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Common and unique components of inhibition and working memory: An fMRI, within-subjects investigation

Fiona McNab^a, Gaëlle Leroux^a, Fredrik Strand^a, Lisa Thorell^{a,b}, Sissela Bergman^a, Torkel Klingberg^{a,*}

^a Developmental Cognitive Neuroscience Group, Stockholm Brain Institute, Karolinska Institutet, Sweden

^b Department of Psychology, Uppsala University, Sweden

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ABSTRACT

Behavioural findings indicate that the core executive functions of inhibition and working memory are closely linked, and neuroimaging studies indicate overlap between their neural correlates. There has not, however, been a comprehensive study, including several inhibition tasks and several working memory tasks, performed by the same subjects. In the present study, 11 healthy adult subjects completed separate blocks of 3 inhibition tasks (a stop task, a go/no-go task and a flanker task), and 2 working memory tasks (one spatial and one verbal). Activation common to all 5 tasks was identified in the right inferior frontal gyrus, and, at a lower threshold, also the right middle frontal gyrus and right parietal regions (BA 40 and BA 7). Left inferior frontal regions of interest (ROIs) showed a significant conjunction between all tasks except the flanker task. The present study could not pinpoint the specific function of each common region, but the parietal region identified here has previously been consistently related to working memory storage and the right inferior frontal gyrus has been associated with inhibition in both lesion and imaging studies. These results support the notion that inhibitory and working memory tasks involve common neural components, which may provide a neural basis for the interrelationship between the two systems.

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1. Introduction

Working memory and inhibition, described as core executive function domains (Goldman-Rakic, 1987; Hasher & Zacks, 1988), are closely related. Both have been linked to IQ (Horn, Dolan, Elliott, Deakin, & Woodruff, 2003), and performance is associated in both normal (e.g. Conway, Cowan, & Bunting, 2001; Kane & Engle, 2000, 2003; Unsworth, Schrock, & Engle, 2004), and clinical populations such as attention deficit hyperactivity disorder (ADHD) (Hervey, Epstein, & Curry, 2004; erté, Geurts, Roeyers, Oosterlaan, & Sergeant, 2006; Willcutt, Doyle, Nigg, Faraone, & Pennington, 2005), high-functioning autism (HFA) and Tourette syndrome (TS) (Verté et al., 2006). It has also been suggested that they may rely on common neural resources (De Fockert, Rees, Frith, & Lavie, 2001; Kane & Engle, 2003). The present study represents an investigation into the extent to which the neural correlates of different forms of inhibition and working memory overlap, and where such commonalities occur.

The right inferior frontal cortex (BA 45/47) has been described as showing the most robust common activation across inhibition tasks (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002) and identified as being central to inhibitory control (e.g. Aron, Robbins, & Poldrack, 2004; Chambers et al., 2006; Kelly, Hester, Foxe, Shpaner, & Garavan, 2006). It has been reported to show significantly greater activation for no-go trials in which participants inhibit a prepotent response compared to go trials in which participants make a prepotent response (Booth et al., 2003; Konishi, Nakajima, Uchida, Sekihara, & Miyashita, 1998; Langenecker & Nielson, 2003), has been strongly implicated in the inhibition of an already initiated manual response, the so-called stop task (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Aron & Poldrack, 2006; Chambers et al., 2006), and has been described as part of a “shared inhibitory neurocognitive network” involved with both go/no-go (GNG) and stop tasks (Rubia et al., 2001). In a flanker task activity in this region has been found to accompany increases in reaction time associated with incongruent trials (Hazelton, Poldrack, & Gabrieli, 2000), with the authors arguing that the strong correspondence between this activity and that reported in GNG and set shifting studies suggests that response inhibition may most appropriately characterize the function of this region.

Inferior parietal activation has also been observed in a number of inhibition tasks (Garavan, Ross, Murphy, Roche, & Stein, 2002;

* Corresponding author at: Karolinska Institutet, MR Centrum, Karolinska Sjukhuset N8:00, 17176 Stockholm, Sweden. Tel.: +46 8 5177 6118; fax: +46 8 5177 3266.

E-mail address: torkel.klingberg@ki.se (T. Klingberg).

Garavan, Ross, & Stein, 1999; Langenecker & Nielson, 2003; Liddle, Kiehl, & Smith, 2001; Peterson et al., 2002; Rubia et al., 2001; Sylvester et al., 2003), although this may be related to the storage of stimulus-response representations rather than inhibition (Hester, Murphy, & Garavan, 2004). Similarly, the dorsolateral prefrontal cortex (DLPFC) activation that has been associated with a range of inhibition tasks (Bellgrove, Hester, & Garavan, 2004; Garavan et al., 2002; Langenecker & Nielson, 2003; Liddle et al., 2001; Sylvester et al., 2003; Van Veen, Cohen, Botvinick, Stenger, & Carter, 2001) might be attributed to working memory demands as significant right DLPFC activation was observed for GNG trials during a counting GNG task, but not during a simple GNG (Mostofsky et al., 2003).

Furthermore, although a relatively consistent set of regions have been implicated in response inhibition paradigms (Wager et al., 2005), different forms of inhibition may be involved in different tasks (Wager et al., 2005). Within this study we adopt the approach taken by Barkley (1997) and consider three inhibition processes (rather than mechanisms); (1) inhibition of an initial prepotent response, (2) stopping an ongoing response or delayed responding, and (3) limiting interference or distractibility. These processes are employed to a different extent in different tasks (Rubia et al., 2001), for example whilst the Stroop and Erikson flanker tasks may rely heavily on limiting interference, GNG and stop tasks are likely to involve a greater reliance on inhibition of a prepotent or previously initiated response (although it should be noted that such conflict resolution tasks may well involve other mechanisms besides inhibition, such as facilitation). Correlations between performance on different inhibitory tasks have generally been low (Wager et al., 2005), but sometimes significant (Fan, Flombaum, McCandliss, Thomas, & Posner, 2003; Miyake, Friedman, Emerson, Witzki, & Howerter, 2000). Although it has been suggested that idiosyncrasies between tasks may obscure the results and account for the low behavioral correlations (Friedman & Miyake, 2004), it is also possible that different mechanisms may be involved in different forms of response inhibition. Therefore, when investigating the commonalities between the neural correlates of working memory and inhibition within the present study, three inhibition tasks were used, corresponding to the three inhibitory processes described by Barkley (1997).

Reviews of the working memory literature have implicated the left inferior frontal cortex, DLPFC, premotor cortex, superior frontal cortex, supplementary motor area, and the parietal cortex (for example, Cabeza & Nyberg, 2000; D'Esposito et al., 1998; D'Esposito, Postle, & Rypma, 2000; Smith & Jonides, 1998, 1999). Working memory tasks that use stimuli from different sensory modalities have been shown to activate overlapping cortical regions, in both prefrontal and parietal cortex (Klingberg, 1998; Klingberg, Kawashima, & Roland, 1996), suggested to be supramodal working memory regions. However, a dissociation has also been reported whereby verbal working memory is primarily associated with left hemisphere regions (in particular the left prefrontal cortex (Gabrieli, Brewer, & Poldrack, 1998)) and spatial working memory is linked to right hemisphere regions, even when the same letter stimuli are used in verbal and spatial working memory task conditions (Smith, Jonides, & Koeppe, 1996). Furthermore, Leung and Zhang (2004) suggested that different subsets of the working memory system may be associated with interference resolution in spatial and verbal domains. It is claimed that whereas the left inferior frontal gyrus is involved in overcoming interfering verbal stimuli, the right precentral sulcus and superior parietal lobe are involved in overcoming interfering spatial stimuli. It is also possible that the cortical representation of interference resolution in working memory may be material specific, which could mean that the relationship between inhibition and working memory differs depending upon whether the working memory task (and/or stim-

ulus) is verbal or spatial. For this reason both verbal and spatial working memory tasks were included within this study.

Evidence from patients suggests that the same right inferior frontal region may be involved in both spatial working memory and response inhibition in a stop task, with correlations reported between damage to this region and both stop signal reaction time (SSRT) and spatial working memory (SWM) performance (Clark et al., 2007). In order to identify commonalities between inhibition and working memory, in healthy participants, one approach has been to draw upon the results of different studies. However, group differences may confound such comparisons. Another approach has been to combine working memory and inhibition demands within the same task, for example Bunge, Ochsner, Desmond, Glover, and Gabrieli (2001) looked at the effects of manipulating the level of proactive interference in a Sternberg-type working memory task, and Kelly et al. (2006) used a task that required inhibition of prepotent responses based on the contents of working memory. However, Hester et al. (2004) reported that maintaining successful inhibitory control under increasing working memory demands tended not to increase activation in overlapping regions, but predominantly in unique inhibition-specific regions. In the present study, working memory and inhibition processes were isolated using different task blocks to avoid confounds associated with the manipulation of inhibition and working memory demands within the same task.

Valid conjunction analysis (Nichols, Brett, Andersson, Wager, & Poline, 2004) was used to localize overlapping activation associated with different forms of inhibition and working memory in the same subjects (to reduce the effects of individual differences). For each task, event related analysis was used to avoid possible confounds associated with using a block design (as described by Aron & Poldrack, 2005), for example unbalanced task maintenance load and switching between blocks which do not include trials that require inhibition and mixed blocks which do include such trials.

Another way in which the present study represents an extension of the approach taken previously is in the design of the GNG and stop tasks. Trials involving inhibition (no-go or stop trials) have typically been compared to go trials in which a prepotent stimulus is presented and a prepotent response is required. Such an approach may introduce confounds associated with differences in the frequency of presentation of certain stimuli (Aron & Poldrack, 2005), with the stimuli associated with inhibition being presented less frequently than the stimuli that do not involve inhibition. To overcome such confounds this study made use of oddball trials, which were control trials that did not require response inhibition, but were matched to no-go trials in terms of frequency of presentation. By comparing no-go or stop trials to these oddball trials we controlled for differences in familiarity associated with the oddball effect, whereby novel stimuli elicit additional cerebral activity (Halgren, Marinkovic, & Chauvel, 1998). Although such oddball trials may require other forms of inhibition, they do not require inhibition of a response, enabling us to isolate this form of inhibition in contrasts between no-go or stop trials and oddball trials.

Five contrasts were generated: three from inhibition tasks (corresponding to the three different inhibitory processes described by Barkley, 1997) and two from working memory tasks (verbal and spatial), and valid conjunction analysis was used to identify regions of common activation within and between working memory and inhibition domains. The results of the within domain conjunctions were also used to generate ROIs which were used to perform small volume corrected conjunction analyses between domains. In this way we were able to test the hypothesis that there are common regions associated with response inhibition and working memory, observe the extent to which each ROI contributes to each task, and determine whether the choice of inhibition and working memory task influences such commonality. This study represents an exten-

sion of the approach by investigating commonalities between three different forms of inhibition and two different forms of working memory and the relative contribution of each ROI to each task, in the same participants, isolating working memory and inhibition within separate task blocks, and using oddball trials in order to control for differences in familiarity within GNG and stop task contrasts.

2. Methods

2.1. Participants

Fourteen right-handed healthy university students were scanned. The data from 11 participants were included in the fMRI analysis (mean age 24 years, $\sigma = 4$ years, range 22–34, 4 males). All participants gave informed consent, and the study was approved by the ethical committee at the Karolinska Institute.

2.2. Procedure

Each participant completed three inhibition tasks (a stop task, a GNG task and a flanker task), and two working memory tasks (spatial and verbal). The data from three participants were excluded due to movement of >4 mm during fMRI recording. One run of each task (of approximately 10 min) was completed prior to entering the scan room, and two runs of each task were completed during scanning. One run of each inhibition task consisted of 152 trials and one run of each working memory task consisted of 40 trials. Responses were made with the right hand and the order of task presentation was counterbalanced across subjects.

2.2.1. Inhibition tasks

Within the GNG task (Fig. 1a) 50% of trials involved the presentation of a yellow square for 1300 ms, followed by a blank screen for 400 ms, and a fixation cross for 300 ms (go trials). In response to presentation of the yellow square participants were required to press a button. For 25% of the trials the stimulus consisted of a yellow triangle which indicated that participants should not make a response (no-go trials). For the remaining 25% of trials the same presentation sequence was used, but the stimulus consisted of a blue square, which also required a button press (oddball trials).

In the stop task (Fig. 1b) 50% of trials (control trials) involved the presentation of a yellow horizontal arrow, displayed for 1500 ms, followed by a blank screen for 400 ms and a fixation cross for 300 ms. The presentation of the yellow arrow required participants to press a button. In 25% of trials the yellow horizontal arrow was followed by a vertical yellow arrow, which signalled that the participant should inhibit their response (stop trials). For the first trial within this inhibition condition the horizontal arrow was displayed for 250 ms and the vertical arrow for 12,500 ms. Following this, if the participant had been successful during the previous inhibition trial, 50 ms was added to the duration of the first arrow. If the participant had failed to inhibit their response, the duration was reduced by 50 ms. Limits were imposed so that the minimum duration was 50 ms and the maximum was 1000 ms. The duration of the second arrow was adapted so that the total duration for the two arrows was always 1500 ms, in keeping with the control condition. This adaptive duration procedure was used to achieve approximately 50% accuracy, and to reduce the likelihood of participants anticipating the onset time of the second arrow, and delaying their response to the first arrow accordingly. In the remaining 25% of trials (oddball trials) the initial horizontal yellow arrow was followed by a second horizontal arrow, which was blue, and a button press was still required. In such oddball trials the duration of exposure of the first arrow was determined by the accuracy and exposure duration in the previous stop trial, the same as for stop trials. However, unlike stop trials, the accuracy of the oddball trials did not influence any subsequent exposure duration.

As discussed previously, in both the GNG and stop tasks, to control for differences in familiarity associated with the oddball effect, we compared no-go and stop trials to the frequency-matched oddball trials. However, it was not possible to control for the additional motor component associated with oddball trials but not with no-go or stop trials. The trials were distributed across blocks containing different relative no-go and stop trial densities in order to improve detection power (Liu, 2004).

Within the flanker task (Fig. 1c) a horizontal array of 5 arrows was presented for 1300 ms, and followed by a blank screen for 400 ms and a fixation cross for 300 ms. A near equal number of congruent trials (75 trials in which all the arrows pointed in the same direction) and incongruent trials (77 trials in which the central arrow pointed in the opposite direction to that of the surrounding arrows) were used, and a near equal number of trials included left pointing surrounding arrows as right pointing surrounding arrows within each condition. Participants were required to press a button on the right if the central arrow pointed to the right and on the left if the central arrow pointed to the left.

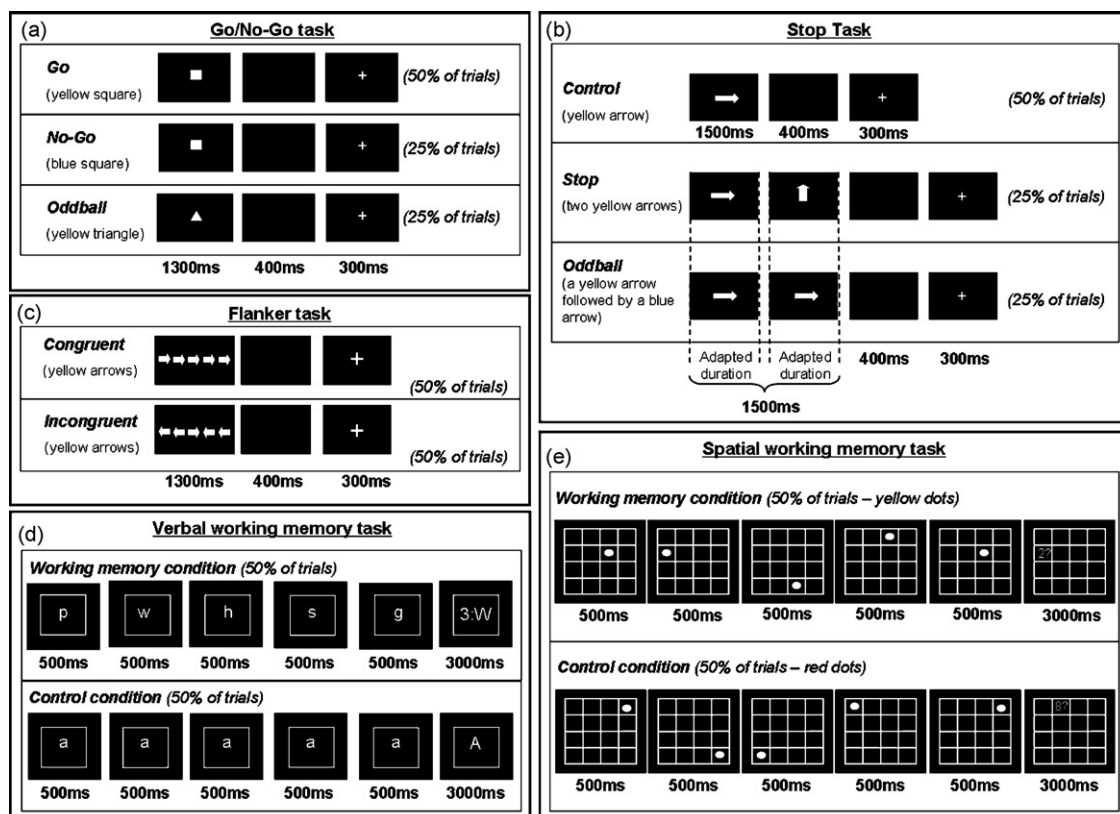


Fig. 1. The inhibition tasks ((a) the GNG task, (b) the stop task and (c) the flanker task) and the working memory tasks ((d) the verbal working memory task and (e) the spatial working memory task).

2.2.2. Working memory tasks

Within the verbal working memory task (Fig. 1d) each trial consisted of the serial presentation of 5 centrally positioned letters. Each letter was displayed for 500 ms. Between each letter the blank screen was shown for 500 ms. A cue was presented 1000 ms after the last letter disappeared. The cue stimulus consisted of a number between 1 and 5 (which referred to the serial position in the stimulus sequence), and a letter (but not the letter “a”). Participants were asked to make a yes/no response to indicate whether the number matched the letter, for example “3:W” would require participants to indicate whether the third stimulus in the trial had been “w”. Within the control condition every stimulus was the lower-case letter “a”, the cue was an upper case letter “A”, and a “yes” response was always required.

Within the spatial working memory task (Fig. 1e) participants were presented with a 4 by 4 grid of white lines on a black background. Within the working memory condition a series of 5 yellow circles appeared within different spaces on the grid, but not in the corner squares. Each circle was displayed for 500 ms. Between each circle presentation the blank grid was shown for 500 ms. 1000 ms after the last circle disappeared a cue was presented within one of the grid spaces. This took the form of a number between 1 and 5, referring to the serial position in the previous stimulus sequence, and a question mark. The participant was asked to indicate whether the second circle had appeared in this particular grid position. In the control condition red circles were presented in the same sequence of corner grid positions, starting in the top left of the grid and progressing clockwise. The cue in the control condition always consisted of the number 8 presented in a non-corner space, and always required a “yes” response.

In an attempt to reduce the risk of implicit working memory processes being employed within the working memory control conditions, the same stimuli were used within every trial of these working memory control conditions, which may have introduced a confound associated with differences in stimulus novelty to the between domain conjunction analyses had oddball trials not been included to control for differences in stimulus novelty within the inhibition task contrasts.

2.3. fMRI scanning

Imaging data were collected using a 1.5 T GE Signa scanner. T2*-weighted, gradient echo, spiral echo-planar images were acquired with TR = 2100 ms, TE = 40 ms, flip angle = 76°, 22 axial slices, 5.0 mm slice thickness, 220 mm × 220 mm FOV, 64 × 64 grid, resulting in voxels that were 3.4 mm × 3.4 mm × 5.0 mm. Each scan included 10 sessions, 2 for each task. Each flanker task and GNG session lasted 308.2 s and included acquisition of 148 volumes. Each stop task session lasted 338.6 s and included acquisition of 162 volumes. Each verbal working memory task session lasted 404.2 s and included acquisition of 194 volumes. Each spatial working memory task session lasted 364.2 s and included acquisition of 174 volumes. T1-weighted spin echo images (FOV = 220 mm × 220 mm, 256 × 256 grid) were acquired in the same position as the functional images.

2.4. Data analysis

There was one behavioural measure associated with each inhibition task. In the GNG task this was the number of commission errors. In the flanker task the difference in reaction time between incongruent and congruent trials was calculated. In the stop task an estimate of the stop signal reaction time was made by first calculating the average stop signal duration for each participant (the average duration of the first arrow in the stop trials after stabilization, i.e. in stop trials 20–38). The stop signal reaction time (SSRT) was then determined by subtracting the mean stop signal duration from the median reaction time for the oddball trials (the median was used because of standard positive skewing of RT data) (Band, van der Molen, & Logan, 2003; Clark et al., 2007). In the spatial and verbal working memory tasks, accuracy and reaction times were recorded. Correlations between these behavioural measures were identified.

The fMRI data were analysed with SPM2 (for the preprocessing and generation of individual contrast images) and SPM5 (for the second level analysis) (Wellcome Department of Imaging Neuroscience, London, UK). Motion during scanning was estimated by 6 parameters (3 translations, 3 rotations), which were used to realign the functional images to the first image in the series. The T1-weighted images

were normalised to MNI305 space. The parameters from this normalization were then used to normalize the functional images, which were sampled to a voxel size of 3 mm × 3 mm × 3 mm and then smoothed with an isotropic Gaussian kernel of 6.0 mm. For each task, events were modeled with the haemodynamic response function and its temporal and spatial derivatives, and contrast images were produced. Event related analysis was used to avoid the confounds associated with using a block design to study inhibition processes (Aron & Poldrack, 2005).

The flanker task was modeled with separate regressors for incongruent and congruent trials (event analysis at stimulus onset), the GNG task was modeled with separate regressors for go, no-go and oddball trials (event analysis at stimulus onset), and the stop task was modeled with separate regressors for control, stop and oddball trials (event analysis at the onset of the second stimulus in stop and oddball trials, and at the onset of the black screen following the horizontal arrow in control trials). The two working memory tasks were modeled with separate regressors for working memory and control trials (epoch analysis beginning at the onset of the first stimulus, with a duration of 8.5 s, corresponding to the trial duration).

No-go trials were compared to oddball trials in the GNG task, and stop trials were compared to oddball trials in the stop task. No-go trials were also compared to go trials in both of these tasks for validation. In the case of the flanker task, incongruent and congruent conditions were compared. Similarly, verbal and spatial working memory tasks were compared to their respective control conditions. This gave rise to 5 contrast images for each participant, which were analysed at the group level using random effects (rfx) analysis. These images were entered into a within-subjects ANOVA. “Valid conjunction inference” (Nichols et al., 2004) (implemented in SPM5) was used to identify regions that were significantly active for each combination of task contrasts, both within and between task domains, with the requirement that each contrast must be individually significant. Such statistical maps were thresholded at $p < 0.001$ uncorrected for multiple comparisons, and effects were considered to be significant if they fulfilled a corrected cluster level requirement of $p < 0.05$ (standard family-wise error (FWE) correction in SPM5).

2.4.1. Region of interest analysis

To more precisely characterise the contribution of these regions to the different tasks, and determine whether there were conjunction effects that were below threshold in the whole brain analysis, an ROI approach was also taken. Twelve ROIs were generated from the within-domain conjunction analyses (and the flanker task contrast image, as this task did not show significant conjunction effects with either of the other two inhibition tasks in the whole brain analysis). For each ROI, the mean relative signal change associated with each task contrast was calculated and correlations were performed between the values of mean relative signal change and the behavioural measure, or measures, associated with that task. The whole brain conjunction analyses were then repeated, and a small-volume correction applied, using the standard small-volume procedure in SPM5, corresponding to each of these ROIs. This enabled us to establish whether any of these regions showed common between-domain activation that had not reached significance in the whole brain analysis.

3. Results

3.1. Behavioral results

In the GNG task significantly longer reaction times were observed for oddball trials (mean = 342 ms, $\sigma = 38$ ms) than go trials (mean = 329 ms, $\sigma = 41$ ms) ($t = 4.141$, d.f. = 13, $p < 0.005$). The mean percentage of commission errors was 9.4% ($\sigma = 7.5\%$), which was significantly greater than zero ($t = 4.849$, d.f. = 13, $p < 0.0005$). In the stop task, as in the GNG task, significantly longer reaction times were associated with the oddball trials (mean = 507 ms, $\sigma = 144$ ms) compared to control trials (mean = 468 ms, $\sigma = 124$ ms) ($t = 5.65$, d.f. = 13, $p < 0.0005$). The mean duration of the first arrow in the two fMRI sessions of the stop task (which was dependent upon the num-

Table 1

Correlation coefficients for the correlations between the behavioural measures associated with each of the tasks, * $p < 0.05$, ** $p < 0.01$ (not corrected for multiple comparisons)

	1	2	3	4	5	6
1. Flanker RT difference						
2. GNG commission errors	−0.29					
3. Stop signal reaction time	0.16	0.60*				
4. Spatial WM accuracy	0.58*	−0.27	−0.15			
5. Spatial WM RT	0.15	0.50	0.49	−0.11		
6. Verbal WM accuracy	0.25	−0.57*	−0.62*	0.62*	−0.29	
7. Verbal WM RT	0.36	0.36	0.45	0.09	0.94**	−0.14

Table 2Rfx results for each inhibition and working memory task ($p < 0.05$ at the cluster level, with a voxel level threshold of $p < 0.001$)

	Voxel-level <i>T</i> value	Cluster extent	Cluster level corrected <i>p</i> value		MNI coordinates
Flanker task *Incongruent > Congruent	4.74	49	0.017	Right inferior/superior parietal BA 40	30, -54, 45
	4.33				39, -45, 51
	4.40	48	0.019	Left anterior cingulate/corpus callosum	-3, 27, 18
	4.21				-24, 27, 9
	3.71				-15, 27, 9
Go/no-go task No-go > Oddball	6.78	54	0.011	Left insula, BA 13/inferior frontal gyrus BA 47	-42, 12, -3
	6.59	318	0.000	Right inferior frontal gyrus BA 47	45, 15, -3
	5.83				33, 24, -6
	5.17				27, 15, -15
	5.88	49	0.017	Right parietal precuneus	12, -75, 48
	5.82	82	0.001	Left superior/middle frontal gyrus BA 9	-42, 36, 36
	5.77	261	0.000	Right superior frontal gyrus BA 9/middle frontal gyrus BA 46	33, 51, 33
	5.63				24, 48, 33
	5.22				45, 42, 30
	5.38	185	0.000	Right parietal supramarginal gyrus/inferior parietal BA 40	63, -45, 33
	4.70				51, -42, 36
	4.62				54, -36, 42
	5.18	42	0.033	Left inferior parietal lobule	-45, -45, 39
	4.14				-42, -51, 48
	4.94	38	0.048	Left inferior occipital gyrus	-33, -90, -6
4.14	39	0.044	Right cingulated gyrus BA 23	6, -36, 27	
3.85				0, -30, 30	
No-go > Go	7.07	150	0.000	Right inferior frontal gyrus BA 47/insula	33, 24, -6
	4.78				48, 15, -9
	4.04				33, 12, 3
	5.06	98	0.000	Right superior frontal gyrus BA 10/middle frontal gyrus BA 46	27, 51, 30
	4.81				36, 42, 27
4.31				48, 39, 27	
Stop task Stop > Oddball	8.28	387	0.000	Right inferior frontal gyrus BA 47/insula	45, 15, -6
	6.92				36, 15, 3
	6.01				36, 18, -18
	7.91	309	0.000	Left inferior frontal gyrus BA 47/insula BA 13	-45, 15, -9
	6.47				-36, 21, 6
	6.31				-36, 12, 12
	7.44	290	0.000	Right superior/middle frontal gyrus	30, 45, 36
	6.28				30, 42, 24
	5.20				42, 42, 27
	7.24	129	0.000	Right superior frontal gyrus BA 6	15, 9, 69
	4.63				15, -9, 72
	3.85				12, 15, 60
	7.02	411	0.000	Right cingulated BA 32/medial frontal gyrus	9, 18, 45
6.51				9, 6, 48	
6.49				6, 24, 30	
5.73	98	0.000	Right parietal supramarginal gyrus BA 40	54, -45, 36	
4.02				63, -54, 30	

Table 2 (Continued)

	Voxel-level <i>T</i> value	Cluster extent	Cluster level corrected <i>p</i> value		MNI coordinates
Stop > Go	5.67	119	0.000	Right thalamus/lentiform nucleus	9, -18, 9
	4.51				9, -24, -6
	4.41				15, -9, -3
	5.42	53	0.012	Right middle occipital gyrus BA 14	24, -87, -15
	4.57				42, -84, -9
	4.11				39, -78, -15
	5.18	81	0.001	Right parietal precuneus BA 7/inferior parietal lobule	27, -54, 51
	4.05				39, -39, 51
	11.30	3337	0.000	Right inferior frontal gyrus BA 47/medial frontal gyrus BA 32	48, 15, -6
	10.56				6, 9, 48
	10.32				33, 24, -6
	11.14	388	0.000	Left inferior frontal gyrus BA 47/insula BA 13	-45, 15, -9
	8.67				-33, 21, 6
	4.35				-30, 6, 15
	Spatial working memory task Working memory > Control	8.69	754	0.000	Left middle temporal gyrus BA 21/inferior occipital gyrus BA 19
7.13					-45, -81, -12
6.80					-57, -54, 18
8.60		2361	0.000	Right parietal precuneus BA 7/inferior temporal gyrus BA 19	12, -72, 45
8.48					51, -72, -6
8.23					51, -57, 12
7.60		275	0.000	Right thalamus	9, -18, 9
5.85					6, -24, -6
5.04					-3, -18, -6
6.23		69	0.000	Left cingulate gyrus BA 23	-3, -27, 30
10.49		1471	0.000	Right superior parietal BA 7/inferior parietal lobule	27, -69, 51
9.86					21, -78, 51
9.28					39, -42, 42
9.88		1636	0.000	Bilateral middle frontal gyrus BA 6	27, -6, 60
9.52					-24, -6, 57
8.18				6, 15, 54	
Verbal working memory task Working memory > Control	8.32	1141	0.000	Left inferior parietal BA 40/superior parietal BA 7	-42, -51, 51
	7.97				-24, -69, 54
	7.91				-33, -54, 45
	7.24	119	0.000	Right inferior frontal gyrus/insula BA 13	36, 21, -6
	3.82				45, 15, -3
	5.65	117	0.000	Left insula BA 13/inferior frontal gyrus BA 47	-33, 21, 3
	5.00				-42, 15, -6
	5.63	304	0.000	Right inferior frontal gyrus BA 9/middle frontal gyrus	48, 6, 27
	5.31				48, 21, 33
	4.71				57, 6, 36
	11.08	2027	0.000	Left inferior frontal gyrus BA 9/left medial frontal gyrus BA 6	-42, 3, 30
	10.35				-3, -3, 63
	9.89				-42, -6, 51
	8.46	798	0.000	Left superior parietal lobule/inferior parietal lobule BA 40	-30, -60, 42
	8.10				-27, -69, 45
7.88				-42, -45, 42	

Table 2 (Continued)

Voxel-level <i>T</i> value	Cluster extent	Cluster level corrected <i>p</i> value		MNI coordinates
7.65	128	0.000	Right inferior frontal gyrus	36, 21, -6
7.60	504	0.000	Right superior parietal lobule BA 7/inferior parietal lobule BA 40	30, -69, 48
6.89				39, -48, 48
6.47				33, -66, 36
5.66	283	0.000	Right inferior frontal gyrus BA 9/middle frontal gyrus BA 46	45, 3, 30
5.29				51, 24, 30
4.58				45, 42, 30
5.26	123	0.000	Right middle frontal gyrus BA 6	33, -3, 66
4.97				27, -6, 60
5.00	62	0.005	Left middle temporal gyrus	-48, -51, 6
4.65	132	0.000	Left caudate/putamen	-15, -3, 15
4.22				-15, 9, 3
4.22				-3, -18, 15

The significant clusters from the contrasts labeled with an asterisk were used to generate regions of interest for further analysis.

ber of commission errors made by each participant) was 339 ms ($\sigma = 155$ ms) for stop trials and 346 ms ($\sigma = 162$ ms) for oddball trials. The mean SSRT was 166 ms ($\sigma = 66$ ms).

In the flanker task, in keeping with incongruent trials involving a greater reliance on the inhibition of interference from surrounding arrows, significantly more errors were made in the incongruent condition (mean = 2.5%, $\sigma = 2.6\%$) compared to the congruent condition (mean = 0.9%, $\sigma = 0.8\%$) ($t = 3.33$, d.f. = 13, $p < 0.005$), and the mean reaction time was significantly longer for the incongruent trials (mean = 449 ms, $\sigma = 43$ ms) compared to congruent trials (mean = 419 ms, $\sigma = 43$ ms) ($t = 8.49$, d.f. = 13, $p < 0.001$).

The mean accuracy for the spatial working memory task was 88.4% ($\sigma = 6.7\%$), and the mean reaction time was 1158 ms ($\sigma = 219$ ms). The mean accuracy for the verbal working memory task was 91.3% ($\sigma = 6.5\%$), and the mean reaction time was 1460 ms ($\sigma = 147$ ms).

The results of the correlations between the behavioural measures are presented in Table 1. Significant correlations were seen between accuracy on the two working memory tasks and between reaction times on the two working memory tasks. Accuracy on the spatial working memory task positively correlated with the reaction time difference between incongruent and congruent trials in the flanker task. Accuracy on the verbal working memory task negatively correlated with the number of commission errors made in the GNG task and the SSRT. The SSRT also correlated with the number of commission errors in the GNG task.

3.2. fMRI results

3.2.1. Whole brain analysis

The results of the group analysis in which the experimental conditions were compared to the respective control condition, for each task, are shown in Table 2. All combinations of tasks were tested using conjunction analysis, the results of such conjunction analysis within and between task domains are presented in Table 3 and Fig. 2. These conjunction effects reached significance at $p < 0.05$ at the corrected cluster level, with a voxel level threshold of $p < 0.001$. The conjunctions that are not reported did not give significant effects at the $p < 0.05$ corrected cluster level previously described.

Although there was no significant conjunction between all three inhibition tasks in the whole brain analysis, significant conjunc-

tions were seen between the GNG task and the stop task within bilateral inferior frontal gyrus (BA 47) and right superior/middle frontal gyrus (BA 46/9). As anticipated, significant conjunctions were also seen between the two working memory tasks within bilateral frontal and parietal regions.

A significant conjunction was seen between both working memory tasks and the GNG and stop tasks within the right inferior frontal gyrus (90 voxels, maximum/minimum: $x = 45/30$, $y = 30/15$, $z = 9/-12$, a cluster which mostly contained voxels within right inferior frontal cortex BA 47, but which also extended to the insula). The mean relative signal change in this right inferior frontal cluster, for each task contrast, is shown in Fig. 2. Fig. 3 shows that this cluster extends across the border between the right inferior frontal cortex and the insula. Within this cluster we also investigated correlations between the mean relative signal change from each task contrast included in the significant conjunction and the behavioural measure, or measures, associated with that task, but no significant correlations were seen.

For validation, additional analysis was conducted using the go trials as the control condition (with the contrast stop vs. go in the stop task and the contrast no-go vs. go in the GNG task) and the conjunction analyses were repeated using these contrast images. Although the right inferior frontal and right middle/superior frontal conjunctions between the GNG/stop tasks remained significant, the left inferior conjunction was no longer significant. The right inferior frontal conjunction between the GNG task, the stop task and the two WM tasks remained significant. No additional effects were observed from these conjunction analyses.

3.2.2. Region of interest analysis

ROIs were generated from the results of the whole brain conjunction analyses. The ROIs were the three clusters that showed a significant conjunction between the stop and GNG tasks, the 7 clusters that showed a significant conjunction between the two WM tasks, and the two clusters that showed a significant effect in the incongruent vs. congruent contrast from the flanker task. Fig. 4 shows the mean relative signal change associated with each task contrast, for each ROI.

For each ROI we performed small volume corrected conjunction analyses to identify between domain commonalities that had not reached statistical significance in the whole brain analysis. Six

Table 3
Conjunction analysis results

	Voxel-level <i>T</i> value	Cluster extent	Cluster level corrected <i>p</i> value	MNI coordinates	
Spatial and verbal working memory tasks	7.71	635	0.000	Left inferior parietal lobule BA 40	
	7.62			–42, –51, 51	
	7.37			–33, –54, 42 –42, –45, 42	
	7.63	951	0.000	Left frontal precentral gyrus BA 6/medial frontal gyrus	
	7.32			–42, –6, 51	
	7.15			–6, 12, 51 6, 12, 54	
	7.60	461	0.000	Right parietal lobule BA 7/BA 40	
	6.89			30, –69, 48	
	6.32			39, –48, 48 36, –57, 51	
	7.24	104	0.000	Right inferior frontal gyrus BA 47	
	3.82			36, 21, –6 45, 15, –3	
	5.63	117	0.000	Left insula BA 13/inferior frontal gyrus BA 47	
	5.00			–33, 21, 3 –42, 15, –6	
	5.48	221	0.000	Right inferior frontal gyrus BA 9/middle frontal gyrus BA 46	
	4.86			45, 3, 30	
4.43	51, 27, 33 42, 39, 21				
5.26	123	0.000	Right middle frontal gyrus BA 6		
4.97			33, –3, 66		
3.61			27, –6, 60		
Go/no-go and stop tasks (With oddball trials as the control condition)	6.59	209	0.000	Right inferior frontal gyrus BA 47	
	5.68			45, 15, –3	
	4.55			33, 24, –6 36, 21, –15	
	6.09	45	0.025	Left inferior frontal gyrus BA 47	
	5.63			–42, 12, –3	
	5.18	161	0.000	Right superior/middle frontal gyrus BA 46/BA 9	
	4.41			24, 48, 33	
	4.41			45, 42, 30 39, 33, 39	
	(With go trials as the control condition)	7.07	143	0.000	Right inferior frontal gyrus BA 47
		4.78			33, 24, –6
		4.04	48, 15, –9 33, 12, 3		
		5.06	91	0.000	Right superior/middle frontal gyrus BA 10/BA 46
4.81		27, 51, 30			
4.31	36, 52, 27 48, 39, 27				
Flanker task and both working memory tasks	4.74	44	0.027	Right inferior parietal BA 40	
	4.33			30, –54, 45 39, –45, 51	
Go/no-go task and both working memory tasks	5.82	102	0.000	Right inferior frontal gyrus BA 47	
	3.82			33, 24, –6 45, 15, –3	
Stop task and both working memory tasks	5.91	91	0.001	Right inferior frontal gyrus BA 47	
	5.60			33, 24, –9	
	3.82	36, 18, –3 45, 15, –3			
	5.69	126	0.000	Right medial frontal gyrus BA 32/cingulate gyrus	
	5.63			6, 6, 51	
4.91	9, 18, 45 12, 21, 36				

Table 3 (Continued)

	Voxel-level <i>T</i> value	Cluster extent	Cluster level corrected <i>p</i> value	MNI coordinates
	5.14	102	0.000	Left insula BA 13/inferior frontal gyrus BA 47 –33, 24, 3
	5.00			–42, 15, –6
	4.97			–36, 21, –6
	4.85	46	0.022	Right superior parietal BA 7/inferior parietal 27, –54, 48
	4.62			33, –57, 54
	4.01			39, –42, 48
Go/no-go task, Stop task and both working memory tasks (With oddball trials as the control condition)	5.68	90	0.001	Right inferior frontal gyrus BA 47 33, 24, –6
	3.82			45, 15, –3
(With go trials as the control condition)	7.07	93	0.000	Right inferior frontal gyrus BA 47 33, 24, –6
	4.39			45, 15, –3

The significant clusters from the contrasts labeled with an asterisk were used to generate regions of interest for further analysis.

ROIs showed a significant conjunction between all 5 task contrasts. These were the right inferior frontal and right middle frontal ROIs generated from the GNG/stop task whole brain conjunction (Fig. 4a and b) and the WM task whole brain conjunction (Fig. 4d and e), the right parietal ROI generated from the WM task whole brain conjunction (Fig. 4h) and the right parietal ROI generated from flanker task group analysis (Fig. 4k). The more superior middle frontal ROI (BA 6) generated from the WM whole brain conjunction showed a significant small volume corrected conjunction between all tasks except the GNG task (Fig. 4i).

A significant small volume corrected conjunction was seen between all tasks except the flanker task in the left inferior frontal ROI generated from the GNG/stop task whole brain conjunction (Fig. 4c), and the left insula/inferior frontal ROI generated from the WM whole brain conjunction (Fig. 4f). A significant small volume corrected conjunction was observed between the stop task and both WM tasks in the left inferior parietal (Fig. 4g) and the left precentral/medial frontal (Fig. 4j) ROIs that were both generated from the WM whole brain conjunction. The anterior cingulate ROI generated from the flanker task contrast showed a significant

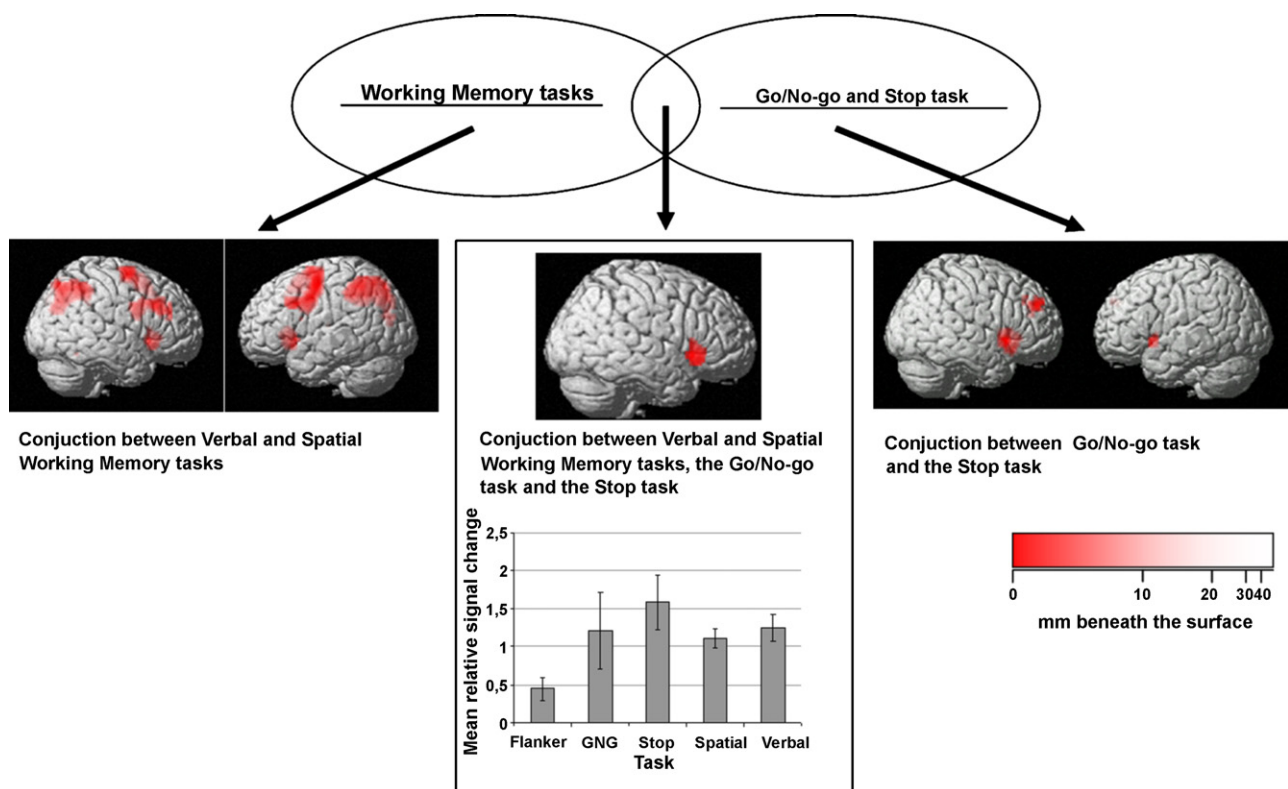


Fig. 2. Significant whole brain conjunction effects within and between the working memory tasks and two of the inhibition tasks (the GNG and stop tasks) (cluster level significance of $p < 0.05$, corrected). The graph shows the mean relative signal change in the right inferior frontal cluster in which the whole brain analysis showed a significant conjunction between both working memory tasks, the GNG task and the stop task, in each task contrast.

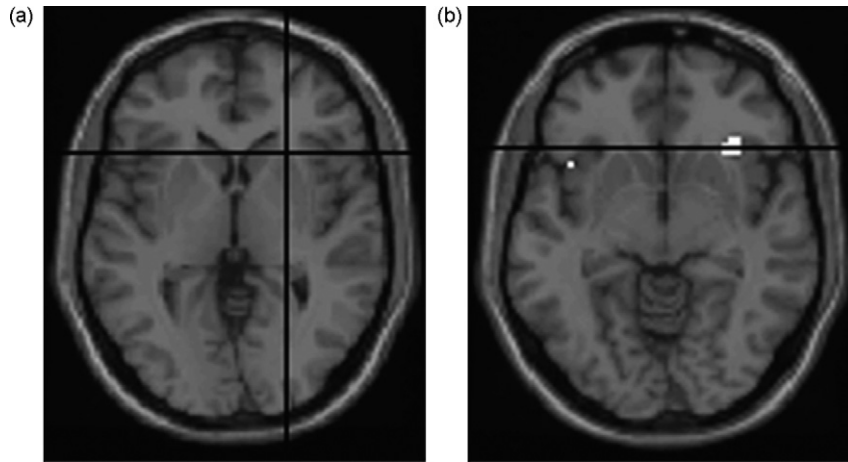


Fig. 3. (a) A template brain with the black lines indicating the localisation of the border between the insula and inferior frontal lobe, at $y = 20$ (MNI), identified according to Naidich et al. (2004). (b) The cluster identified from the whole brain conjunction between all tasks except the flanker task extended across the anterior border of the insula, as indicated by the black line at $y = 20$ (MNI).

small volume corrected conjunction between the flanker task and the stop task.

All of these small volume corrected conjunction results remained significant when the no-go vs. oddball contrast was

replaced with the no-go vs. go contrast and the stop vs. oddball contrast was replaced with the stop vs. go contrast, except for the conjunction between the flanker task and the stop task in the anterior cingulate ROI generated from the flanker task group analysis.

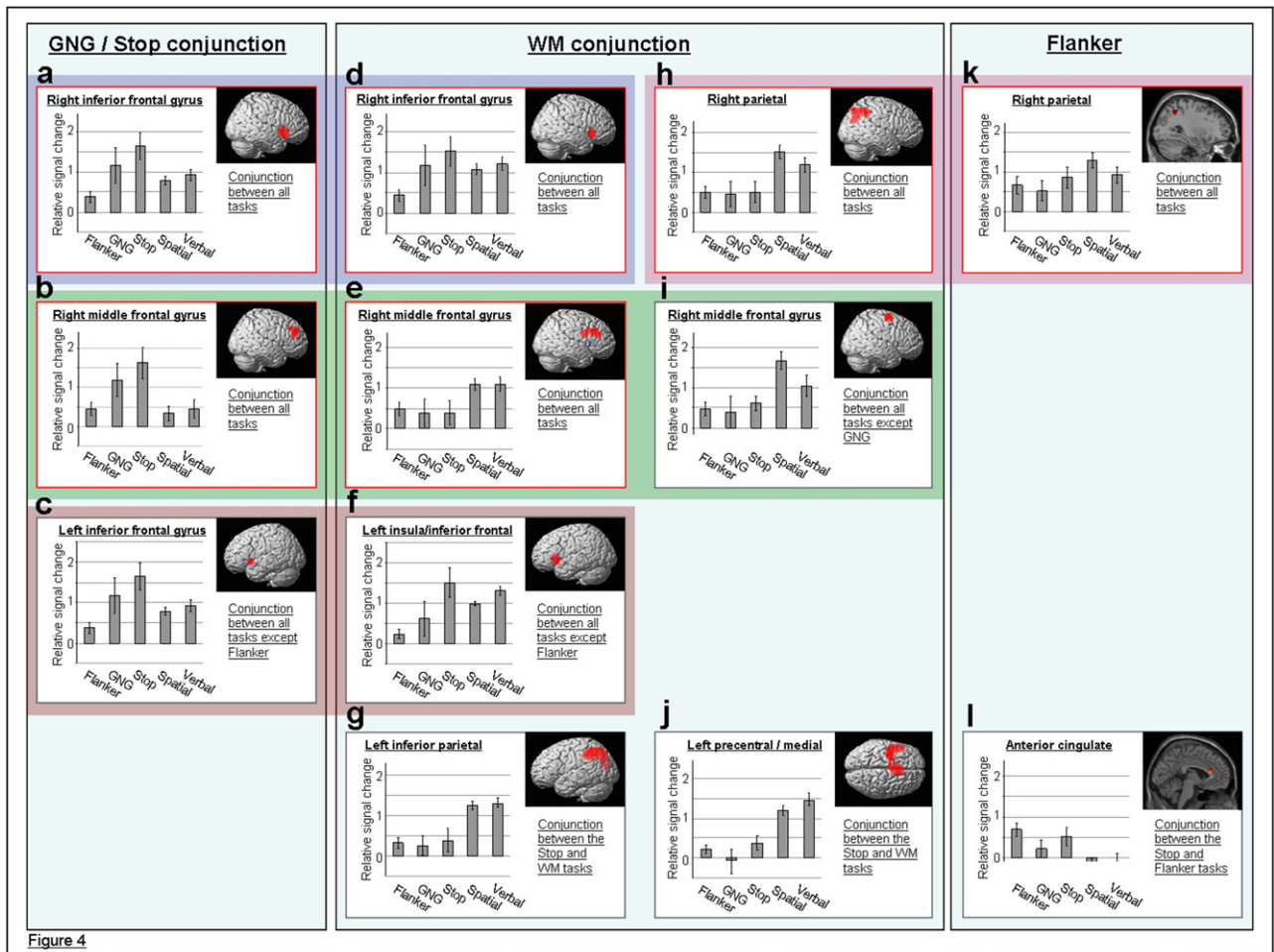


Fig. 4. The 12 ROIs used for the small volume corrected conjunction analyses, generated from the whole brain conjunction analysis between the GNG and stop tasks (a–c), from the whole brain conjunction analysis between the two working memory tasks (d–j), and from the flanker task group analysis (k and l). The graphs show the relative signal change associated with each task contrast, for each ROI. Within each ROI, the combination of tasks that gave a significant conjunction, while including the maximum number of tasks, was identified, and is indicated within this figure.

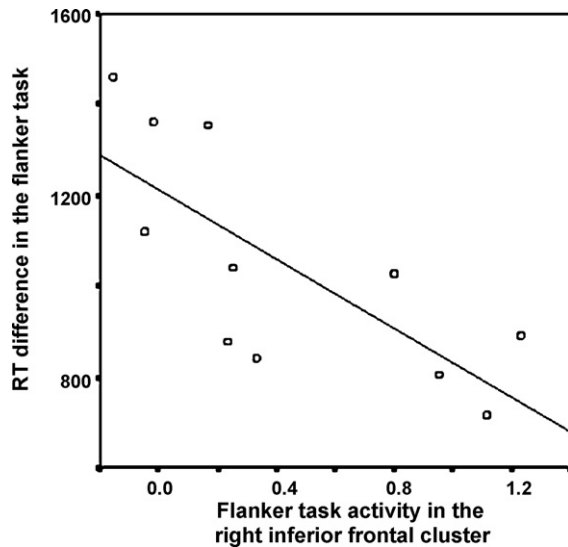


Fig. 5. The correlation between the flanker task activity (from the incongruent vs. congruent contrast) in the right inferior frontal cluster (identified by the conjunction between the two working memory tasks, the GNG task and the stop task), and the difference in reaction time between the two conditions ($r = -0.75$, $p < 0.01$).

Within each ROI, the mean relative signal change associated with each task contrast contributing to the generation of that ROI was correlated with the respective behavioural measure. The flanker task was the only task that showed such a correlation. The mean relative signal change associated with the incongruent vs. congruent contrast significantly correlated with the difference in reaction time between the two conditions in two ROIs. These were the right middle frontal ROI generated from the conjunction between the GNG and stop tasks (Fig. 4b) ($r = -0.68$, $p = 0.020$), and the right middle frontal ROI generated from the conjunction between the two WM tasks (Fig. 4e) ($r = -0.74$, $p = 0.009$). As the right inferior frontal cluster identified by the whole brain conjunction between all tasks except the Flanker task (Fig. 2) showed a significant conjunction between all five tasks when the small volume correction was used (now including the flanker task), correlation analyses was performed between the Flanker task activity within this ROI and the difference in reaction time between the two Flanker task conditions. This was significant ($r = -0.75$, $p < 0.01$, Fig. 5), indicating that greater activity in this region predicted more effective inhibition in incongruent trials.

4. Discussion

Conjunction analysis was used to examine commonalities between the neural correlates of different forms of inhibition and working memory, within the same subjects, and using separate task blocks to avoid the effects of interactions that may occur when inhibition and working memory demands are manipulated within the same task (e.g. Hester et al., 2004). From the whole brain analysis, one area (right inferior frontal gyrus) was identified as showing common activation between the two working memory tasks, the GNG task and the stop task. ROIs were identified from the whole brain within-domain conjunctions, and significant small-volume corrected between-domain conjunctions were identified which did not reach significance in the whole brain analysis. As a result of this additional analysis, significant conjunctions were seen between all tasks (the two working memory tasks, the GNG task, the stop task and the flanker task) within right inferior frontal, right middle frontal and right parietal regions. A significant

conjunction between all tasks except the flanker task was seen in the left inferior frontal gyrus.

In terms of the behavioural measures, there was a significant correlation between SSRT and the number of commission errors made in the GNG task, but not between these measures and the difference in RT between incongruent and congruent trials in the flanker task. These results support the notion that the flanker task may rely more heavily on a different type of inhibition, as indicated by the results of the whole brain conjunction analysis and the small volume corrected conjunction in the left inferior frontal ROI.

4.1. Conjunction analysis—Inhibition tasks

Although the conjunction between all three inhibition tasks was not significant in the whole brain analysis, this analysis did show common activation between the GNG and stop tasks, and significant small volume corrected conjunctions between all inhibition tasks in ROIs within the right inferior frontal gyrus, right middle frontal gyrus and right parietal regions (BA 7/40), and between the GNG task and the stop task in left inferior frontal cortex. These ROI results show some similarity with the common activation reported by Rubia et al. (2001), who also observed common activation between GNG and stop tasks within bilateral inferior frontal (BA 47/44), right middle frontal (BA 9/6) and right inferior parietal (BA 40) regions.

The right inferior frontal gyrus is the region that has most consistently been linked to inhibition by both lesion and neuroimaging studies (reviewed by Aron et al., 2004). The reduced right inferior frontal gyrus activation associated with the flanker task (Fig. 4), which was below threshold in the whole brain analysis, may therefore suggest a reduced reliance on such response inhibition processes in the flanker task, and perhaps a greater reliance on alternative mechanisms. Flanker tasks are believed to involve inhibition of the perceptual processing of competing stimuli (Van Veen et al., 2001), so the flanker task may differ from the other two tasks in that irrelevant information may be inhibited at the perceptual level, rather than at a response-selection stage of processing (Kornblum, Hasbroucq, & Osman, 1990). Similarly, Wilson and Kipp (1998) distinguish between an active suppression process (GNG and stop task) and resistance to interference (flanker task), described as a gating mechanism. There are, however, a number of other task differences which could account for the reduced inferior frontal activation seen in the flanker task, for example, the extent to which the task involves response selection (Rubia et al., 2001) and withholding a prepotent response versus producing an alternative response (Wager et al., 2005). Finally, the three inhibition tasks differ with regard to the relative number of trials that require inhibition, which has been reported to affect the magnitude of Stroop and Stroop-like interference (e.g. Logan & Zbrodoff, 1998). Whereas the GNG and stop tasks within this study involved a smaller percentage of trials requiring inhibition, the numbers of congruent and incongruent trials within the flanker task were approximately equal.

A reliance on a resistance to perceptual interference in the flanker task contrast might also account for the finding of significant ACC activation in this task, which was also seen for the stop task, but not for the GNG task (although differences between the inhibition tasks were not specifically investigated here). ACC has been described as part of a network of cortical regions involved in spatial selective attention (Mesulam, 1990), and is activated by various cognitive/attentional inhibition tasks (for example, a flanker task, a stroop task and a spatial conflict task) (Fan et al., 2003; Peterson et al., 2002; Wager et al., 2005), although not consistently linked to the flanker task (Hazelton et al., 2000). The control of inhibitory processes required for ignoring the distracting arrows within incon-

gruent trials of the flanker task, and for monitoring the area in the center of the screen for the appearance of a vertical arrow in the stop task, may account for the activation of ACC, and the conjunction between the flanker task and the stop task in the ACC ROI, observed here.

The initial conjunction analysis failed to detect right inferior frontal commonality between the flanker task and the other inhibition tasks, because of the relatively low signal change associated with the flanker task (Figs. 2 and 4c and f). However, the correlation between the right inferior frontal flanker task activity and flanker task performance (Fig. 5) is strong evidence that the inferior frontal gyrus is important for performance in the flanker task. One possibility is that the involvement of the inferior frontal gyrus in the flanker task is different, for example that it is activated for shorter periods of time in flanker trials, but that this activation is nevertheless crucial for correct performance.

A conjunction between all inhibition tasks was also seen within ROIs in the right middle frontal gyrus (BA 9/6), an area previously found to be activated by three different types of inhibition task (Wager et al., 2005), and described as part of a “core set of commonly activated regions”. Similarly, right inferior parietal ROIs also showed significant commonality between all three inhibition tasks, in keeping with the results of the study by Wager et al. (2005), which also associated this region with three different inhibition tasks. Such findings will be discussed in more detail later.

4.2. Conjunction analysis – Working memory tasks

Significant conjunctions were seen between spatial and verbal working memory task contrasts within bilateral middle frontal gyrus/precentral gyrus (BA 6), bilateral inferior frontal gyrus (BA 47), and bilateral parietal cortex (BA 40). Although a number of studies have focussed on differences between working memory for different types of stimuli, for example spatial versus nonspatial (Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Courtney, Ungerleider, Keil, & Haxby, 1996), others have argued against domain specificity (Owen, 1997a, 1997b). Overlapping activation patterns have been observed which suggest that any division between different types of working memory is not absolute (Sala, Rämä, & Courtney, 2003). A common prefrontal involvement has been reported in working memory tasks that use verbal, spatial, object and shape stimuli (Baker, Frith, Frackowiak, & Dolan, 1996; Hautzel et al., 2002; Nystrom et al., 2000; Postle, Sten, Rosen, & Corkin, 2000). Klingberg et al. (1996), Klingberg and Roland (1997), and Klingberg (1998) identified parietal and prefrontal regions activated by both visual and auditory working memory tasks.

4.3. Conjunction between inhibition and working memory tasks

Studies that have combined inhibition and working memory demands within the same task have reported overlapping activation in a variety of frontal and parietal regions. For example, common activation has been identified in left middle frontal (BA 9/46) and bilateral inferior frontal regions (BA 47), left inferior parietal lobe (BA 40), the left precuneus and right putamen (Kelly et al., 2006) and left prefrontal cortex (BA 45) (Smith & Jonides, 1998). By manipulating working memory demands within an inhibition task, regions of spatial overlap were identified within right (BA 9) and left (BA 6) middle frontal gyrus, bilateral inferior parietal lobule, ACC, right insula and left putamen (Hester et al., 2004). Working memory and inhibition manipulations have shown overlapping activation in the lateral prefrontal cortex (ventral and dorsal), insula, ACC and parietal cortex (Bunge et al., 2001). Perlstein, Dixit, Carter, Noll, and Cohen (2003) used separate working memory and inhibition tasks and identified the right DLPFC as forming part of a cognitive control

mechanism that appeared to be involved in both working memory and inhibition of a preponent response.

Besides potential problems associated with interactions between inhibition and working memory manipulations within the same task, discussed in the introduction, another possible source of the disparity between the regions of commonality identified within these studies might be the wide variety of tasks employed. Such tasks may involve different forms of inhibition and working memory processing. In the present study three different inhibition tasks were used (designed to correspond to three different types of inhibition) and two working memory tasks were used (spatial and verbal) in an attempt to identify between domain commonality that was not influenced by the choice of task.

With this approach small volume corrected between-domain conjunction analysis revealed significant commonality between all 5 tasks within right inferior frontal (Fig. 4a and b), right middle frontal (Fig. 4b, e and i) and right parietal ROIs (Fig. 4h and k). Three other ROIs showed small volume corrected between domain conjunctions for a subset of these tasks; the left inferior parietal (Fig. 4g) and left precentral/medial frontal (Fig. 4j), which both showed commonality between the stop task and the two WM tasks, and the anterior cingulate (Fig. 4l), which showed commonality between the flanker task and the stop task.

Such between domain commonality may reflect an involvement of response inhibition processes within the working memory tasks (Barkley, 1998; Borgo et al., 2003; Goldman-Rakic, 1995; Roberts & Pennington, 1996), for example, such inhibition processes may play a role in resistance to distraction, which has been closely linked to working memory (McNab & Klingberg, 2008; Oberauer & Kliegl, 2001; Vogel, McCollough, & Machizawa, 2005). Alternatively, commonality may reflect common mechanisms within the two task domains (Braver & Barch, 2002; Casey, Giedd, & Thomas, 2000) or an involvement of working memory processes in the inhibition tasks (Aron & Poldrack, 2005; Roberts, Hager, & Heron, 1994), for example in the retention of task rules.

The observation of between domain commonality within the right inferior frontal gyrus is consistent with correlations between damage to this region and both stop signal reaction time and spatial working memory performance (Clark et al., 2007). Although this region extended to the insula, as was also the case in other studies of inhibition (Bunge et al., 2002; Kelly et al., 2006; Rubia et al., 2001), it seems unlikely that such commonality reflects general arousal. The use of the oddball condition was designed to reduce confounding effects associated with the appearance of infrequent stimuli, including differences in arousal. Furthermore, this is the region that has most consistently been linked to inhibition by the results of both lesion and neuroimaging studies (reviewed by Aron et al., 2004) and activation in this region has been specifically related to response inhibition (Kawashima et al., 1996; Rubia et al., 2001). The observation of enhanced right inferior frontal activation associated with the GNG and stop inhibition tasks, and to a lesser extent the flanker task and working memory tasks, further supports the notion that this region is essentially linked to response inhibition.

In a previous study, DLPFC activity was observed for GNG trials during a counting GNG task, but not during a simple GNG task (Mostofsky et al., 2003), suggesting that the DLPFC may be linked to working memory rather than inhibitory demands. However, in working memory tasks, a requirement for stimuli to be manipulated has been shown to involve the additional recruitment of DLPFC (Owen, Evans, & Petrides, 1996; Owen et al., 1999; Postle, Berger, & D'Esposito, 1999), suggesting an association between DLPFC and executive control. A common executive component may therefore account for the DLPFC conjunction between the WM and inhibition tasks studied here. In line with this suggestion, following a systematic comparison of 5 cognitive demands as diverse

as response selection, working memory maintenance and stimulus recognition, Duncan and Owen (2000) reported a high degree of similarity in terms of mid-dorsolateral, mid-ventrolateral and dorsal anterior cingulate recruitment. One of the interpretations offered for such a finding is that these frontal regions are associated with functions that are sufficiently general to contribute to a broad range of cognitive problems.

Whereas, in the whole brain analysis, a more anterior right middle frontal region was associated with the conjunction between the GNG and stop inhibition tasks, a more posterior right middle frontal region showed a significant conjunction between the two working memory tasks. As comparisons between activity in the different task conditions, within these ROIs, would be confounded by the procedure in which the ROIs were selected, a domain-specific dissociation in the localization of right middle frontal inhibition/working memory effects may exist, but further studies would be required to confirm this.

A right parietal ROI was identified from the working memory task conjunction. This region closely corresponds to the load sensitive region identified by Todd and Marois (2004) and McNab and Klingberg (2008). The cluster extent was $x = 12/48$, $y = -36/-77$ and $z = 25/56$ within this study, and in McNab and Klingberg (2008) the cluster extent was $x = 24/59$, $y = -50/-77$ and $z = 36/51$. Furthermore, with the whole brain analysis, this region was associated with the conjunction between the two working memory tasks, and not with conjunctions between inhibition tasks. It is therefore possible to speculate that such activity may represent working memory storage particularly within the working memory tasks, but also, to a lesser degree, within the inhibition tasks, perhaps associated with the storage of task rules and stimulus-response representation, as previously suggested (Hester et al., 2004).

Within the two left inferior frontal ROIs (identified from the conjunction between the inhibition tasks and from the conjunction between the GNG and stop tasks) a significant small volume corrected conjunction was seen between all tasks except the flanker task. Although studies of inhibition have tended to show right-sided prefrontal activation (Garavan et al., 1999; Hazeltine et al., 2000; Kawashima et al., 1996; Konishi et al., 1998), the left inferior frontal gyrus has been associated with the inhibition of conflicting verbal information (D'Esposito, Postle, Jonides, & Smith, 1999; Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998). It is therefore possible to speculate that the reduced left inferior frontal activity may be linked to a reduced demand upon verbal processes in the flanker task.

Although it is only possible to speculate about the nature of the underlying mechanisms accounting for such observations of commonality, the between domain conjunctions observed here provide a neural basis for the interrelationship between working memory and inhibition, and particularly implicate the right inferior frontal gyrus, right middle frontal gyrus and right parietal region. Commonality in the left inferior frontal gyrus and a more superior region of the right middle frontal gyrus seems to be dependent on the nature of the inhibition task, possibly due to different tasks involving different forms of inhibition.

The use of oddball trials enabled us to control for stimulus frequency (and familiarity) differences within the GNG and stop task contrasts, so it seems unlikely that differences in stimulus novelty could account for the significant conjunction between task domains. Significantly longer reaction times for oddball trials compared to go trials are in keeping with the oddball effect and justify the use of such oddball trials as a control condition. Additional analyses were performed using contrasts in which go trials rather than oddball trials acted as the control condition. Although this resulted in small changes to the results of the within-domain conjunctions (left inferior frontal gyrus showed a significant whole brain con-

junction between the GNG task and the stop task, and the ACC ROI showed a significant small volume corrected conjunction between the flanker task and the stop task, only when oddball trials were used), the choice of control condition did not influence the identification of between domain conjunctions in either the whole brain or the ROI analysis.

It should be noted that the hypothesis of inhibitory and working memory demands both placing strain on a common neural network assumes that cognitive processes that share brain loci also share underlying cognitive components. This suggestion may not necessarily be true, for example there is evidence from single cell research that cells in the same region can have different functions (Hanes, Patterson, & Schall, 1998). However, by using conjunction analysis to identify commonalities between inhibition and working memory processing in separate task blocks, with a repeated measures design, this study extended the approach beyond the comparison of results from different inhibition and working memory studies involving different subjects, and beyond the use of a single task in which working memory and inhibition manipulations are combined. In this way we aimed to reduce confounds associated with individual differences, and reduce the effects of interactions between inhibitory and working memory demands. By using different inhibition and working memory tasks we were able to identify regions of overlap that were unaffected by the choice of task, apparently indicative of commonality between domain general effects.

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