuroimaging approaches for identifying the default network including task-induced deactivation (Shulman et al., 1997), resting state functional connectivity (Greicius et al., 2003) and anticorrelations between networks (Fox et al., 2005), similarly converge on a consistent set of five regions that include the anteromedial prefrontal cortex (amPFC), posterior cingulate cortex (PCC), inferior parietal lobule (IPL), medial temporal lobe (MTL) including the hippocampal formation (HF), and lateral temporal cortex (LTC). Although each of these regions may be further subdivided (e.g., the IPL into the temporo-parietal junction [TPJ] and the angular gyrus [AG]), these five “core” regions are the focus of the present study/model. The model divides the default network into two subsystems. The first, referred to here as the ‘cortical midline subsystem (CMS)’, is comprised of the amPFC and PCC, and may primarily mediate self-referential processing. The second, referred to here as the ‘parieto-temporal subsystem (PTS)’, includes the IPL, MTL and LTC, and may primarily contribute to memory retrieval processes.

A recent study (Andrews-Hanna et al., 2010b) has proposed a more refined, tripartite model of the default network in which the network is subdivided into 11 componential regions. However, given that the default network is still an evolving construct that requires further validation, in terms of both anatomy and function, a simpler model may have distinct advantages. It is worth noting that complex interactions are likely to exist alongside information flows among the network's componential processes. Thus, any simple anatomical/functional fractionation of the default network, including the present one, should be viewed as a heuristic tool that can further guide research efforts rather than as establishing a strict categorization.

The CMS likely plays critical roles in self-referential processing, which involves stimuli or information that is personally significant or relevant to the self (Northoff et al., 2006). Studies have indicated that the amPFC and PCC are among the regions that are most consistently activated across a range of contrasts when comparing high versus low self-referential tasks such as trait judgments of the self versus trait judgments of others (Kelley et al., 2002), recollection of self- versus non-self-specific events (Summerfield et al., 2009), personal versus non-personal thinking (Abraham et al., 2008), and taking first- versus third-person perspectives (Vogeley et al., 2004). Recent meta-analyses of self-referential processing (Northoff et al., 2006; Qin and Northoff, 2011; van der Meer et al., 2010) has also confirmed the importance of the CMS regions in self-referential processing, but these studies have also tended to indicate more consistent involvement of the amPFC than PCC regions. Furthermore, the two CMS regions share particularly extensive and reciprocal connections with one another, as observed by both structural (Greicius et al., 2009) and functional connectivity studies (Buckner et al., 2009), leading to the notion that they constitute a “core” system of the default network (Andrews-Hanna et al., 2010b). Finally, neuropsychological studies have revealed that lesions in the amPFC are associated with prominent deficiencies in self-control, spontaneity and initiative (Devinsky et al., 1995), indicating the critical role of this region in self-representation. The effects of PCC lesions on self-related processing remain unclear due, in part, to the clinical rarity of this type of lesion (Vann et al., 2009). However, a study of ‘reversible’ functional lesions induced by repetitive transcranial magnetic stimulation (rTMS) highlighted the critical involvement of the PCC in self-referential processing (Lou et al., 2004).

The PTS likely contributes to memory retrieval processes which may encompass both episodic and semantic memory retrieval. Extensive evidence both from lesion (Squire et al., 2004) and neuroimaging studies (Diana et al., 2007) indicated that the MTL and, in particular, the HF are the key structures associated with episodic memory retrieval. Although not traditionally considered to play an important role in episodic memory, the IPL is among the regions that show the most consistent level of activation in neuroimaging studies for both AM and LM retrieval (Kim, in press; Svoboda et al., 2006; Wagner et al., 2005). The consistent engagement of this region is thought to reflect bottom–up attentional processes captured by the retrieval output (the attention-to-memory model [AtoM]; Cabeza et al., 2008; Ciaramelli et al., 2008), or the maintenance or representation of retrieved information (the episodic buffer hypothesis; Vilberg and Rugg, 2008). Recent neuropsychological studies also demonstrated subtle memory deficits associated with the parietal regions such as impaired free, but not cued, recall of AM (Berryhill et al., 2007), a syndrome aptly termed “memory neglect” (Cabeza, 2008). Moreover, functional connectivity analyses (Vincent et al., 2006) showed strongly correlated activity between the HF and several parietal regions, suggesting the existence of a hippocampal–parietal memory network. The left IPL is also likely to have an association with verbal semantic processing as various language and semantic impairments may result from the development of AG lesions (Ardila et al., 2000).

The critical roles of the LTC in semantic memory retrieval have been supported by studies of conditions associated with lesions in this area, such as semantic dementia following temporal atrophy, as well as by neuroimaging data (for a review, see Patterson et al., 2007). Many theorists (Conway and Pleydell-Pearce, 2000) have underscored the fact that most “everyday” remembering (e.g., AM retrieval) represents “an integration of episodic and semantic contents” (Cabeza and St Jacques, 2007). Moreover, Binder et al. (2009) has argued that semantic memory retrieval is a logical prerequisite for episodic memory retrieval in the sense that to recall “I watched a movie last Sunday” necessarily entails retrieval of the concepts “watch”, “movie” and “Sunday”. Thus, episodic and semantic retrieval may co-vary in most remembering and thinking contexts. These considerations suggest that a hippocampal–parietal memory network may also interact closely with the LTC regions. In fact, an aforementioned connectivity analysis (Vincent et al., 2006) also indicated significant correlated activity between the HF and LTC regions.

In summary, the model presented in this paper divided the default network into two subsystems: one that included the amPFC and PCC, and mediates self-referential processing, and the other which involves the IPL, MTL and LTC, and supports memory retrieval processes. This model is partially a restatement of predominant view of the roles of cortical regions such as the association of the amPFC with self-referential processing and the contribution of the MTL to episodic memory retrieval. However, the model proposed by this report synthesizes these predominant views with more tentative ones within the context of the default network, and establishes a new hypothesis based on anatomical/functional fractionation. The relevance of this model with respect to findings from the literature, especially the results of recent meta-analyses, will be further discussed after data from the current meta-analysis are presented.

AM retrieval and related reference tasks

AM retrieval is a prototypical example of cognitive tasks that strongly demand both self-referential processing and memory