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Individual differences in parietal and frontal cortex structure predict dissociable capacities for perception and cognitive control

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A R T I C L E I N F O

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A B S T R A C T

Capacity limits in perception can lead to failures of awareness in situations that overload capacity, resulting in various phenomena of 'inattentional blindness'. In contrast, capacity limits in cognitive control over attention by working memory lead to increased processing of irrelevant distractors (reduced inattentional blindness). Here, using Voxel-Based Morphometry combined with Principal Components Analysis, we establish distinct brain-structural correlates of perceptual capacity, dissociable from those of cognitive control. Perceptual capacity was measured as the principal component accounting for variance across tasks of multiple object tracking, change blindness and rapid visual enumeration (i.e. 'subitizing'). Cognitive control capacity was measured as the principal component underlying performance of three different complex working memory span tasks (involving spatial, semantic and numerical domains). Volumetric differences in the right Inferior Parietal Lobule (IPL) were predictive of individual differences in perceptual capacity, while volumetric differences in left Middle Frontal Gyrus (MFG) (as well as lateral frontal and posterior cingulate cortex in a non-parametric analysis) were predictive of individual differences in cognitive control capacity. IPL remained a significant predictor of perceptual capacity when controlling for variance accounted for by cognitive control capacity and vice versa for the neural correlates of cognitive control. These results suggest that perceptual and cognitive control capacities represent dissociable and lasting, trait-like attributes which can be predicted from distinct signatures in regional grey matter.

1. Introduction

A great deal of research over many years has demonstrated the limits on human perceptual processing capacity. Numerous demonstrations have accumulated to show that when people attend to tasks involving a high level of perceptual processing load this results in reduced neural response to unattended stimuli leading to various perceptual phenomena of "inattentional blindness" outside the focus of attention (e.g., Rees et al., 1997; Rees et al., 1999; see Lavie, 2005; Lavie et al., 2014 for reviews). These effects of perceptual load have been established across visual cortex, including category-selective regions (e.g. the response in parahippocampal place area to images of places; e.g. Yi et al., 2004; or V4 responses to images of everyday objects, Pinsk et al., 2004); extrastriate visual cortex (Rees et al., 1997; Schwartz et al., 2005) and primary visual cortex (e.g. Schwartz et al., 2005; Torralbo et al., 2016), and in subcortical regions including the superior colliculus (e.g. Rees et al., 1997), the LGN (O'Connor et al., 2002) and the amygdala (Bishop et al., 2007; Lim et al., 2008). Behavioural research has clearly established increased rates of inattentional blindness and reduced detection sensitivity for stimuli outside the focus of attention in tasks involving high (compared to low) perceptual load (Cartwright-Finch and Lavie, 2007; Macdonald and Lavie, 2008; Simons and Chabris, 1999). These findings have more recently been extended to demonstrate load induced inattentional deafness, reflected both in detection reports (e.g. Macdonald and Lavie, 2008; Raveh and Lavie, 2015) and cortical response to unattended stimuli; Molloy et al. (2015); Molloy et al., 2019).

Importantly, the diversity of perceptual load manipulations converging on the same pattern of results, suggests these reflect a generalised limit on perceptual capacity. In addition, the effects of perceptual load have been clearly dissociated from the effects of load on higher-level cognitive control resources, used for executive control over task performance, clarifying further that the effects demonstrate limits on perceptual capacity rather than a generalised cognitive capacity. For example, 'cognitive control load', involving increased demands on working memory or task-switching has been shown to result in increased cortical responses to unattended distractors (De Fockert et al., 2001;

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Kelley and Lavie, 2010) as well as increased distractor effects and reduced rates of inattentional blindness (e.g. Lavie et al., 2004; Lavie and De Fockert, 2005; Brand-D'Abrescia and Lavie, 2007; De Fockert and Bremner, 2011). These effects of cognitive control load have been explained as reflecting the diminished capacity to actively maintain processing priorities of task-relevant stimuli over irrelevant stimuli when cognitive control resources are depleted (e.g. Lavie, 2000; Lavie et al., 2004). Together the opposite effects of perceptual load and cognitive control load on unattended processing are taken to indicate that perceptual processing depends on a capacity-limited resource which is distinct from the higher-level resources mediating the capacity for cognitive control.

The behavioural distinction between perceptual capacity and cognitive control capacity has received some support in neuroimaging research that has implicated different regions in studies on the effects of perceptual load to those found in studies of cognitive control load. Specifically, the main effect of increased perceptual load in a task was associated with increased activity in posterior parietal cortex (PPC). For example, Wojciulik and Kanwisher (1999) found that increased load on attention was selectively associated with increased activity in the intraparietal sulcus across a variety of tasks involving different manipulations of load on attention. PPC activity has also been shown to increase with the relevant set size for attended processing in tasks of Multiple Object Tracking (MOT; Culham et al., 2001; Jovicich et al., 2001), visual search (Mitchell and Cusack, 2007; Nobre et al., 2003; Torralbo et al., 2016) and rapid serial visual presentations requiring either feature detection (low load) or discrimination between conjunctions of features (high load, Schwartz et al., 2005). Furthermore, this activity could be attributed to capacity limits manifested in task performance in studies that demonstrated PPC activity related to the effects of perceptual load reached a plateau at the behaviourally-observed capacity limit (Mitchell and Cusack, 2007; Cutini et al., 2014).

Load on cognitive control resources on the other hand is most often associated with activity in prefrontal cortex (PFC; e.g. De Fockert et al., 2001; Lavie and De Fockert, 2006; Tomasi et al., 2007). However, various other regions throughout the fronto-parietal network have also been implicated in the effects of perceptual load (e.g. Jovicich et al., 2001; Culham et al., 2001; Christophel et al., 2017; Torralbo et al., 2016). Cognitive control and working memory load have also been associated not only with increased PFC activity but also with increased activity in the PPC especially when visual working memory tasks have been employed (e.g. Chein et al., 2011; Mackey and Curtis, 2017; Osaka et al., 2003; Todd and Marois, 2004). Thus, while perceptual capacity can be dissociated from cognitive control capacity through their opposite effects on distractor processing, the functional distinction between the brain regions mediating these capacities is less clear.

In the present research we therefore sought to examine whether there are distinct neural substrates underlying perceptual capacity that are dissociable from those mediating cognitive control capacity using an individual differences approach combined with Voxel Based Morphometry (VBM). Importantly, given that performance of any task alone (be it either a task that mainly draws on perceptual capacity or one that mainly draws on cognitive control functions) would involve various task-specific factors and their associated neural substrates, we employed a battery of perceptual and complex working memory span tasks. We used Principal Component Analysis (PCA) to delineate the common variance attributed to perceptual capacity and cognitive control and VBM to identify the neural substrates associated with each. This approach thus allowed us to assess whether differences in perceptual and cognitive control capacities are associated with distinct structural cortical differences. A recent behavioural study established that individual differences in diverse measures of perceptual capacity indeed share a common underlying source of variance, and can predict the occurrence of inattentional blindness phenomena (Eayrs and Lavie, 2018). Moreover, a factor analysis demonstrated that the perceptual capacity factor was dissociable from a cognitive control capacity factor.

We investigated individual differences in perceptual capacity further by examining whether these individual differences in behavioural performance are associated with differences in the brain: Participants performed a battery of tasks designed to load either perceptual capacity or cognitive control capacity. Perceptual capacity tasks required participants to detect changes in flickering real world scenes (change detection), report the number of stimuli presented in brief displays (subitizing), and track a set of moving targets among identical nontargets (i.e. multiple object tracking – MOT). While the capacity for cognitive control was measured using three separate complex working memory span tasks which require participants to memorise sets of letters or spatial locations while simultaneously performing cognitive operations such as mathematical problems, semantic judgements or image symmetry judgements.

2. Method

2.1. Participants

A sample of $n = 44$ people participated in exchange for course credit or payment of £7.50 per hour. Participants were aged 18 to 43 ($mean = 25.73$, $SD = 5.86$) and 24 were female. All participants provided written informed consent prior to both the behavioural testing session and the MRI scan.

2.2. Behavioural testing

Participants completed six behavioural tasks, three complex span tasks and three perceptual load tasks. The complex span tasks were the same as those described by Oswald et al. (2015), downloaded from http://englelab.gatech.edu/tasks.html and run using E-Prime 2.0; the enumeration, change detection and MOT tasks were programmed in Matlab (Mathworks Inc., Natick, MA) using the Cogent toolbox. Testing was conducted in a quiet and dimly lit room; the tasks were all run on a Dell PC with a 15-inch flat screen monitor and participants were seated 60 cm from the screen. Behavioural testing preceded the MRI scan by approximately one week except for 4 participants who completed both parts of the experiment on the same day.

2.2.1. Enumeration task

Each trial of the enumeration task began with the presentation of a fixation point for 1 s, followed by a stimulus set of black squares, presented on a mid-grey background for 100 ms. The number of squares varied randomly on each trial between one and nine. Each of the squares was positioned in an area subtending 7.15° by 7.15° in the centre of the screen, individual square positions were determined randomly with the constraint that no square could be presented within 0.38° of the edge of another square. The size of each square varied randomly from a minimum of 0.38° to a maximum of 3.8°, with each size selected from a uniform distribution (in steps of .1°). This was followed immediately by a mask of 100 overlapping black and white squares with their size and position randomised in the same manner as the stimulus squares (but allowed to overlap with one-another) and covering the same (7.15° by 7.15°) area as the enumeration display. After 400 ms a '?' was presented centrally which remained onscreen for a further 2,400 ms or until a response was recorded. Participants were instructed to indicate the number of squares as quickly as possible by pressing a key from one to nine on the right-hand number pad of the keyboard at any time following the initial enumeration display. The task comprised of one practice block of nine trials, followed by four experimental blocks of 81 trials each.

2.2.2. Change detection task

Each trial of the change detection task began with a fixation point for 1s, followed by a photograph of an outdoor scene subtending 21.2° by 12.8° at the centre of the screen (see Fig. 1). The scene image alternated between two versions, each presented successively for 200 ms and

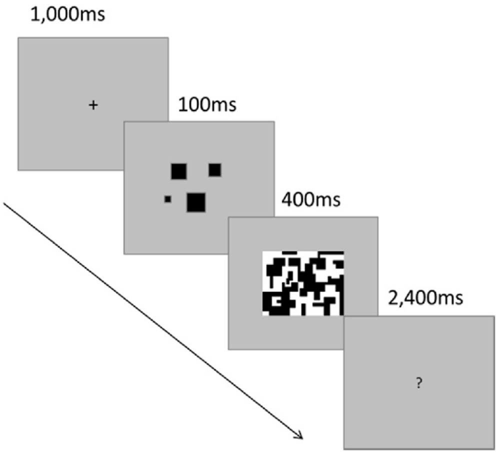

Fig. 1. Stimulus schematic of a typical trial in the enumeration task in which the correct response is '4'.

interspersed by a grey rectangle of the same dimensions for 100 ms. The images alternated on each presentation in an ABAB pattern between the two versions, which were either identical (50% of trials) or contained a small but conspicuous change (50% of trials, Fig. 2). Participants responded by pressing the right or left shift keys on the keyboard if a change was present or not respectively. If no response was made after 15 s then a 'no-change' response was recorded. After receiving instructions, participants completed a single demonstration practice before completing the 52 experimental trials.

2.2.3. *MOT task*

In the MOT task (Fig. 3) participants were instructed to track four target dots which moved around the screen among four identical non-target dots. Each of the dots subtended 0.5° by 0.5° and moved randomly within an invisible central box subtending 5.7° by 5.7°. On each trial, eight black dots were presented against a grey background for 500 ms before the colour of four dots changed to blue for 1.5s. The dots then turned back to black for another 500 ms before beginning to move at a rate of 2.15° per second. They were deflected by one-another and by the edges of the movement area. The dots ceased moving after 8 s and a single probe dot turned blue. Participants responded by pressing the '1' key on the keyboard number pad if the probe was a target and the '2' key if it was not. There was no time-limit on responses. Following the response the probe turned either green or red for 1 s to indicate a correct or incorrect response respectively. Participants received one block of five practice trials, and then completed four blocks of 20 experimental trials.

2.2.4. *Complex span tasks*

There were three complex working memory span tasks; these were the 'Operation Span' (OSPAN), 'Reading Span' (RSPAN) and 'Symmetry Span' (SSPAN) tasks (Fig. 4). The use of a variety of shortened tasks in place of a single full length task has been validated in recent research and is recommended as a means of measuring working memory capacity in a non-domain-specific manner (see Oswald et al., 2015 and Foster et al., 2015 for a detailed discussion).

In all three tasks, the memory set size varied randomly on each trial between set sizes four and six (two trials per set size) In the OSPAN task, a series of sums were presented (e.g. (8/2) + 9 = 13) and participants responded by clicking 'yes' or 'no' icons on the screen to indicate whether or not the answer was correct. A single letter was presented after each sum for 1 s and participants were instructed to memorise it. After four to six sum and letter pairs, a memory test screen was presented, containing 12 letters, including each of the memorised letters and six to eight (depending on the set size for that trial) non-target letters, chosen randomly without replacement. The participant then selected the letters in the order in which they had been presented via mouse-click, if uncertain of any individual letter they responded by clicking the 'blank' icon. The 'span score' for each participant was calculated as the total number of letters reported in the correct sequential position over all of the experimental trails.

Before starting the experimental trials, participants first completed a series of practice trials. The first practice included only the 'sum' component with no memory stimuli; the second practice included only the 'memory' component with no sums and the final practice included both together as in experimental trials. Participants completed two trials of each practice and their average response time plus 2.5 standard deviations was used as the time limit in experimental trials. The participant's accuracy in the sum portion of the task was continuously displayed onscreen with the instruction to maintain a minimum of 80%.

The RSPAN task followed the same trial structure in both practice and experimental trials. However instead of a series of sums, the participant read a sentence and was instructed to indicate whether the sentence made semantic sense (e.g. 'The prosecutor's dish was lost because it was not based on fact.'). The SSPAN task and practice also had the same structure, but instead of a sum or sentence, a black and white block image was presented and participants were instructed to indicate whether or not the left and right sides were mirror symmetrical. Instead of memorizing letters, in the SSPAN task the position of a red square in a white grid was memorised on each trial and participants responded by clicking these locations on an empty grid at the end of each trial.

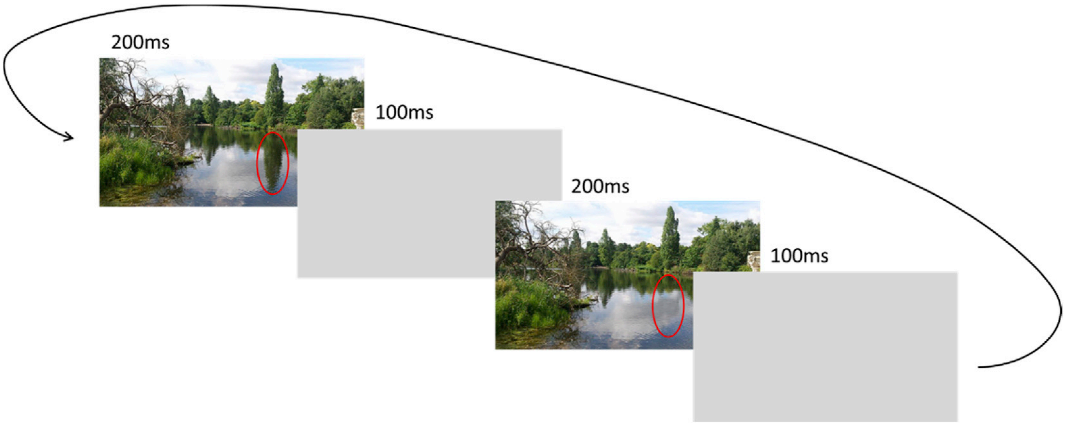

Fig. 2. A typical trial in the change detection task. A red oval (not present in the actual stimulus) was added to the figure to highlight the change.

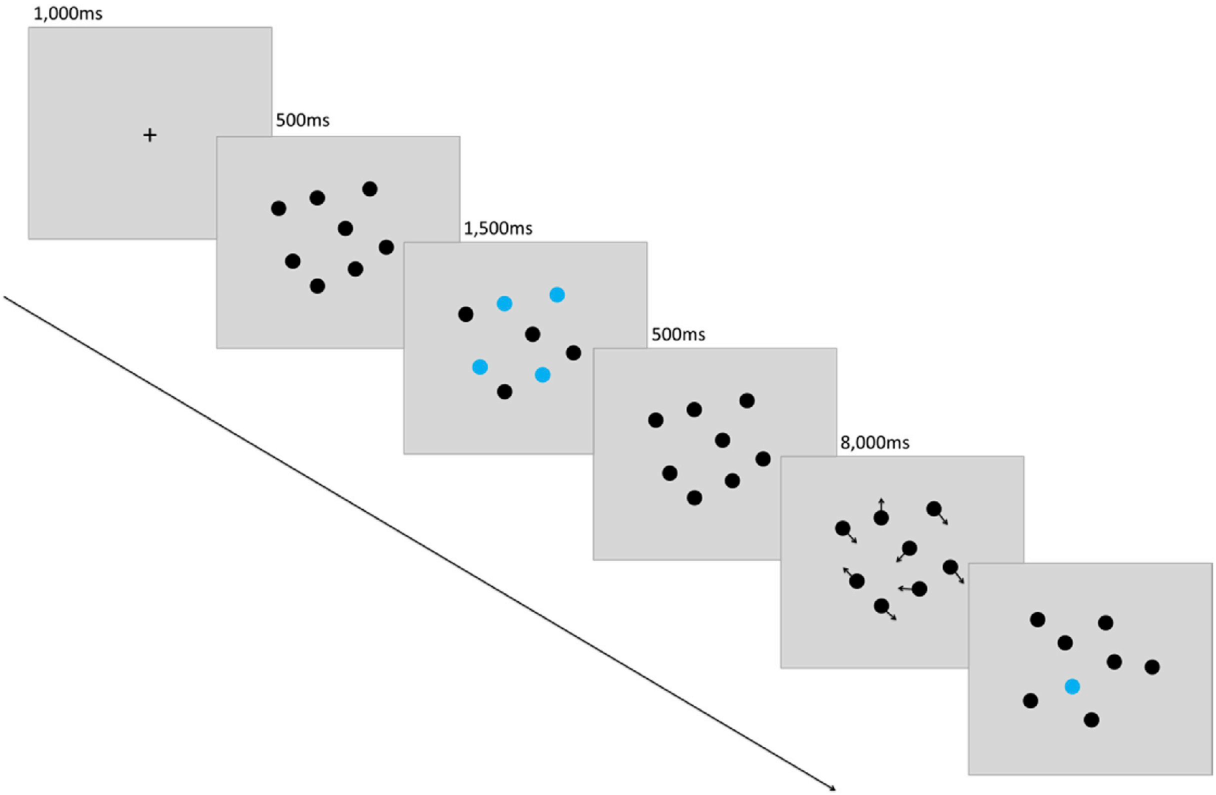

Fig. 3. A typical trial of the MOT task.

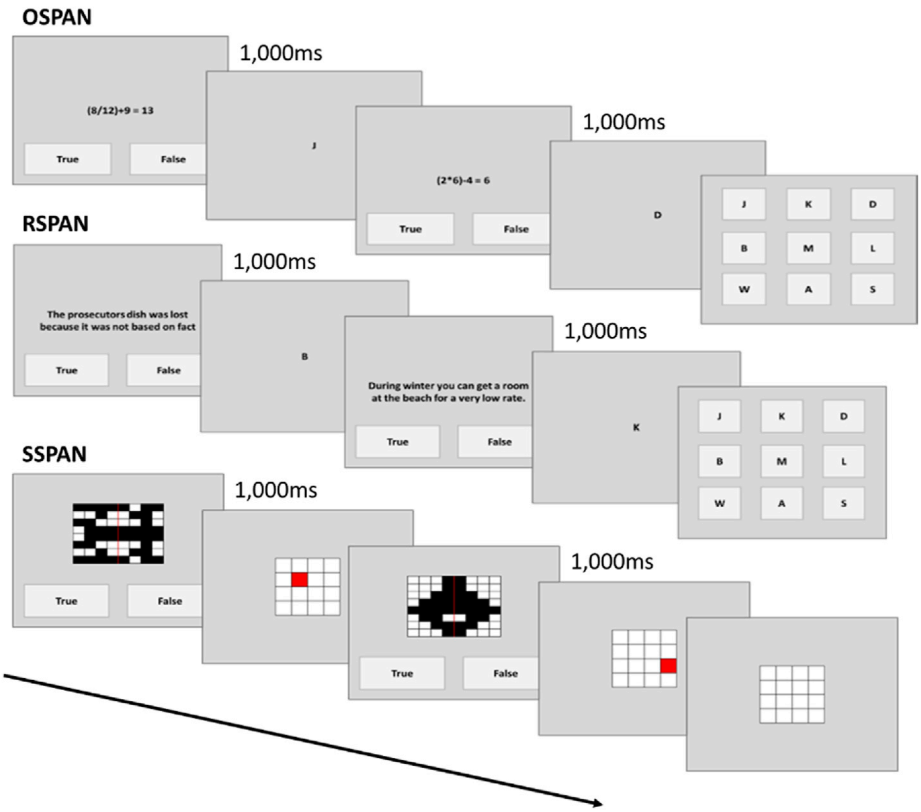

Fig. 4. Simplified example trials in each of the three complex working memory span tasks: In the actual tasks memory set size varied randomly between four and six operation and memoranda pairs rather than the two displayed for each task here. The memory response display (the last image in the figure) remained until participant response. Time limits for responses on the operation portion of each trial were determined idiosyncratically for each participant based upon their average response time during practice plus two and a half standard deviations (the stimulus remained onscreen until this time limit or until the participant made a response by clicking the 'true' or 'false' icon).

2.3. Image acquisition

Brain images were acquired at the Birkbeck-UCL Centre for Neuroimaging (BUCNI) using a 1.5 T (Siemens Avanto) MRI scanner, with a 32-channel head coil. The whole brain was imaged using a high resolution T1-weighted 3D magnetization-prepared rapid acquisition gradient-echo sequence (MPRAGE; voxel size = 1.00 x 1.00 × 1.00 mm).

2.4. Image pre-processing

The T1-weighted scans were first segmented into separate tissue types using SPM12's segmentation tool, which uses six tissue classes to optimally characterise the voxels of interest. This was followed by inter-subject registration of the grey and white matter images independently using Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra (DARTEL; Ashburner, 2007; Ashburner and Karl, 2000) also in SPM12. During co-registration the local grey and white matter volumes are conserved by modulating the intensity at each voxel by the Jacobian determinants of the deformation fields as computed by DARTEL. The co-registered images were smoothed using a Gaussian kernel (FWHM = 10 mm) before being transformed to MNI stereotactic space in SPM12 through affine nonlinear spatial normalisation.

All statistical analyses of MRI data controlled for total intracranial volume (TIV), calculated as the total volume accounted for by grey matter, white matter and cerebrospinal fluid (CSF) for each participant. Analyses were constrained to grey matter by applying optimized masks generated using the masking toolbox developed by Ridgway et al. (2009). Multiple regression analyses were conducted on the pre-processed images in SPM12 to investigate the relationship between behavioural predictors and voxel-wise intensity values. A cluster-forming threshold of $p < .001$ was employed with a Family-Wise Error-corrected (FWE) statistical threshold of $p < .05$ (two tailed, 0.025 per tail) for cluster size as is typical in VBM analyses and default in the SPM software.

3. Results

3.1. Behavioural results

3.1.1. Enumeration performance

Average accuracy in each set size of the enumeration task is presented in Table 1, the task was designed to assess capacity using accuracy, with very brief (100 ms) and masked displays to preclude serial counting, thus rendering accuracy too low at the highest set sizes for reliable measurement of response times. To characterise the subitizing capacity for each participant a bilinear function and a sigmoid function were fit to each participant's accuracy at each set size excluding set size nine (which was excluded to eliminate 'end effects' common in enumeration tasks, which involve participants guessing the largest set size when they are uncertain of the answer, thereby artificially inflating their accuracy at this set size. See Trick, 2008 and Green and Bavelier, 2006 for a similar approach).

Table 1
Average accuracy and corresponding standard deviation for each set size of the enumeration task.

Set size	% correct (SD)
1	93.94 (7.70)
2	94.60 (6.88)
3	89.87 (13.40)
4	70.08 (19.15)
5	54.26 (15.76)
6	51.33 (15.19)
7	39.39 (13.34)
8	34.56 (16.19)
9	40.53 (21.89)

Note: Mean proportion of correct responses at each set size in the enumeration task, with standard deviation displayed in parentheses.

We first fit a sigmoid function to the average accuracy at each set size (excluding set size nine) for each participant individually. The function was defined by four parameters representing the upper and lower asymptote points, the inflection point and the slope, these were adjusted using Matlab's nlinfit function to find the best fitting solution. The sigmoid function produced an average RMSE of 10.81 (SD = 2.85) and an average adjusted R^2 value of 0.84 (SD = 0.14), demonstrating a good fit to the data.

The bilinear function was similarly fit to the average accuracy at each set size for each participant (once again excluding set size nine). This function consisted of two linear components The first slope used starting values of 90% accuracy for the intercept and 0 for the slope, the second used a starting value of −15 for the slope and each integer set size value as a candidate 'bifurcation point' parameter. The model was tested with each integer set size value as a candidate bifurcation point parameter and the other parameters of the function were then adjusted using Matlab's fminsearch function to identify the best fitting values. The bilinear function fit to the accuracy data for each participant produced an average RMSE of 9.01 (SD = 5.13) and an average adjusted R^2 value of 0.88 (SD = 0.11) suggesting a slightly better fit to the data than that provided by the sigmoid function.

The average subitizing capacity for the sample (as estimated from the bilinear fit) was 3.06 (SD = .65) which is in good accordance with the typically observed subitizing range of three to four items (e.g. Eayrs and Lavie, 2018; Burr et al., 2010).

3.1.2. Change detection performance

Change detection performance was measured using a non-parametric measure of detection sensitivity (A; Zhang and Mueller, 2005). The average detection sensitivity was 0.83 (SD = .07), consistent with our previous results using a similar change detection task (Eayrs and Lavie, 2018).

3.1.3. MOT performance

Average accuracy in the MOT task was 75.69% (SD = 9.44), tracking capacity was estimated using the formula for 'Effective Number of Objects Tracked' (ENOT) as described by Scholl et al. (2001). ENOT scores were calculated as: $m = n(2p-1)$, where m is the estimated tracking capacity (ENOT), n is the number of target dots and p is the proportion of correct responses. The average tracking capacity using this formula was 2.06 (SD = 0.76), which is similar to capacity estimates reported previously using similar tasks (e.g. Eayrs and Lavie, 2018; Oksama and Hyönä, 2004).

3.1.4. Complex span performance

Average performance data for the OSPAN, RSPAN and SSPAN tasks are presented in Table 2 expressed as total scores for which the maximum is 30 for OSPAN and RSPAN and 24 for the SSPAN task. Accuracy in the 'operation' portion of each task (i.e. sums, reading and symmetry judgements) is also presented. Operation accuracy was consistently above 90% and did not drop below 80% for any participant, indicating that they attended both components of the task as instructed. Average task performance was high (see Table 2) and in line with previous reports using these paradigms (e.g. Oswald et al., 2015).

Table 2
Average scores and accuracy in the complex working memory span tasks.

Task	Score (SD)	Accuracy (SD)
OSPAN	25.75 (4.15)	92.27% (5.32)
RSPAN	24.89 (4.47)	92.88% (6.92)
SSPAN	17.32 (4.26)	93.09% (5.75)

Note: Mean working memory scores and proportion of correct responses for each task, with standard deviation displayed in parentheses.

Table 3
Pearson correlation matrix for each of the behavioural measures, with Spearman-Brown corrected split half reliability on the diagonal.

	1	2	3	4	5	6
1. Subitizing	.77***					
2. Change detection	.35*	.82***				
3. ENOT	.39*	.44**	.78***			
4. OSPAN score	.18	.22	.24	.69***		
5. RSPAN score	.08	.38*	.22	.47**	.79***	
6. SSPAN score	-.03	.10	.19	.41*	.29†	.77***

Note: Subitizing refers to the intersection point of the bilinear function fit to enumeration data; Change detection refers to detection sensitivity (A) for the Change blindness task; ENOT refers to the 'Effective number of object tracked' for the MOT task; OSPAN refers to the operation span task; SSPAN refers to the reading span task and SSPAN refers to the symmetry span task. All p-values are two-tailed: * = p < .05, ** = p < .01, *** = p < .001, † p = .059.

3.1.5. *Measure reliability and inter-task correlations*

Table 3 presents a pearson correlation matrix for each of the key behavioural performance measures with Spearman-Brown corrected split-half reliability estimates on the diagonal of the matrix. As can be seen from Table 3, reliability estimates were strong for each of the tasks, all of which were within a range of .77 to .82. All of the perceptual capacity variables were significantly, positively correlated with one-another (Table 3). Each of the complex span tasks were also correlated, with the exception of SSPAN and RSPAN (which was marginally significant at p = .059).

3.1.6. *Principal components analysis of behavioural measures*

Behavioural performance scores were entered into a principal components analysis (PCA). The PCA was conducted upon the pearson correlation matrix (Table 3) of the primary performance measures from each task (i.e. subitizing capacity from the enumeration bilinear function; detection sensitivity from the change detection task; ENOT from the MOT task and memory scores from each of the three complex span tasks). Orthogonal (Varimax) rotation was used in order to maximally differentiate the two components and their neural substrates. The Kaiser-Meyer-Olkin measure of sampling adequacy indicated that the sample size was adequate (KMO = .67; Kaiser, 1970; Field, 2009). Bartlett's test for sphericity was significant, ($\chi^2(15) = 45.18$, $p < .001$), indicating that inter-item correlations were sufficient for PCA. Principal components were extracted with Eigenvalues greater than one (Kaiser, 1974), resulting in a two component solution; which was supported by examination of a scree-plot. The first component accounted for 39.21% of the overall variance and the second component accounted for an additional 21.61% (60.82% cumulatively).

The first component was strongly indicated by the three working memory tasks, all of which had loadings greater than .70 (see Table 4). The second component was indicated most strongly by the three perceptual variables which also had loadings consistently over .70. In contrast, the loadings of complex span variables on the second component and perceptual variables on the first component were much smaller (consistently less than .25). These results therefore indicate two separate constructs representing cognitive control (Component 1) and perceptual (Component 2) capacities.

Table 4
Varimax-rotated principal component loadings from PCA of behavioural task performance.

Measure	Component 1 loading	Component 2 loading
OSPAN	.78	.20
RSPAN	.77	-.08
SSPAN	.72	.24
Subitizing	-.09	.79
Change blindness	.21	.74
MOT	.24	.74

3.2. *VBM results*

3.2.1. *Component scores*

Scores were calculated for each participant on each of the two varimax-rotated principal components in order to investigate the grey matter correlates of perceptual and working memory capacities. We conducted separate VBM analyses predicting regional grey matter volume from each of the principal component scores while controlling for TIV for each individual.

For the perceptual capacity component there was a significant correlation with grey matter volume in the angular gyrus of the right Inferior Parietal Lobule (IPL): cluster size = 20 voxels, p = .009 FWE corrected for the whole brain, peak t = 5.93 coordinates: x = 41, y = −68, z = 35 (Fig. 5). This correlation remained significant when including cognitive control capacity component scores as a covariate (cluster size = 12 voxels, p = .03 FWE corrected for the whole brain, peak t = 5.63, coordinates: x = 41, y = −68, z = 35) demonstrating the specificity of the relationship between parietal cortex and perceptual capacity, rather than any general task-performance factors (e.g. motivation).

The cognitive control capacity component was correlated with grey matter volume in left Middle Frontal Gyrus (MFG): cluster size = 80 voxels, p = .002 corrected for the whole brain, peak t = 5.7, coordinates: x = −39, y = 21, z = 42 (Fig. 6). Again, this correlation remained significant when controlling for the perceptual task component scores as a covariate to rule out general task-performance factors (cluster size = 49 voxels, p = .01 FWE corrected for the whole brain, peak t = 5.45, coordinates: x = −41, y = 21, z = 44).

There were no other significant clusters (p > .05) and no significant clusters in white-matter volume associated with either the perceptual or cognitive control component scores (p > .05).

3.2.2. *Regions associated with individual tasks*

VBM analyses predicting regional grey matter volume associated with performance measures from each task independently were conducted. Each analysis included only one behavioural measure as a predictor. The complex span tasks did not reveal any significant cluster of grey matter associated with any of the specific tasks. However, individual differences were found in task-specific regions in relation to subitizing and change detection task performance.

Individual differences in subitizing capacity were significantly correlated with grey matter volume in a cluster within the right angular gyrus (cluster size 130 voxels, p < .001 FWE corrected for the whole volume, peak t(43) = 8.36, peak coordinates: x = 39 y = −66 z = 33; Fig. 8). A similar analysis using estimation accuracy for set sizes outside the subitizing range did not significantly correlate with any region of grey matter throughout the brain. Thus, individual differences in subitizing capacity were associated with grey matter in IPL and this effect was specific to subitizing capacity and not to general task performance factors (such as motivation) or general enumeration ability (involved in number estimation for larger set sizes).

Individual differences in change detection were significantly correlated with grey matter volume in a similar cluster in right angular gyrus (cluster size = 36 voxels, p = .005 FWE corrected for the whole volume, peak t(43) = 5.75, peak coordinates: x = 47, y = −60, z = 36; Fig. 7). There was also a very small but significant cluster in left orbitofrontal cortex (cluster size = 9 voxels, p = .028 FWE corrected for the whole volume, peak t(43) = 5.54 peak coordinates: x = 33, y = 65, z = −9). Change detection ability was therefore also associated with the same region of parietal cortex as subitizing capacity, suggesting a common resource underlying performance of the two tasks.

Tracking capacity (ENOT) was not significantly correlated with grey matter in any region. This could perhaps be due to the possibility for participants to recruit a diverse range of strategies (mediated by different brain regions) to aid their performance (for example creating an imaginary polygon linking each of the items, as suggested by Yantis, 1992). Indeed a large number of regions are reported in fMRI studies using the

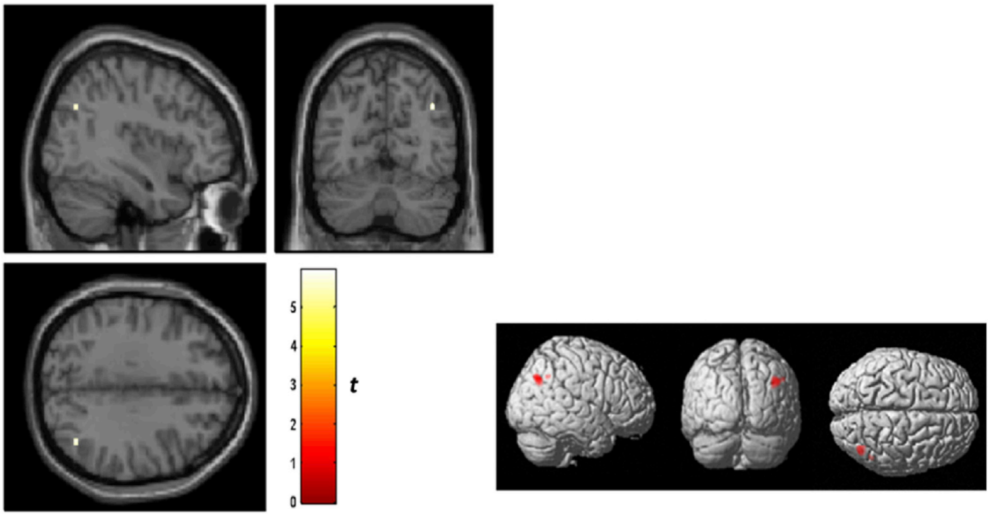

Fig. 5. Results of a VBM analysis with the second varimax-rotated principal component (perceptual capacity) as a predictor of grey matter volume.

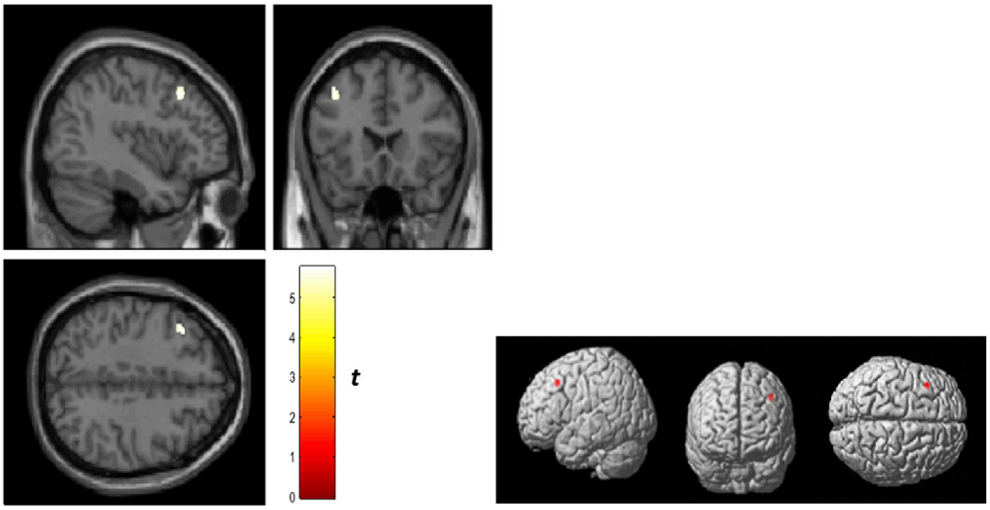

Fig. 6. Results of a VBM analysis with the first varimax-rotated principal component (cognitive control) as a predictor of grey matter volume.

MOT paradigm (e.g. Culham et al., 2001; Jovicich et al., 2001). The variance in the reliance of different task trials on different regions (related to different strategies e.g. a polygon may be easier to imagine on some trials compared to other trials due to the movement pattern) could preclude the finding of a common region explaining individual differences in task-specific performance. Importantly the potential variance in the recruitment of regions related to the task-specific activations did not hinder the findings of a significant loading on the perceptual component. Thus despite any variance in regions related to common individual differences in task specific performance, the perceptual component in PPC, was stable enough to be revealed.

3.2.3. *Nonparametric analyses*

In light of the concerns raised by Eklund et al. (2016) regarding the validity of parametric assumptions for cluster-size in MRI analysis, we replicated these analyses using a non-parametric, permutation-based approach (see supplementary materials for details). All of the significant clusters reported above were also significant using this approach, with the addition of several other significant clusters. Briefly, these included a right inferior frontal gyrus (IFG), bilateral cingulate cortex and right lateral temporal cortex associated with cognitive control component scores. These analyses also revealed extensive regions of significant correlation in bilateral orbitofrontal cortex and precuneus for detection sensitivity in the change blindness task as well as clusters in lateral frontal cortex, premotor cortex and posterior cingulate cortex associated with individual complex working memory span tasks. Crucially, the right parietal and left middle-frontal clusters associated with perceptual capacity and cognitive control respectively were replicated in these analyses and were still only associated with their respective capacities.

4. Discussion

The present research establishes distinct grey matter correlates in right PPC (specifically in the Angular gyrus of the right IPL) and left MFG underlying individual differences in perceptual capacity versus those in the capacity for cognitive control respectively. Individual differences in grey matter volume in right IPL were predictive of a common component in the performance of the tasks of change detection, MOT and subitizing, despite their differences in task specific factors. Similarly, individual differences in grey matter volume in left MFG were predictive of the component accounting for variance underlying the performance of the complex working memory tasks despite their differences in the memory content and secondary task domain during maintenance.

Specifically, while change detection required perception of a

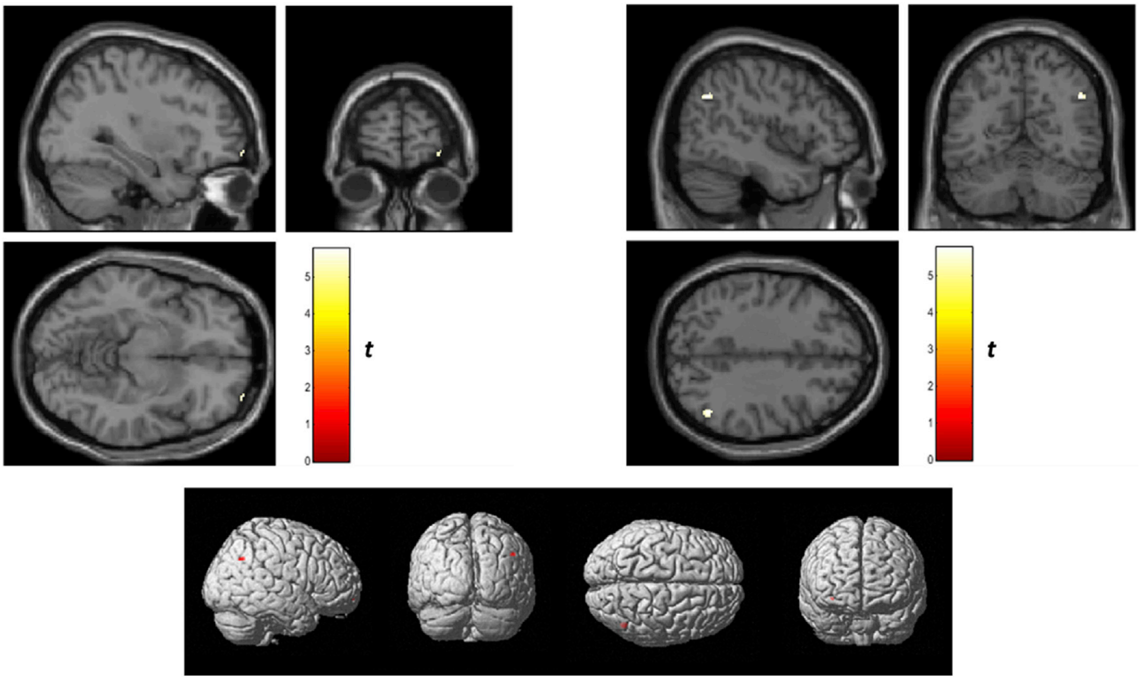

Fig. 7. Results of a VBM analysis with detection sensitivity (A) in the change blindness task as a predictor of grey matter volume.

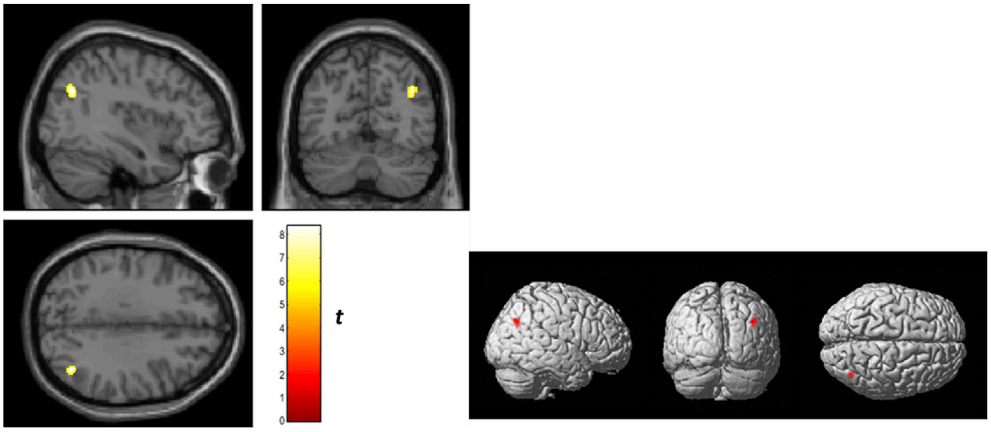

Fig. 8. Results of a VBM analysis with subitizing capacity as a predictor of grey matter volume.

transient change among complex meaningful scenes (e.g. a London street), the MOT task required sustained focus over time on a group of moving target objects while filtering distractors, and the subitizing task required the instant detection and individuation of items from very brief presentations. The tasks also diverged in terms of their stimulus content and presentations (e.g. complex meaningful scenes versus abstract shapes, dynamic versus static displays, brief versus prolonged presentations). Despite all these differences, they all tax the ability to perceive and consciously detect multiple stimuli in parallel and this perceptual ability could be predicted from individual differences in IPL grey matter volume.

The complex span tasks on the other hand all required participants to actively maintain information in memory while responding to secondary task demands but differed both in the working memory content (digits, letters, or location) and the relevant processing domain required for the 'operation' of the secondary tasks: arithmetic, semantic reasoning or symmetry judgements. While performance of each of these tasks involves demand on content-specific memory maintenance, the common limiting factor between the tasks is their load on domain-general top-down cognitive control of processing priorities (Oswald et al., 2015). Importantly, this cognitive control ability could be predicted from grey matter volume in left MFG (as well as from right inferior frontal gyrus, bilateral cingulate cortex and right lateral temporal cortex regions in our nonparametric results, see supplementary materials) but not in parietal cortex, further distinguishing this from perceptual capacity.

The distinct grey matter correlates for perceptual capacity and cognitive control were consistent with behavioural results which support the distinction between perceptual and working memory capacities. The two-component solution to the PCA indicated clearly that perceptually demanding tasks load on one component, while complex span tasks load on a separate, orthogonal component. The two component solution also ruled out accounts for the variance in task performance in terms of general factors, such as motivation which would not be expected to diverge across perceptual and working memory tasks.

4.1. *Relation to functional dissociations*

The dissociation between the neural correlates of perceptual capacity and working memory capacity is consistent with the functional distinction between perceptual and cognitive control capacities previously revealed with the effects of different types of load (Lavie, 2000; Lavie et al., 2004; Tomasi et al., 2007). Specifically, opposite effects of working memory load and perceptual load have been found on unattended processing. High perceptual load in an attended task leads to reduced distractor processing (Lavie, 1995, 2005), indicating reduced processing due to exhausting perceptual capacity in high load conditions. In contrast, working memory load has been shown to have opposite effects – increased distractor processing, indicating depletion of cognitive control capacity used to actively maintain task priorities between relevant and irrelevant stimulus processing (De Fockert et al., 2001; Lavie et al., 2004).

Functional imaging studies have also implicated PPC activity underlying the effects of load on perceptual capacity, and PFC activity underlying the impact of load on cognitive control functions. For example, increased PPC activity has been related to increased perceptual load (e.g. Mitchell and Cusack, 2007; Tomasi et al., 2007) together with reduced visual cortex activity related to distractor processing (e.g. Schwartz et al., 2005; Torralbo et al., 2016).

Activity in PPC has been shown to mediate awareness and perceptual processing involved in target detection in various paradigms including visual search, change detection and binocular rivalry (e.g. Beck et al., 2001; Lumer et al., 1998; Nobre et al., 2003; Nobre et al., 2002). Furthermore, TMS to this region, in particular the right angular gyrus, has been shown to disrupt perceptual processing involved in visual search and to elicit change blindness, thus establishing a causal role for this activity in awareness (e.g. Beck et al., 2005; Muggleton et al., 2008; Silvanto et al., 2009).

Conversely, our findings that grey matter volume in MFG was associated with cognitive control capacity accords with the functional imaging reports of this region as one of the key regions shown to be selectively activated during performance of complex working memory span tasks (Chein et al., 2011; Osaka et al., 2003, 2004). For example, Chein et al. (2011) found that numerous regions were activated during complex memory span tasks, but a contrast comparing storage-only conditions against the complex span conditions similar to those used in the present study demonstrated that complex span demands (i.e. maintaining stimuli in memory while simultaneously performing cognitive operations) produced significantly greater activation in lateral PFC and anterior cingulate. In our results the left MFG was the region most consistently associated with complex span performance. There is some limited evidence for lateralisation to the left MFG in particular (Osaka et al., 2003). However, other studies using similar tasks (e.g. Chein et al., 2011) found bilateral activation in MFG and other regions. Our results suggest that the left MFG may be particularly important in determining individual capacity limits in cognitive control.

4.2. *Evidence for dissociable perceptual and cognitive control capacities from lesion studies*

Our findings that structural differences in the healthy brain reflect an individual's capacity are consistent with established findings from brain lesion studies. The association between right PPC and perceptual capacity relates to the pattern of symptoms arising from parietal lesions which can lead to hemispatial neglect and Balint's syndrome (e.g. Driver and Mattingley, 1998; Egly et al., 1994; Luria, 1959), both of which can involve strong deficits in attention and awareness. Relatedly, right parietal lesions have been associated with specific deficits in subitizing (in contrast deficits in general task performance and in serial counting were associated with more distributed lesions in frontal cortex and in left parietal cortex respectively, see Demeyere et al., 2012). Our findings are also in good accordance with the long-established effects of frontal lesions on cognitive control (i.e. Dysexecutive syndrome, Baddeley and Wilson, 1988). Left lateral frontal lesions including those encompassing the region of MFG highlighted in our analyses have in fact been specifically associated with impaired working memory capacity (e.g. Zheng et al., 2014) and task switching (e.g. Aron et al., 2004) as well as deficits in 'task setting' (Stuss and Alexander, 2007) manifesting for example in a cost to performance of stroop-like tasks (e.g. Alexander et al., 2007) and the Wisconsin Card-Sorting Task (Stuss et al., 2000), all of which place high demands upon cognitive control.

In the context of the well-known divergent effects of lesions to PPC and lateral frontal cortex, our results suggest that these regions contribute critically to distinct and fundamental capacity limits in perceptual and executive functioning in the healthy brain. With a relative reduction in the available grey matter in a given region (either due to lesion, disruption from TMS, or normal inter-individual variability), a person has reduced perceptual processing capacity (in the case of PPC) or ability to exercise cognitive control (in the case of MFG), manifesting as reduced capacity.

4.3. *Differences in regional cortical volumes and distraction*

While there is considerable evidence that right PPC is associated with capacity limitations in visual attention as supported by our results, there is also evidence for an association between grey matter volume in left PPC and the top-down guidance of attention. For example, Soto et al. (2014) demonstrated that guidance of attention by the contents of visual working memory is correlated with grey matter volume in left PPC. Their participants performed a visual search task while maintaining stimuli in visual short-term memory which were irrelevant to the search task. In this paradigm it is well-established that distractors which match the contents of working memory will capture attention to a greater extent than distractors which do not match memory contents (e.g. Olivers et al., 2006). Soto et al. (2014) showed that the extent of this memory-driven capture of attention was positively associated with grey matter differences in left superior PPC. Relatedly, grey matter volume in left superior PPC has been shown to be positively correlated with self-reported distractibility in daily life. Thus, while increased volume in right PPC is associated with increased perceptual capacity, increased volume in left PPC is associated with greater processing of distractors (Kanai et al., 2011). This association could perhaps also reflect increased capacity, leading to a 'spillover' to irrelevant distractor processing and so enhanced attention capture effects (e.g. Forster and Lavie 2008a; 2008b). However, this interpretation remains speculative given that somewhat surprisingly TMS disruption of activity to the left PPC has been shown to increase distractor processing in a laboratory task (rather than decrease it as one might expect from the positive association between left PPC volume and distractor processing as reported by Kanai et al., 2011).

4.4. *Training versus hereditary contributions*

An interesting question that arises from these findings is whether the effects reflect hereditary differences in capacity or differences due to training or experience. There is good evidence from twin studies that genetic factors play a significant role in determining individual differences in various aspects of brain structure: from total brain volume (Baaré et al., 2001) to regionally specific differences in grey and white matter (e.g. Chiang et al., 2009; den Braber et al., 2013; Thompson et al., 2001). Specifically, grey matter in frontal cortex, including the left MFG, has been shown to be highly heritable (up to 78%; Hulshoff Pol et al., 2006). Parietal grey matter has also been shown to be hereditary, albeit to a lesser degree than that of frontal regions (Thompson et al., 2001).

However, it is also well-established that the environment and gene-environment interactions can influence individual differences in brain structure (Gu and Kanai, 2014; May, 2011). Multiple studies have shown that acquiring a skill or knowledge base over the course of months or years can have a significant impact on regionally specific grey matter volume. For example, skill acquisition, such as learning to golf (Bezzola et al., 2011) or to juggle (Draganski et al., 2004) has been shown to lead to significant localised grey matter changes. Similarly, academic mathematicians (Aydin et al., 2007), London taxi drivers (Maguire et al., 2000) and action video-game experts (Tanaka et al., 2013) have all been shown to possess regionally specific differences in grey matter volume. In fact, the angular gyrus specifically has been noted as a region which is often observed to respond to training interventions, especially those which involve visuospatial cognition (Seghier, 2013). The same region associated with capacity in the present results was found to be enhanced in expert (i.e. professional) action video game players relative to non-gamers (Tanaka et al., 2013) and previous work has shown enhancement of both subitizing and MOT capacities from action gaming experience (Green and Bavelier, 2006). Together these findings can be taken to suggest that perceptual capacity may be subject to enhancement through extensive action game play. We note however that Tanaka et al. (2013) compared pre-existing groups of gamers and non-gamers, and so it is impossible to be certain that this is a training effect and not an effect of self-selection (Boot et al., 2011).

4.5. *Future research*

Here, we used PCA to identify common variance attributed to different capacities from behavioural data and used these components as predictors of grey matter volume throughout the brain using VBM. This approach allowed us to refine our analysis to the common capacities underlying the behavioural measures (see Garrido et al., 2009; for a similar approach in developmental prosopagnosia). One benefit of this approach is that it allows a whole brain analysis of the substrates of the two capacities. An alternative method would be to apply a confirmatory analysis to both the neuroimaging and behavioural data simultaneously (such as in the structural equation modelling approach employed by Kievit et al., 2012, 2014). This would allow formal comparisons of models in which different latent factors such as perceptual capacity and cognitive control are associated with predefined regional differences in grey matter volume. This approach would require strong a-priori hypotheses regarding which regions of interest to include in the model and would benefit from very large sample sizes and from large numbers of behavioural indicators of latent measures. As such it may be beneficial for large-scale neuroimaging initiatives to take into account the distinction between perceptual capacity and cognitive control highlighted here and attempt to include distinct measures of each capacity. This would provide a means for future research to further delineate the distinction between these capacities in the brain.

5. Conclusions

In conclusion, our results support the hypothesis that a grey matter resource in IPL underlies perceptual processing capacity; and this is distinct from the grey matter resources underlying cognitive control capacity. These findings are compatible with prior observations from studies testing the load theory of attention and cognitive control (e.g. Lavie, 2005; Lavie et al., 2004; Lavie et al., 2014) and with the well-established distinctions between frontal and parietal functions drawn from lesion and functional neuroimaging studies. The distinct relationship between capacity and regionally specific differences in grey matter volume suggests that this correlation relates to a lasting individual attribute with a distinct signature in cortical structure. Whether this is hereditary or the result of enhancement through extensive training is an interesting avenue for future research.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.116148.

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