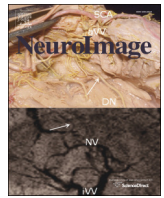




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Q1 Default mode network connectivity during task execution

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ABSTRACT

Initially described as task-induced deactivations during goal-directed paradigms of high attentional load, the unresolved functionality of default mode regions has long been assumed to interfere with task performance. However, recent evidence suggests a potential default mode network involvement in fulfilling cognitive demands. We tested this hypothesis in a finger opposition paradigm with task and fixation periods which we compared with an independent resting state scan using functional magnetic resonance imaging and a comprehensive analysis pipeline including activation, functional connectivity, behavioural and graph theoretical assessments. The results indicate task specific changes in the default mode network topography. Behaviourally, we show that increased connectivity of the posterior cingulate cortex with the left superior frontal gyrus predicts faster reaction times. Moreover, interactive and dynamic reconfiguration of the default mode network regions' functional connections illustrates their involvement with the task at hand with higher-level global parallel processing power, yet preserved small-world architecture in comparison with rest. These findings demonstrate that the default mode network does not disengage during this paradigm, but instead may be involved in task relevant processing.

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34 Introduction

35 Extensive neuroimaging research has identified a set of brain regions
36 that displays relative deactivation during goal-driven, attention demanding
37 paradigms (Binder et al., 1999; Mazoyer et al., 2001; Shulman et al., 1997).
38 Despite the difficulty in assigning functional significance to these observations,
39 the detected activity in the posterior cingulate, medial prefrontal cortices and
40 bilateral angular gyri has been attributed to a “default mode of brain function”
41 (Raichle et al., 2001), prominent in the absence of any external task demands
42 (Gusnard and Raichle, 2001; Gusnard et al., 2001).

44 Initial findings reported on the activity/inactivity of default mode
45 regions during cognitive paradigms were later complemented by functional
46 connectivity analyses of task-free functional magnetic resonance imaging
47 (fMRI) data. Acquired during no-task conditions, resting state fMRI has
48 provided remarkable insight into the human brain organization by revealing
49 synchronous oscillations of distant brain regions that form distinct large-scale
50 brain networks (Biswal et al., 1995). Using this technique, Greicius and colleagues
51 advanced our understanding of the default mode brain by showing not only that
52 the same set of regions,

53 which deactivate during cognitive tasks, form an intrinsic default mode
54 network (DMN) at rest (Greicius et al., 2003), but also that this network
55 is mirrored by direct structural connections (Greicius et al., 2009). Further
56 exploration of both rest and task-based fMRI data revealed interactions
57 between DMN and other large-scale brain networks. A prevailing anti-correlation
58 was reported between DMN and dorsal attention networks (Fox et al., 2005)
59 at rest, and DMN coupling with the frontoparietal control network has been
60 observed during task execution (Spreng et al., 2010). Moreover, the quantification
61 of such neural communication through network level graph theoretical analyses
62 also provided robust support for the economical organization of the brain into
63 biologically relevant complex architecture (Achard et al., 2006; Buckner et al.,
64 2009; Bullmore and Sporns, 2012; Fransson and Marrelec, 2008; Hagmann et al.,
65 2008) with a central role attributed to the DMN (van den Heuvel and Sporns,
66 2011).

68 The volume of research demonstrating the existence of the DMN
69 mechanistically is now substantial; nonetheless, explanations for its exact
70 contribution to brain function remain scarce. A meta-analytic comparison of
71 DMN to task-based activation maps (Smith et al., 2009) reported substantial
72 overlap with tasks that encompassed theory of mind, social cognition, episodic
73 recall and imagined scenes (Laird et al., 2011). Furthermore, many task-free
74 studies have all revealed alterations in this network's properties in different
75 patient populations such as Alzheimer's disease (Buckner et al., 2009) and
76 traumatic brain injury (Sharp et al., 2011), following pharmacological
77 interventions such as propofol (Stamatakis et al., 2010), and with normal
78 ageing (Damoiseaux et al., 2008). Overall, existing evidence advocates for a
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fundamental, possibly adaptive role that spans a variety of cognitive domains (Hasson et al., 2009; Schacter et al., 2012).

Although not extensively investigated, some recent studies concur with this view by revealing changes in DMN topography during task conditions and alluding to a possible involvement in cognitive processing. Specifically, differential changes in DMN functional connectivity and network properties have been demonstrated in tasks such as working memory, auditory oddball, and autobiographical planning (Arbabshirani et al., 2013; Fransson and Marrelec, 2008; Harrison et al., 2008; Newton et al., 2011; Spreng et al., 2013). Furthermore, there have been claims for a positive relationship between DMN connectivity and performance during a working memory task (Hampson et al., 2006). These studies, which may appear disparate at first sight, display one important commonality: the persistence of DMN functional connectivity during task execution, with some connectivity attenuation during paradigms of high mental load (Fransson, 2006). Given this evidence for DMN reconfiguration and its interaction with other large-scale brain networks during tasks, we would expect DMN to persist and exchange information with task related networks in a variety of experimental paradigms with a comprehensive role that implies direct contribution to cognitive processing.

We discuss here our initial approach to testing this hypothesis during a task of relatively low cognitive demand, in which participants followed visual cues to execute purposeful movement (finger opposition). Our specific questions pertained to the possible task-induced alterations in the DMN topography with potential behavioural significance, and interaction with the task related somatomotor network (SMN). We aimed to identify mechanisms of DMN engagement or disengagement during task and fixation conditions as well as rest by investigating them with activation, functional connectivity, behavioural correlation and graph theoretical analyses. In comparison with traditional subtractive activation/deactivation approaches, such multifaceted analysis could further quantify DMN engagement during task execution. In line with these objectives, our findings provide evidence on the nature and extent of DMN involvement in task execution and may advance our understanding of its contribution to brain function.

Materials and methods

Participants

The study was approved by the local ethics committee and all participants gave informed consent following the presentation of a study specific information sheet. The exclusion criteria comprised of a score below 70 on the National Adult Reading Test (NART) and 23 on the Mini Mental State Exam (MMSE), any history of drug or alcohol abuse, psychiatric and neurological disorders, head injury, medication use affecting cognitive performance (e.g. tricyclic antidepressants), physical handicap hindering the completion of the study, left-handedness, contraindication to MRI scanning and severe claustrophobia. Complying with these conditions, 22 healthy participants were recruited (19–57 years old, mean = 35.0, SD = 11.2, 9/13 female to male ratio) with average scores of 117.1 (SD = 5.76) on NART and 29.33 (SD = 0.85) on MMSE.

Behavioural assessment

The participants were assessed with an extensive set of neuropsychological tests using the Cambridge Neuropsychological Test Automated Battery (CANTABeclipse). In the simple reaction time test the participants were instructed to press a button in response to the visual presentation of a white box stimulus over a black background. Our measure of choice, the mean simple reaction time denoted the speed of motor response, in which shorter latency implied faster processing.

Paradigm specifications

In addition to the 5 min resting state scanning (eyes closed), a self-paced, right-handed finger opposition paradigm was employed in a boxcar design with 5 alternating cycles of task and fixation blocks. A visual “move” command indicated for participants to initiate and repeat the movement, while “rest” signalled the fixation state. The participants were instructed to touch the remaining fingers with their right thumb moving sequentially from the index to little finger, and to continue the cycle for the duration of the task period. Since we did not have access to the scanner compatible equipment to assess speed of finger opposition during task performance, we instead related latencies obtained from the CANTAB simple reaction time task to functional connectivity strengths.

Image acquisition and preprocessing

The MRI data was obtained using a Siemens Trio 3 T scanner at the Wolfson Brain Imaging Centre, Cambridge. The imaging session started with a high resolution T1-weighted, magnetization-prepared 180 degrees radio-frequency pulses and rapid gradient-echo (MPRAGE) structural scan (TR = 2300 ms; TE = 2.98 ms; TA = 9.14 min; flip angle = 9°; field of view (FOV) read = 256 mm; voxel size = 1.0 × 1.0 × 1.0 mm, slices per slab = 176), followed by whole-brain echo planar imaging (EPI) for the resting state scanning and the finger opposition paradigm (TR = 2000 ms; TE = 30 ms; flip angle = 78°; FOV read = 192 mm; voxel size = 3.0 × 3.0 × 3.0 mm; volumes = 160; slices per volume = 32). The preprocessing and image analysis were all performed using the Statistical Parametric Mapping (SPM) Version 8.0 (<http://www.fil.ion.ucl.ac.uk/spm/>) and MATLAB Version 12a platforms (<http://www.mathworks.co.uk/products/matlab/>). All imaging data were preprocessed following a standard pipeline of slice-time and motion correction, normalization to the Montreal Neurological Institute (MNI) space in combination with the segmented high-resolution grey matter structural image and an a priori grey matter template, and smoothing with an 8 mm FWHM Gaussian kernel.

Task-induced activation analysis

This analysis was carried out in order to validate the task and to derive a set of regions of interest (ROIs) to be used for subsequent functional connectivity analyses. For each subject, the functional images acquired during the task were entered into a first level general linear model with the fixation and task onsets modelled as regressors convolved with a canonical HRF. Further, the data was temporally filtered with a high pass filter (cut-off of 128 s) and no global normalization was performed. A one-sample t-test examined group level effects for the contrast of *task > fixation*. The resulting statistical maps were conservatively corrected for multiple comparisons at the voxel level using family wise error (FWE), alpha = 0.05, and the local peaks were assessed for further use as ROIs in the functional connectivity analyses.

ROI definitions

Depending on their source of identification (anatomical atlas, task or resting state scanning), the definitions of ROIs can have substantial influence on the subsequent functional connectivity and graph theoretical analyses (Smith et al., 2011). Task-based definition is a method shown to reproduce valid network topologies (Dosenbach et al., 2007; Power et al., 2011; Spreng et al., 2013). The employed finger opposition task provided us with 14 somatomotor ROIs, selected according to the local peaks in the *task > fixation* contrast of the activation analysis (voxel level multiple comparison correction, FWE $p < 0.05$). Sixteen seeds defining the DMN were chosen from the current literature (Andrews-Hanna et al., 2010). The MNI coordinates and the corresponding

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