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Comparing brain activations associated with working memory and fluid intelligence

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A B S T R A C T

Working memory (WM) and fluid intelligence (Gf) are thought to be highly related, though psychometrically distinct cognitive constructs. Both are important in a wide range of cognitively demanding tasks, and predictive of success in educational, occupational, and social domains. From a cognitive perspective, WM and Gf may share a capacity constraint due to the shared demand for attentional resources. Neuroimaging investigations of these two cognitive constructs have suggested similar shared frontal and parietal areas of neural activation as well, though to our knowledge the two have not been investigated in the same population. Here, we examine group level functional activations for tasks of WM (dual n-back), Gf (Raven's Standard Progressive Matrices; RSPM), as well as a theoretically unrelated comparison task of visual word/pseudoword decoding (lexical decision task) in a large sample of healthy young adults (N = 63) aged 18–40. Consistent with previous research, results indicate large areas of fronto-parietal activation in response to increasing task demands for the n-back task (dorsolateral, ventrolateral, and rostral prefrontal cortex, premotor cortex, and posterior parietal cortex), which largely subsume similar but more circumscribed regions of activation for the RSPM and lexical decision tasks. These results are discussed in terms of a task-general central network which may underlie performance of WM, Gf, and word decoding tasks alike, and perhaps even goal-directed behaviour more generally.

1. Introduction

Working memory (WM), or the ability to maintain and manipulate task-relevant information over short periods of time, is a core cognitive ability in humans. Though WM shares much in common with the concept of 'short term memory' (i.e. cognitive architecture, capacity limitation, and functional neuroanatomy), it is the prospective use of information in the service of some goal or objective which distinguishes the two, and has largely motivated the use of the descriptor "working" (Eriksson, Vogel, Lansner, Bergström, & Nyberg, 2015; Linden, 2007). In this sense, WM is highly utilized in a wide variety of challenging tasks both in the laboratory and in everyday life, and is in fact highly related to general intellectual and reasoning abilities, or 'fluid intelligence'. In the theory of Cattell (1963), fluid intelligence (denoted Gf) is the ability to adapt one's reasoning abilities to solve novel cognitive problems involving new information, and stands in contrast to 'crystallized intelligence' (denoted Gc) which draws heavily upon previously learned declarative information acquired from education or previous experience (Carpenter, Just, & Shell, 1990; Carroll, 1996; McGrew, 2009).

Fluid intelligence and WM are highly related psychological constructs, and are often described as being 'almost' isomorphic. Studies investigating the specific strength of the relationship between WM and Gf have noted moderate correlations with coefficients in the 0.3 to 0.9 range (see Burgess, Gray, Conway, & Braver, 2011; Colom, Rebollo, Palacios, Juan-Espinosa, & Kyllonen, 2004), and Martínez et al. (2011) reported that WM and Gf could not in fact be distinguished at the latent variable level. Thus, although WM is defined much more narrowly than Gf, research over the past several decades has identified it as a core psychological process responsible for driving much of the observable variation in human cognitive abilities. Indeed, making recently experienced stimuli subsequently accessible for brief periods is an essential component of our ability to act outside the bounds of the immediate moment, and to coordinate complex goal-directed behaviours (Baddeley, 1992; Repovs & Baddeley, 2006). Given the relative necessity and ubiquity of WM processes in day-to-day cognitive functioning, previous research has indicated a surprisingly small capacity of the WM system (Chuderski, 2013). Luck and Vogel (1997) estimated the average capacity to be approximately four items, with most individuals demonstrating a capacity between two and six items (Cowan,

2001). Though small in absolute terms, these inter-individual differences in WM capacity appear to account for much of the variance observed in cognitively demanding tasks and situations, including reading comprehension, language abilities, mathematics, reasoning, problem solving, overall academic performance, and even 'fluid intelligence' more generally (Engle, Tuholski, Laughlin, & Conway, 1999; Eriksson et al., 2015).

A parallel approach to studying the psychometric association between WM and *Gf* is the investigation of the neural mechanisms associated with each, and their potential overlap in terms of observed patterns of activation in response to task-load (i.e. task difficulty/complexity). Shared components between tasks might represent capacity constraints in the domain of attention (see Halford, Cowan, & Andrews, 2007), or perhaps shared neural circuitry or cortical involvement between the two tasks (Buschkuehl, Hernandez-Garcia, Jaeggi, Bernard, & Jonides, 2014). Burgess et al. (2011) note that a better understanding of the core psychological and neural mechanisms involved in WM may help in developing better targets for intervention in training studies, and more accurate predictions about success or failure of such interventions. To this end, here we review literature examining typical activation patterns associated with two of the most commonly utilized tasks of WM and *Gf* in WM training studies: the dual n-back task, and Raven's Standard Progressive Matrices (RSPM) respectively. In addition, we examine functional activation patterns associated with a comparison task that is theoretically unrelated to the domains of WM or *Gf*, in order to assess the specificity of observed activations for tasks in those domains. For this purpose, we chose a word/pseudoword decoding task (lexical decision task; LDT) that, contrary to *Gf*, draws heavily upon previously learned information (i.e. crystallized intelligence; Carpenter et al., 1990; Carroll, 1996; McGrew, 2009).

1.1. Neural mechanisms associated with the n-back task

The n-back task has been widely utilized in recent years to study WM both in the context of its neural bases (Owen, McMillan, Laird, & Bullmore, 2005; Rottschy et al., 2012), as well as how training with the task may serve to improve WM (see von Bastian & Oberauer, 2013 for a review; though see also Redick & Lindsey, 2013). The n-back task requires participants to monitor consecutive presentation of visual and/or auditory stimuli, and respond via button-press when the current stimuli matches that presented 'n' trials ago, where *n* typically ranges from one to three. As *n* is increased, task difficulty rises sharply and places larger demands on a number of key processes involved in WM, including monitoring, updating, and manipulation of remembered information (Owen et al., 2005). We chose to utilize a dual n-back task in this study to most closely match the training tasks implemented in trials of working memory training (see Jaeggi, Buschkuehl, Jonides, & Perrig, 2008). While the dual n-back task is considerably more difficult due to the multiple modalities of task demands (i.e. visual and auditory), at least one investigation has shown it to be similarly effective compared to a single n-back training task (i.e. visual only) in terms of training gain and transfer to untrained domains (Jaeggi et al., 2010). However, transfer of training gains from working memory tasks to untrained domains (e.g. fluid intelligence) remains an unresolved and controversial issue in the literature (see Clark, Lawlor-Savage, & Goghari, 2017; Simons et al., 2016).

Owen et al. (2005) conducted a meta-analysis of 24 imaging studies utilizing the n-back task in healthy adult populations. Their analysis revealed five consistent areas of activation across task variants, falling exclusively within the frontal and parietal lobes. First, the bilateral dorsolateral prefrontal cortex (DLPFC) is thought to be involved in organizational control of WM, reducing overall cognitive load in WM tasks by selecting appropriate organizational chunks. Interestingly, neuropsychological data appears to support this claim, as patients with damaged frontal lobes appear to be impaired on only some WM tasks

(Owen, Morris, Sahakian, Polkey, & Robbins, 1996). Second, the bilateral mid-ventrolateral prefrontal cortex was implicated in n-back activity and is thought to be associated with explicit encoding and retrieval of information, as well as attentional processes. Third, the bilateral rostral prefrontal cortex is thought to combine or integrate multiple cognitive processes, specifically when the operation of a single cognitive process is insufficient to meet the particular demands of a task. Fourth, bilateral medial premotor cortex was implicated and is thought to be involved in maintenance of visuospatial attention during working memory tasks. Finally, bilateral medial posterior parietal cortex (including precuneus and inferior parietal lobule) was implicated in n-back activations and has previously been associated with mediating shifts in attention, retaining task-related temporal information, and preparing for a given task.

Similarly, Rottschy et al. (2012) undertook a broader neuroimaging meta-analytic approach to model the neural correlates of working memory by investigating several WM-related tasks (e.g. the Sternberg Task, the delayed matching to sample task, and the delayed simple matching task) as well as the n-back. They identified what they called a "core" WM network which included areas predominantly in the frontal and parietal regions across both hemispheres: dorsolateral prefrontal cortex, lateral prefrontal cortex, anterior insula, premotor cortex, pre-supplementary motor area, intraparietal sulcus, superior parietal lobule, and anterior parietal area. Rottschy et al. (2012) note that their results are quite similar to the earlier findings of Owen et al. (2005), despite including a wider variety of WM tasks in their meta-analysis and perhaps divergent naming practices of given stereotaxic spaces or neural structures. The consistency of these results across task and stimuli types strongly implicate the above areas as comprising a "core" WM network, perhaps forming the neural underpinnings of all WM cognitive processes.

Interestingly however, this core WM network closely resembles patterns of activation observed in a wide variety of tasks beyond WM, particularly when task demands increase. For example a similar, though right-dominant, network is associated with selective attention (see Shulman, D'Avossa, Tansy, & Corbetta, 2002; Shulman et al., 2009), and largely similar networks studied outside the realm of intelligence have been termed the attention and working memory system (Cabeza & Nyberg, 2000), the cognitive control network (Cole & Schneider, 2007), and the task-positive network (Fox et al., 2005). The involvement of these same cortical areas in such a diversity of tasks suggest an even more fundamental role in cognition, and coordinating behaviour beyond WM. Indeed, the frontoparietal network implicated in WM processes has also been discussed in terms of an executive control network, a dorsal attention network (Yeo et al., 2011), a core executive (discussed in Rottschy et al., 2012), and a multiple demand network (Duncan, 2010) which may mediate goal-directed behaviour by rapidly organizing mental focus and separation of successive task steps. In this sense, the cortical areas involved in successful navigation of WM tasks, or what Duncan (2010) calls 'multiple-demand cortex', may be essential to keeping the mind focused on the task-relevant information at hand without regard to its cognitive modality (e.g. perceptual, mnemonic, motor-related), thus playing a central role in virtually all non-routine cognitive functions. Recall that this matches the traditional description of fluid intelligence quite well – i.e. the ability to adapt one's reasoning abilities to solve novel cognitive problems involving new information (Carpenter et al., 1990; Carroll, 1996; McGrew, 2009).

1.2. Neural mechanisms associated with Raven's progressive matrices

Raven's Progressive Matrices (RPM; Raven, 1975; Raven, Raven, & Court, 1994) scores are highly correlated with a wide range of other tests of intelligence, and is regarded as the most general single test of non-verbal (i.e. fluid) intelligence (Alderton & Larson, 1990; Carpenter et al., 1990). The task presents participants with a series of

complex designs or grids of visual puzzle elements with a single piece missing, and requires that they choose the correct missing piece from several alternatives. Both the standard set of puzzles (Raven's Standard Progressive Matrices; RSPM; Raven, 1976) and the more difficult set (Raven's Advanced Progressive Matrices; RAPM; Raven et al., 1994) require participants to infer and integrate rules, manage goal hierarchies, as well as form abstractions on the basis of novel non-verbal information. While Raven's Advanced Progressive Matrices are often utilized as pre- versus post-training measures of *Gf*, here we chose to use the easier Standard progressive matrices in order to 1) shorten administration time in the scanner; and 2) reduce overall variability in reaction time.

RPM-type tasks have not received as much attention as the n-back task in terms of neuroimaging studies, however early investigations have revealed activity in frontoparietal regions. Prabhakaran, Smith, Desmond, Glover, and Gabrieli (1997) found increasing activation of the prefrontal cortex with progressively more complex (and therefore more difficult) RPM problems. Consistent with this, Duncan and Owen (2000) found increased DLPFC perfusion (assessed via positron emission tomography; PET) in response to performing a variety of *Gf* tasks, including RPM-type tasks. Two subsequent studies obtained similar results, and additionally found engagement of increasingly anterior areas of the prefrontal cortex with increased task difficulty (Christoff et al., 2001; Kroger et al., 2002). Selective activation of the DLPFC and posterior parietal cortex in these studies is thought to reflect the verbal working memory and visuospatial processes utilized during the reasoning process. Similarly, activation of the rostrolateral prefrontal cortex is variously thought to support the more executive processes of working memory during reasoning, or the manipulation of self-generated information to support abstraction, or perhaps the integration of information from longer-term memory with the demands of the current task (reviewed in Krawczyk, 2012). More recent studies have further implicated additional brain areas in non-verbal reasoning in RPM tasks including the basal ganglia (Melrose, Poulin, & Stern, 2007), and the cerebellum (Kalbfleisch, Meter, & Zeffiro, 2006). Most recently, Shokri-Kojori, Motes, Rypma, and Krawczyk (2012) demonstrated increasing involvement of prefrontal cortex, as well as occipital and parietal cortices as task complexity increased from one to three relations in an RPM-type visuospatial reasoning task.

Two studies have investigated neural activation differences for RPM in high- and low-ability healthy adult samples. Perfetti et al. (2009) found that high-ability participants responded to increasing task complexity with commensurate increases in activation in frontal and parietal areas, whereas low-ability participants showed decreased activation in the same areas. Further, low-ability participants demonstrated greater activity overall in response to less difficult problems, particularly in medial and lateral frontal areas. The authors suggest that these patterns reflect the discrepancy in mental effort required between the groups, and indicate considerable differences in problem solving strategies, executive control, and/or modulation of attention as task demands increase. Lee et al. (2006) found similar results in comparing high- and low-ability participants, though noted relatively stronger differences in posterior parietal cortex.

1.3. Neural mechanisms associated with the lexical decision task

By including a task clearly outside the domain of WM or *Gf* (i.e. semantic knowledge, or vocabulary, or 'crystalized intelligence'), we can gain a better understanding of the degree to which tasks of WM and/or *Gf* exclusively activate whichever regions they are found to. The lexical decision task presents participants with four letters, and requires that they decide as quickly as possible whether these letters constitute a 'real' word in English, or merely a pronounceable pseudoword. Though not the specific cognitive domain or neural activation pattern of interest, this task was included here as a comparison to speak to the specificity of potential overlapping neural activations for the WM and

Gf tasks. Unfortunately however, little is known about neural activation patterns associated with the lexical decision task when contrasting different levels of task difficulty in blocked designs. The vast majority of fMRI-based neuroimaging studies on the lexical decision task have utilized event related designs, and investigated real word versus pseudoword contrasts (Taylor, Rastle, & Davis, 2013). Haut, Lim, and Macdonald (2010) did contrast easier and harder blocks of this task, though only reported on null findings for cortical areas of change following cognitive intervention in a sample of participants with schizophrenia. In this sense, our findings for patterns of functional neural activation in response to task load for the lexical decision task are novel, though will still serve the purpose of speaking to the specificity of findings for the two central tasks of interest (i.e. dual n-back, and RSPM).

The strong behavioural, neuroanatomical and psychometric associations between general intelligence, WM, and *Gf* suggest similar functional networks for these constructs (Barbey, Colom, Paul, & Grafman, 2014; Barbey et al., 2012; Glascher et al., 2010; Gray, Chabris, & Braver, 2003). However, relatively few studies have worked to directly and accurately characterize the similarities and differences between the networks responsible for WM and *Gf* which support critical cognitive skills such as adaptive behaviour and novel problem solving. Given this background, the central goal of the present investigation is to clarify the nature of the neural networks that support WM versus *Gf* processes in human cognition. To this end, we studied a relatively large sample of 63 healthy adult participants in an fMRI design. Importantly, by utilizing in-scanner tasks that have become ubiquitous in the working memory training literature (i.e. dual n-back task, and RPM), our results are uniquely positioned to comment on the potential overlap in functional activation for WM training (i.e. dual n-back) tasks and potential transfer to tasks of *Gf* (i.e. RPM).

2. Method

2.1. Participants and recruitment

Healthy adults (N = 63) aged 18 to 40 years were recruited from the community through online advertisements and physical postings directing them to an online eligibility screener. Exclusion criteria included: 1) left-handedness; 2) history of traumatic brain injury or other neurological condition causing sensory or motor impairment; 3) presence of self-reported mental illness; 4) less than normal or corrected-to-normal visual acuity; and 5) MRI contra-indications. Recruitment was shared with that of larger investigation of online working memory training, thereby necessitating the additional exclusion criteria of: 6) insufficient access to a computer and high-speed internet; and 7) recent or previous use of the n-back training task or other online cognitive training paradigms. Participants provided online consent and completed online surveys of demographic, behavioural, and health information also used to confirm eligibility. Participants were compensated $20 per cognitive testing session, and $20 per MRI session. Written consent was obtained from all participants, and ethics approval was obtained from the University of Calgary's Conjoint Health Research Ethics Board (CHREB).

2.2. Procedure and materials

Following initial recruitment and eligibility screening, participants underwent MRI scanning. MRI sessions consisted of structural scans for anatomical registration, and functional scans of the dual n-back task, Raven's Standard Progressive Matrices, as well as a lexical decision task. Participants were introduced to these tasks before the MRI session, and were asked to practice with them until they indicated full comprehension of task instructions and requirements. These practice trials included immediate feedback for responses, whereas the trials in the scanner did not. In the scanner, participants viewed stimuli on a screen

suspended behind their heads in the magnet bore via a mirror attached to the head coil. Participants were additionally fitted with headphones for presentation of audio stimuli, and utilized a scanner-compatible two-button response box placed in their right hand in order to indicate their responses to task trials with their index and/or middle fingers. All stimuli were presented electronically using E-Prime software (Psychology Software Tools, 2012). MRI sessions typically ranged from 60 to 75 min in duration. The three tasks described below were completed in a random order for each participant. Some of the 63 participants described here went on to complete working memory training, or processing speed training (active control condition), described elsewhere (Clark et al., 2017). However, all scores and measures reported here were completed at baseline, and are therefore not impacted by subsequent cognitive training.

2.2.1. Dual n-back functional imaging task

Jaeggi et al.' (2008) description of the dual n-back training task was followed as closely as possible, though modified for use in the scanner. For each trial in a block-design, participants viewed a blue square presented at one of eight locations around the periphery of a 3 × 3 grid with a fixation cross at centre, and simultaneously listened to an auditorily presented letter (D, F, H, J, M, Q, R, or X). Visual stimuli were presented for 500 milliseconds (ms), followed by 2500 ms of fixation which also served as the window within which participants could indicate their responses for that trial. Participants indicated a visual match to n trials previous via button-press with their index finger, auditory match to n trials previous via button-press with their middle finger, and combined visual and auditory match via button-press with both fingers. No response was required on trials not containing a match. Participants underwent four blocks each of 1-back, 2-back, and 3-back conditions, where each block included 20 + n trials. Visual stimuli location, and letter presentation were randomized within each block, though each bock was structured to contain four visual matches, four auditory matches, and two combined visual plus auditory matches. Each block was preceded by 5 s of instructions, and separated from subsequent blocks by 15 s of fixation in order to allow the hemodynamic response to return to baseline. Block order was fixed for all participants: 1-back, 2-back, 3-back repeated four times, split into two separate scan runs lasting 8:51 each, for a total task time of 17 min, 42 s.

2.2.2. Raven's progressive matrices functional imaging task

Raven's standard set of matrix problems (Raven, 1976) were modified for use in the scanner such that participants could respond using the same scanner-compatible two-button response box utilized for the n-back task. This was achieved within a block-design by first presenting participants with each matrix problem for 5000 ms, after which one of the multiple answer options was highlighted with a superimposed red box. Participants were then required to indicate whether this highlighted answer was correct via button press with their index finger, or incorrect with their middle finger. The matrix problem and highlighted answer option remained on the screen for 8000 ms, and trials were separated by 1000 ms of fixation cross at the centre of the screen. The highlighted answer was the correct answer for exactly half of the trials, and the increased difficulty of 'good wrong answers' (i.e. those that closely resemble the actual correct answer) was controlled by ensuring an equal number in each block. The total set of 60 matrix problems that comprise Raven's Standard Progressive Matrices was split into two sets (for pre- versus post-training comparisons as part of the larger working memory training study), and further divided into three levels of difficulty: Easy, Medium, and Hard – yielding six sets of 10 problems each. Participants completed one block of each difficulty level in a randomized order, in a single scanner run. Trials within blocks were also randomized. Task instructions were displayed for 5 s before the first block, and each block was preceded by 15 s of fixation in order to allow the hemodynamic response to return to baseline. Total task time was

8 min.

2.2.3. Lexical decision functional imaging task

For this block-design task, participants viewed sequences of four letters, and were asked to indicate whether they composed a real word in English via button-press; index finger for 'yes', middle finger for 'no'. Four-letter combinations were generated ahead of time using The English Lexicon Project database (Balota et al., 2007), which classifies words and non-words along several empirically derived dimensions, including accuracy of lexical decision (i.e. word versus non-word). For example, 'blue' and 'jume' have perfect accuracy ratings in the database, indicating that they are relatively easy to distinguish as a word and non-word respectively. In contrast, 'faze' and 'thew' have considerably lower accuracy ratings reflecting their nature as harder series' of letters to lexically classify. Participants completed three blocks each of Easy and Hard four-letter combinations, in a single scanner run. Blocks consisted of 30 trials each in which half were real words and half were non-words. Block order was randomized, as were items within each block. Task instructions were displayed for 5 s before the first block, and each block was preceded by 15 s of fixation in order to allow the hemodynamic response to return to baseline. Total task time was 10 min, 45 s.

2.3. MRI data acquisition

Whole-brain images were collected for all participants on a 3T General Electric Discovery MR750 system using an 8-channel head coil at the Seaman Family Magnetic Resonance Research Centre at the University of Calgary. Functional echo planar imaging (EPI) data were acquired in an interleaved bottom-up slice order with 40, 3.4 mm thick slices, echo time (TE) = 30 ms, repetition time (TR) = 2500 ms, flip angle = 77°, field of view (FOV) = 22, and matrix = 64 × 64. A total of 424 volumes were collected for the n-back task, 192 volumes for Raven's Progressive Matrices, and 258 for the lexical decision task. T1-weighted 3D magnetization-prepared rapid gradient-echo (MP-RAGE) anatomical scans were also acquired for each participant to register the functional data (256, 1 mm slices, TE = 3.1 ms, TR = 7.4 ms, inversion time (TI) = 650 ms, FOV = 25.6, matrix = 256 × 256). Additionally, T2-weighted high resolution scans were collected as expanded functional images to aid in registering the functional images to standard space (40, 3.4 mm thick slices, TE = 120 ms, TR = 7500 ms, FOV = 22, and matrix = 256 × 256).

2.4. Data analysis

Functional MRI data was analysed with fMRI Expert Analysis Tool (FEAT) and other utilities from FMRIB Software Library (FSL; www.fmrib.ox.ac/fsl) version 5.0.9 for Linux. Preprocessing of functional and anatomical images included reorientation to standard orientation, removal of non-brain tissue, slice-timing correction (Smith, 2002), spatial smoothing (using a 7 mm FWHM kernel), grand-mean intensity normalization, and high-pass temporal filtering. Time-series statistical analyses were carried out using FMRIB's improved linear model (FILM) with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). Careful inspection of plots representing head movement revealed < 2 mm of translation for all participants, so motion correction parameters were not included in the preprocessing stage. Functional images were registered first to T2-weighted high resolution images, then to participants' structural images, and then to standard the MNI avg152 T1-weighted template with non-linear transformations with seven, seven and 12 degrees of freedom respectively using FSL's FMRIB Linear Image Registration Tool (FLIRT; Jenkinson & Smith, 2001; Jenkinson, Bannister, Brady, & Smith, 2002). Manual inspections were performed after each preprocessing step for each scan, and reanalyses were performed where necessary. Mean group activations for all harder > easier task condition contrasts were modeled for each task
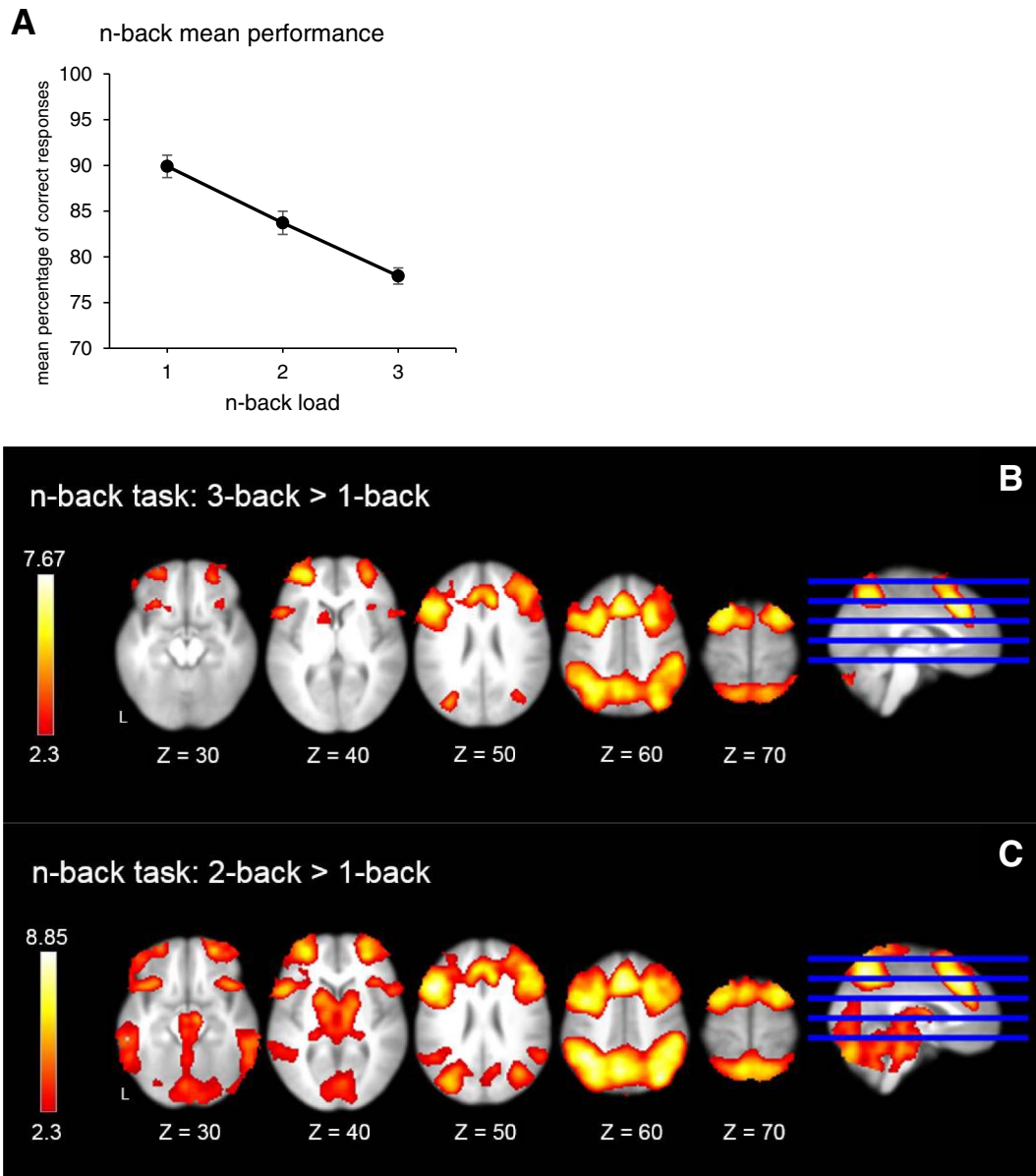
A

n-back mean performance

B

n-back task: 3-back > 1-back

C

n-back task: 2-back > 1-back

Fig. 1. Mean performance accuracy (A), and observed patterns of activation for the 3-back > 1-back contrast (B), and 2-back > 1-back contrast of the dual n-back task. Error bars represent 95% confidence intervals.

contrast using a Z threshold of 2.3 and a cluster threshold of 0.05 (Worsley, 2001). Two task scans were lost due to problems in data acquisition. Therefore, the group mean analyses were based on 62 participants for the Dual n-Back Task, 63 participants for RSPM, and 62 participants for the Lexical Decision Task.

Participant behavioural responses to task stimuli in the scanner were collected via E-Prime software, and exported to SPSS for analysis. Specifically, one-way within-subject ANOVAs were utilized to assess for significant differences in performance and reaction times across task difficulty levels for the n-back task and Raven's Standard Progressive Matrices (e.g. 1-back, 2-back, 3-back; Easy, Medium, Hard matrix problems). A dependent samples t-test was used to asses for analogous differences between the two difficulty levels of the Lexical Decision Task (Easy versus Hard).

To quantitatively assess the degree of overlap between observed activations for each pairwise combinations of cognitive tests Dice coefficients were computed. Specifically, activation maps for the 2-back > 1-back contrast of the dual n-back task, hard > medium and hard > easy contrasts of the Raven's progressive matrices task, and the

hard > easy contrast of the lexical decision task were binarized at the 2.3 cluster threshold, and resulting cluster volumes (i.e. number of voxels) were fed into the following formula:

$$s = \frac{2 \, |V_1 \cap V_2|}{|V_1| + |V_2|}$$

This method computes the number of shared 'activated' voxels between two sets of activation patterns, and divides it by the total number of activated voxels in both sets, which results in an easily interpretable number between 0 (no spatial similarity) and 1 (total spatial similarity) representing the overall spatial similarity between observed patterns of activation. Dice coefficients have been used previously for similar investigations of task activation overlap (see Barbey et al., 2014; Roman et al., 2014).

3. Results

3.1. Participant demographics and cognitive characteristics

The 63 participant sample was composed of 28 males and 35 females, with an average age of 30.91 (SD = 6.01), and an estimated average educational attainment of 15.44 (SD = 1.90) years. Cognitive testing revealed intelligence quotients (IQ) ranging from 69 to 143 with an average of 109.95 (SD = 14.93) based on scores from eight split-half WAIS-IV subtests.

3.2. In-scanner behavioural data

As expected, increasing task difficulty resulted in fewer correct responses from participants across all tasks: n-back, [F(2, 124) = 231.76, p < 0.001]; RSPM, [F(2, 124) = 38.93, p < 0.001]; Lexical Decision Task, t(62) = 7.54, p < 0.001. Follow-up pairwise analyses using the Bonferroni correction revealed that correct responses for each of the three difficulty levels of the n-back task were in fact significantly different from each other: 1-back, 143.83 ± 1.96 total correct responses (of a possible 160); 2-back, 133.95 ± 2.03; 3-back, 124.65 ± 1.42. However, follow-up pairwise analyses for the RSPM task revealed significant differences in participant performance only between the easiest level of difficulty and the harder two. On average, participants answered 9.21 ± 0.29 (of a possible 10) easy matrix problems correctly, versus only 7.68 ± 0.28 medium questions (p < 0.001 compared to easy), and 7.91 ± 0.29 hard questions (p < 0.001 compared to easy). Performance on medium and hard matrix problems was statistically indistinguishable (p = 0.60). Increasing task difficulty also increased reaction times for both the RSPM task [F(2, 124) = 63.55, p < 0.001], and the Lexical Decision Task t(63) = − 15.45, p < 0.001. Interestingly, follow-up pairwise analyses of reaction times, again using the Bonferroni correction for the RSPM task revealed statistically different reaction times for each of the three levels of difficulty (p < 0.001 for each pairwise comparison). Reaction time was not considered for the n-back task, as on exactly half of all trials, the correct response was to not press a button. Mean in-scanner task performance and reaction times are displayed graphically in panel A of Figs. 1–3.

3.3. Whole brain fMRI analyses

3.3.1. Dual n-back task, by level of difficulty
3.3.1.1. 3-Back > 1-back contrast. Mean group activation was observed when contrasting the hardest and easiest conditions of the task – specifically in the bilateral middle and superior frontal gyri, paracingulate gyri, frontal poles, frontal orbital cortex, insular cortex, precuneus, superior parietal lobule, supramarginal gyrus, angular gyrus, the left caudate, and areas of the right cerebellum. This suggests that the WM network discussed above is indeed activated by the present task, even at the hardest level of difficulty with relatively poor performance. See Fig. 1, panel B.

3.3.1.2. 3-Back > 2-back contrast. However, when comparing the more difficult 3-back condition to the 2-back condition, this WM-related network was not observed. Mean group activation was not observed to increase commensurate with the increase in task difficulty, revealing no significant areas of activation for this contrast.

3.3.1.3. 2-Back > 1-back contrast. Mean group activation was observed to increase in a wide variety of areas as a function of WM load (i.e. task difficulty) in comparing the 2-back and 1-back task conditions. These areas were consistent with the 'core WM network' discussed above, including large bilateral frontal and parietal regions, bilateral basal ganglia and thalamus, as well as more circumscribed regions of the temporal and occipital cortices, and cerebellum. See Fig. 1, panel C.

3.3.2. Raven's progressive matrices task, by level of difficulty
3.3.2.1. Hard > medium contrast. Mean group activation was observed to increase as a function of task difficulty in comparing the hardest and intermediate matrix problem sets. Specifically, in right frontal and left inferior temporal cortical areas. See Fig. 2, panel B.

3.3.2.2. Hard > easy contrast. Similar to the comparison of the hardest and intermediate matrix problems, comparison of the hardest versus easiest problems indicated increased activation in left lateral occipital cortex, left superior parietal lobule, and bilateral occipital poles. See Fig. 2, panel C.

3.3.2.3. Medium > easy contrast. Easy and Medium matrix problems were indistinguishable on the basis of their group level activations, suggesting that the two groupings may not have engaged significantly different cognitive processes.

3.3.3. Lexical decision task, by level of difficulty
3.3.3.1. Hard > easy contrast
Consistent with the n-back and RSPM tasks, mean group activations were observed to increase as a function of task difficulty for the lexical decision task. Activation increases occurred in a wide variety of regions including bilateral medial and lateral frontal lobes, insula, anterior cingulate, lateral occipital cortex, basal ganglia, cerebellum, and left superior parietal cortex. See Fig. 3, panel B. Detailed whole-brain activation results (e.g. number of voxels, as well as magnitude and co-ordinates of Z_{max}) is provided in Table S1 of the Supplementary information.

3.4. Activation overlap

Binarized maps of activation for the three tasks discussed above were rendered onto a 3-dimensional standard brain in MRIcroGL. Results are displayed in Fig. 4, and corresponding Dice coefficients are displayed in Table 1.

4. Discussion

Functional MRI of the tasks most typically utilized in the literature for WM training (i.e. dual n-back task), and as a gauge of transfer to *Gf* (i.e. RPM-type tasks) revealed considerable overlap in neural activation in response to increasing task demands. Similar areas of the frontal and parietal cortices were also activated by increasing task demands in our comparison lexical decision task which is not thought to implicate WM or *Gf* cognitive processes at all, but rather relies on previously learned declarative information, or crystallized intelligence. To our knowledge, the present study is the first to investigate neural activations associated with the dual n-back and RSPM tasks in a single population. Specifically, and consistent with previous literature, increasing *n* in the dual n-back task from one to two was associated with widespread activation increases in frontal and parietal cortices bilaterally, as well as basal ganglia, thalamus and cerebellum in our relatively large sample of healthy adults. Each of the frontal and parietal areas identified as part of the 'core WM network' by comprehensive meta-analyses of n-back tasks (Owen et al., 2005; Rottschy et al., 2012) were included in our very large activation cluster for this contrast, including: dorsolateral prefrontal cortex, lateral prefrontal cortex, anterior insula, premotor cortex, pre-supplementary motor area, intraparietal sulcus, superior parietal lobule, and anterior parietal area. Furthermore, present findings are consistent with the small number of studies which have investigated functional activation in response to simultaneous visual-spatial and/or auditory-verbal n-back task (i.e. *dual* n-back; Buschkuehl et al., 2014; Jaeggi et al., 2007; Thompson, Waskom, & Gabrieli, 2016; Yoo, Paralkar, & Panych, 2004). Interestingly however, increasing *n* from two to three was not associated with additional areas of activation despite the observed difference in performance accuracy between the
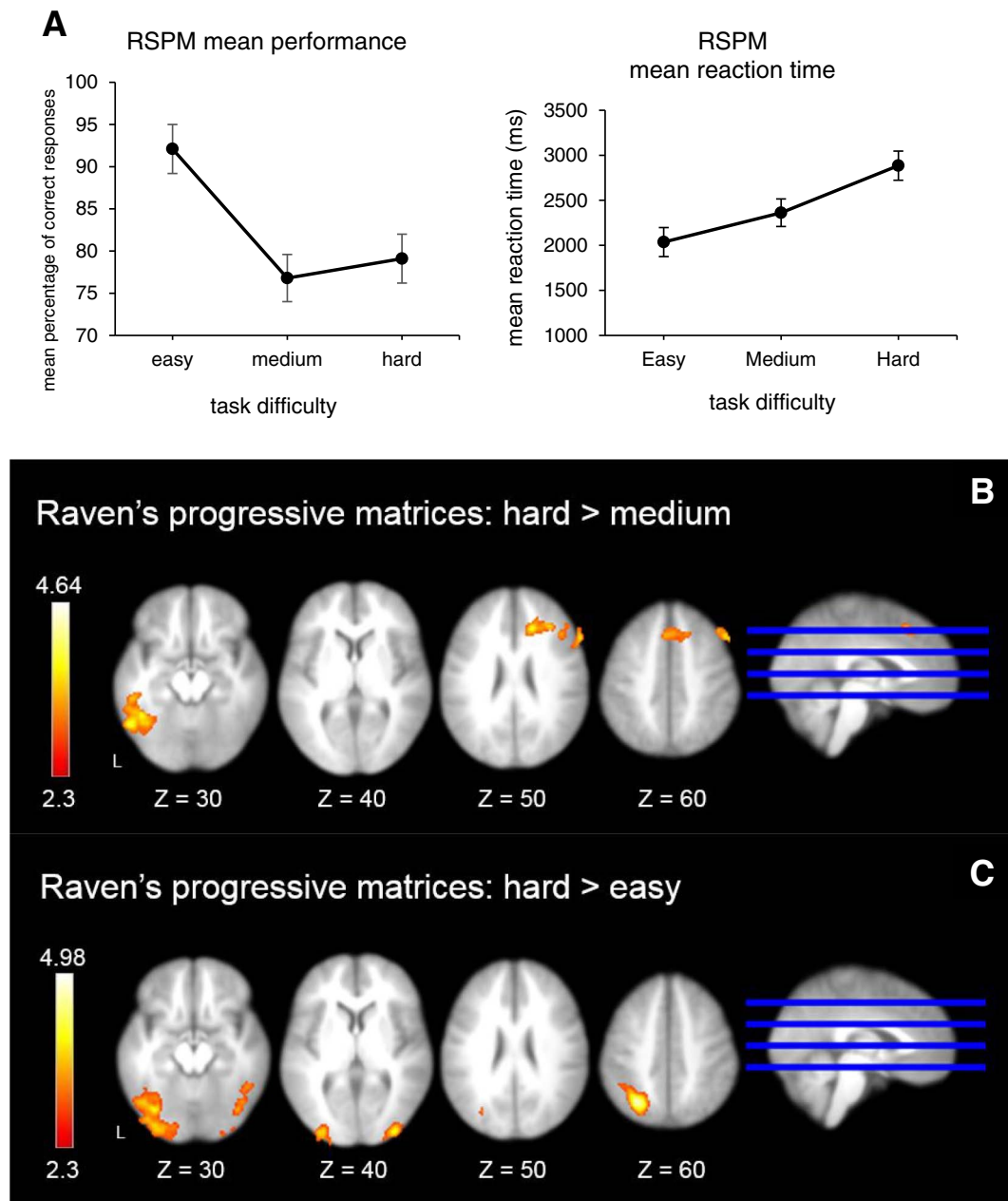
Fig. 2. Mean performance accuracy, reaction time (A), and observed patterns of activation for the hard > medium contrast (B), and hard > easy contrast of the Raven's progressive matrices task. Error bars represent 95% confidence intervals.

two conditions. This is perhaps not surprising because failing to accurately complete the 3-back condition due to WM capacity constraints is, in theory, quite similar to completing an easier version of the task. That is, above one's individual WM capacity threshold, all more difficult versions of the task may in fact evoke activation similar to that observed at that threshold. This is an empirical question that was not specifically tested in the current experimental design. Other studies have investigated n-back task conditions greater than $n = 3$ however. For example, Buschkuehl et al. (2014) included a 4-back auditory condition in their investigation, and Schweizer, Grahn, Hampshire, Mobbs, and Dalgleish (2013) included a 5-back condition in a modified emotionally-laden version of the n-back task. It should be noted here that the lack of significant activation observed for the group average contrast between the 3-back and 2-back conditions may obscure variability in ability and activation patterns for different individuals within the group. For example, Jaeggi et al. (2007) found that as n-back task demands grew, lower-ability participants demonstrated load

dependant increases in activation, whereas higher-ability participants evinced less activation while continuing to perform the task accurately.

From a cognitive perspective, failure to complete higher difficulty conditions of the n-back task may be accounted for by a failure of any of the involved component processes that the task is thought to require. For example, 3-back task requirements may 1) exceed participants' ability to store or update individual spatial location and auditory letter items or sequences in memory (i.e. primary memory); 2) exceed participants' ability to effectively search for target items that may be stored in memory (i.e. secondary memory); or 3) may exceed participants ability to effectively attend only to relevant task stimuli (i.e. attentional control; Unsworth, 2014). Based on estimates of average WM capacity between two and six items (Cowan, 2001; Luck & Vogel, 1997) it is plausible that any or all of the above constraints limit participant performance accuracy (and consistent functional activation) at the 3-back level of difficulty. Less difficult levels of the n-back task appear not to have exceeded participants' abilities in these cognitive subdomains of
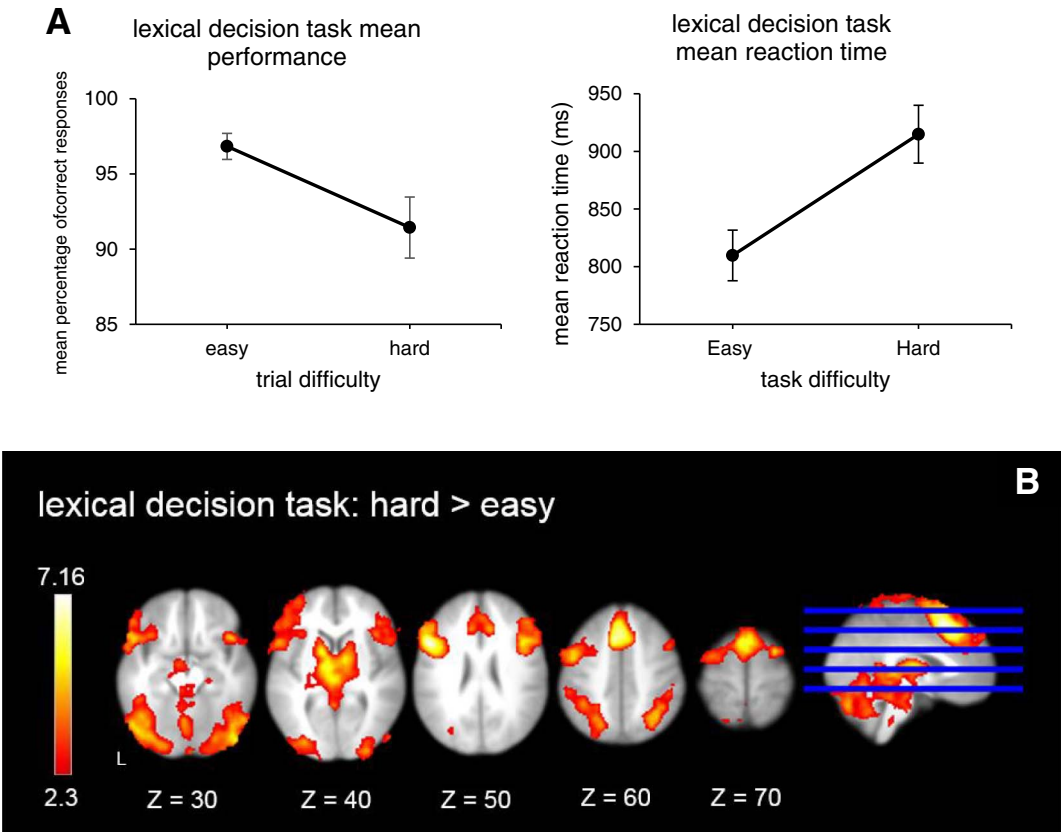
Fig. 3. Mean performance accuracy, reaction time (A), and observed patterns of activation for the hard > easy contrast (B) of the lexical decision task. Error bars represent 95% confidence intervals.

WM.

The present findings for n-back task activations are also consistent with several of the finer differences between WM task characteristics noted by Rottschy et al. (2012) in their meta-analytic review. For example current results are expectedly more similar to the bilateral WM load-dependent effects (i.e. more versus less difficult WM tasks) observed in ventral premotor cortex, lateral prefrontal cortex, inferior frontal gyri, supplementary motor area, and middle cingulate cortex, versus the primarily left-hemispheric set-related network (i.e. WM tasks vs. control tasks) observed in left rostral prefrontal cortex, superior
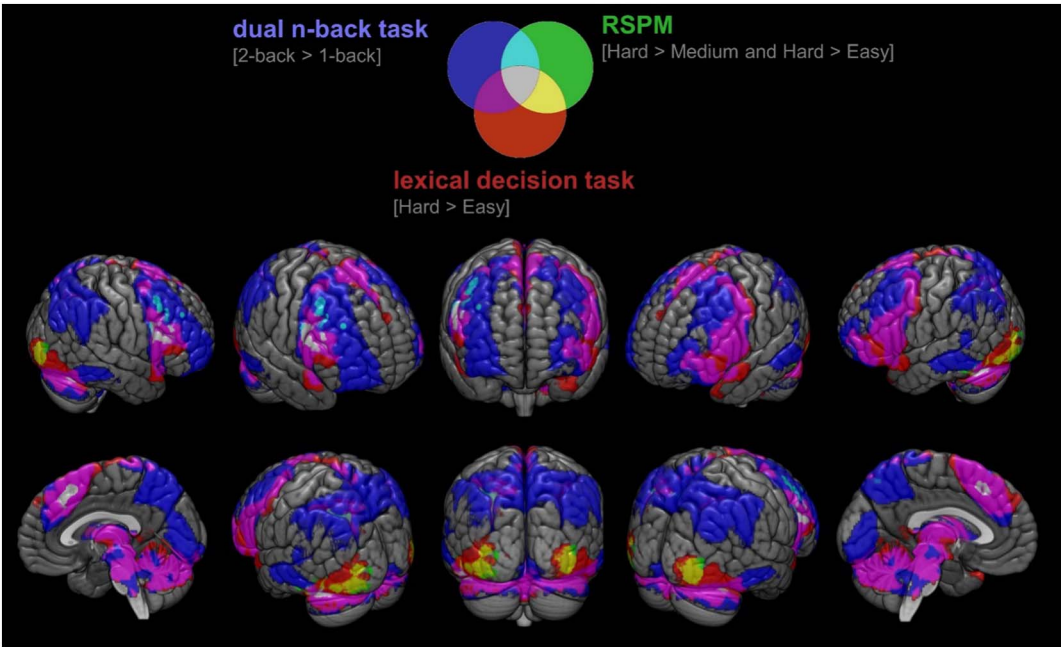

Fig. 4. Binarized activation maps for harder > easier contrasts of the dual n-back task (blue), Raven's Standard Progressive Matrices (RSPM; green), and the lexical decision task (red). Overlap in activation is displayed as per the provided colour legend. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Dice coefficients of spatial overlap for observed patterns of activation for harder > easier contrasts of the dual n-back task, Raven's Standard Progressive Matrices, and the lexical dcision task.

	Dual n-back task	RSPM	Lexical decision task
Dual n-back task	1.0	0.085	0.505
RSPM		1.0	0.205
Lexical decision task			1.0

Note. RSPM, Raven's Standard Progressive Matrices.

parietal lobule/intraparietal sulcus, postcentral sulcus, dorsal premotor cortex, and posterior superior frontal gyrus. Rottschy and colleagues also identified a stable WM "core" network that appeared to activate in response to a wide variety of WM task variants. This network consisted of bilateral dorsal area 44 and premotor cortex, anterior insula, pre-supplementary motor area, intraparietal sulcus, left inferior parietal cortex, and right lateral prefrontal cortex.

Also consistent with previous literature, analysis of the RSPM task revealed much smaller areas of increased frontal and parietal activation in response to increasing task difficulty. However as discussed above, the Medium and Hard levels of the task were behaviourally differentiated only by reaction time, not task performance. Regardless, the increase in difficulty from Medium to Hard revealed increased activation of the right lateral inferior and superior frontal gyri, and the left lateral inferior temporal gyrus. Contrasting the Hard and Easy conditions additionally revealed increased activation of the occipital poles bilaterally, and the left superior parietal lobule. The overall smaller area of activation observed for the RSPM task compared to the n-back task may have arisen from the less challenging nature of the task altogether, or perhaps from the more gradually graded levels of difficulty compared to the present implementation of the n-back task. For example, the difference between 1-back and 2-back conditions of the n-back task is likely much larger than that of the difference between easy and medium problem sets of RSPM, particularly for our well-educated, above average intelligence sample. Consequently, comparing more similar difficulty levels of the RSPM task may have resulted in 'cancelling out' areas of activation that would not have occurred if the problem set were split into two rather than three levels of difficulty (see below for further discussion).

Regardless of this potential difference, of particular interest here is the degree to which observed activation patterns for these tasks of WM and *Gf* converge, and where they do not. As can be seen in Fig. 4, the areas of activation observed for the RSPM task are largely subsumed by the much larger activation changes observed for the dual n-back task, with the exception of left lateral occipital cortex, and the left occipital poles. Interestingly however, this pattern matches that which might be predicted by the task differentiation analyses performed by Rottschy et al. (2012). For example, in comparing different types of WM task implementation, they found that matching of memorized items (versus verification or reproduction) in a WM task relied to a greater extent on right inferior frontal gyrus – a precise area implicated in the Hard > Medium task difficulty contrast for the present task, but not implicated in the larger 2-back > 1-back contrast, nor the 3-back > 2-back contrast for the n-back task. In this context, the current implementation of the RSPM task might be thought of as a primarily visuospatial, nonverbal, object location centered WM task (versus it's traditional conceptualization as a test of *Gf*; Alderton & Larson, 1990; Carpenter et al., 1990) that requires matching of memorized stimuli in order to produce the correct answer on a given trial. This is consistent with Martínez et al.' (2011) latent-variable approach to behavioural cognitive testing data indicating not only that short-term storage, WM, and WM updating are 'hardly distinguishable', but also that *Gf* itself is almost perfectly correlated with these cognitive abilities. This is perhaps not surprising upon closer inspection of RSPM task demands. In visually

searching through the problem set for any given item of the RSPM task, participants must populate a list of relations amongst all permutations of adjacent matrix items, temporarily hold those relations in memory, and subsequently search the multiple potential answers looking for a match for these relations to rule out incorrect answers and find the correct one. In this sense, patterns of neural activation for the dual n-back and RSPM tasks show good convergence with their high degree of overlap from a cognitive (Burgess et al., 2011) and psychometric perspective (Chuderski, 2013) despite typically being thought of as tasks representative of distinct cognitive domains (i.e. WM and *Gf*).

Another way to conceptualize this overlap in neural activation for these cognitively distinct, though related, tasks is to appreciate their shared reliance on key areas of the frontal and parietal cortices not dissimilar from what has been described as the core WM network (Owen et al., 2005; Rottschy et al., 2012), or any of the other monikers it has been given to highlight its importance in cognition more broadly: attention and working memory system (Cabeza & Nyberg, 2000), the cognitive control network (Cole & Schneider, 2007), the task-positive network (Fox et al., 2005), the executive control network, or the dorsal attention network (Yeo et al., 2011), multiple demand network (Duncan, 2010), or more simply, those areas outlined by Jung and Haier's (2007) P-FIT model of intelligence. Similar regions have also been implicated in executive functioning related measures of task switching (Wager, Jonides, & Reading, 2004), inhibition (Nee, Wager, & Jonides, 2007), as well as lower-level cognitive functions including motor tasks involving planning (Bortoletto & Cunnington, 2010), movement integration (Wolynski, Schott, Kanowski, & Hoffmann, 2009), and even orientation (Marangon, Jacobs, & Frey, 2011). Indeed, the centrality of these select areas of cortex to such a vast range of cognitive activity support the notion that this "executive committee" network (Baddeley, 1996) may play an even more fundamental role in all human cognitive processes outside the circumscribed domains of WM and *Gf*. This nearly-ubiquitously engaged fronto-parietal network has even been described as essential in keeping the mind focused on task-relevant and goal-directed information regardless of task-type (e.g. perceptual, mnemonic, or motor-related), and even as mediating the control of goal directed behaviour more generally (Rottschy et al., 2012). Rottschy and colleagues end their review on this important note regarding the centrality of the WM core network in all cognition: "We would hence conclude that the robustly engaged fronto-parietal core network, as demonstrated here for working memory, may sustain extremely basal processes or computations that are required for virtually all cognitive function, but whose exact nature remains to be further elucidated" (pp. 18). Thus, while from a behavioural perspective the dual n-back and RSPM tasks may appear completely different and representative of distinct domains of cognitive functioning, neuroimaging evidence presented here and elsewhere suggests that the brain may treat RSPM-type problems more parsimoniously as simply another type of WM/attention/executive control task.

Further evidence of the centrality of this core WM network in widespread areas of cognition is provided by our lexical decision task. While classifying letter strings into categories of words or non-words would not typically be considered a task of WM or certainly *Gf*, our analyses revealed activation in areas quite similar to those of the dual n-back task and RSPM when task demands increased, including: bilateral medial frontal cortex, insula, anterior cingulate, basal ganglia, as well as left superior parietal areas (see Fig. 2, panel B). Despite this apparent overlap in neural activation, decades of cognitive psychology would suggest that these tasks are in fact representative of very discrepant domains of psychological functioning (i.e. crystallized intelligence versus fluid intelligence; Gottfredson & Saklofske, 2009). Rather than to suggest that lexical decision making involves similar psychological processes to dual n-back or RSPM on the basis of this observed pattern of neural activation, a more likely explanation here is that all novel and difficult tasks robustly activate domain- and process-general areas of

the brain such as the WM core network. In fact, recent work by Fedorenko, Duncan, and Kanwisher (2013) has carefully identified a network which shows increased activation for hard > easy contrasts across a wide range of cognitively demanding tasks, including: precentral gyrus, anterior insula/frontal operculum, middle frontal gyrus, intraparietal sulcus, supplementary motor area, pre-supplementary motor area, anterior cingulate cortex, as well as posterior temporal and adjacent occipital regions. Interestingly, though perhaps not surprisingly, this primarily frontal and parietal network very closely resembles the core WM network, the network associated with Jung and Haier's (2007) P-FIT model of intelligence, and the regions evoked by harder > easier contrasts for all three tasks used in this study.

While a particular strength of the current study is the examination of both WM and *Gf* functional neuroimaging tasks within the same population, several weaknesses may arise from their specific implementation. First, the dual n-back task was implemented in an ordered sequence from easiest (i.e. 1-back) to most difficult task blocks (i.e. 3-back), rather than a randomized order. While randomizing task block difficulty may have caused confusion in our participants, not doing so may have caused some ordering effects, in which performance on latter difficulty levels was systematically influenced by earlier ones. Another limitation is the temporally imprecise nature of our block-design paradigm. For example, during the RSPM task, participants were given 8000 ms to decide whether the highlighted answer was correct. While some responses from participants did approach this timeframe, the average response time was in the range of 2000 ms to 3000 ms depending on the difficulty level. Thus, while the response window was required to be sufficiently long to account for all responses, current analyses potentially capture a large proportion of time unrelated to specific task completion. Much shorter response windows for the n-back and lexical decision tasks (2500 ms and 2000 ms respectively) mitigated this issue for these tasks. Our in-scanner RSPM task additionally failed to produce significantly different performance between difficulty levels for some metrics. For example, the medium and hard question sets were indistinguishable in terms of performance accuracy, and the easy and medium question sets were likewise indistinguishable in terms of neural activation patterns (despite statistical difference between all three levels of difficulty in terms of mean reaction time). These equivalencies suggest that splitting the original RSPM question set into two rather than three levels of difficulty may have made for more distinct comparisons between difficulty levels.

Finally, the imprecision of using group level averages to comment on specific task activations should be acknowledged here. Inter-subject variability in neuroanatomy or true functional activation in response to a given task may contribute to overestimating task activation when averaged together in traditional group analysis (discussed in Nieto-Castañón & Fedorenko, 2012). This is particularly concerning in this case because we are acutely interested in functional activation overlap across two potentially exaggerated mappings. However, Fedorenko et al. (2013) comprehensively tested multiple-demand cortex via single subject analyses and found similar activation patterns to those resulting from traditional group level analyses, which provides some support for the validity of the current results. It is also worth mentioning here that with respect to the n-back task, different strategies for completing the task (e.g. exclusively relying on verbal rehearsal of auditorily presented letters, or visuospatial rehearsal of visual location stimuli) may result in differential patterns of activation regardless of ability level at any of the observed levels of difficulty. In other words, the n-back task poses a large enough cognitive problem that participants may focus variously on specific sub-tasks which may be reflected in variability in activation patterns in response to the task that are obscured at the level of the group average. Our current analyses are not able to exclude this possibility.

These limitations aside, the current study adds to the present understanding of the neural bases of WM and *Gf* in several important ways, particularly in the context of potential clinical, educational or remedial applications such as WM training. First, the demonstrable overlap observed in dual n-back and RSPM tasks provides preliminary support for the neural basis of WM training, in that dual n-back and RSPM tasks do indeed activate similar areas of cortex associated with task-specific and goal-directed behaviour. Secondly however, the large functional activation overlap between the supposed training task and a wide variety of other cognitively demanding tasks (e.g. our comparison lexical decision task) presents a challenge to notion that overlapping activation alone is sufficient to account for any observed effects behavioural effects resulting from training. Future research can clarify the relationship between WM and *Gf* by investigating overlapping activations with a more diverse set of representative tasks in each domain, and with a more diverse participant or patient populations (e.g. elderly populations, brain injured patients, or persons with schizophrenia). With regard to the WM training and its feasibility on the basis of overlapping neural activations for training and transfer tasks, future research should seek to gain a refined understanding of the conditions under which overlapping task activations ought to have behaviourally transferrable effects, and when they ought not to.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.intell.2017.06.001.

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