Examining a supramodal network for conflict processing:

A systematic review and novel fMRI data for related visual and auditory Stroop tasks

Katherine L Roberts, Deborah A Hall*

MRC Institute of Hearing Research

University Park

Nottingham

NG7 2RD

* corresponding author

email : D.Hall@ihr.mrc.ac.uk

Tel : +44 (0)115 922 3431

Fax : +44 (0)115 951 8503

Abstract

Cognitive control over conflicting information has been studied extensively using tasks such as the colour-word Stroop, flanker, and spatial conflict task. Neuroimaging studies typically identify a fronto-parietal network engaged in conflict processing, but numerous additional regions are also reported. Ascribing putative functional roles to these regions is problematic, since some may have less to do with conflict processing *per se*, but could be engaged in specific processes related to the chosen stimulus modality, stimulus feature, or type of conflict task. In addition, some studies contrast activation on incongruent and congruent trials, even though a neutral baseline is needed to separate the effect of inhibition from that of facilitation.

In the first part of this paper, we report a systematic review of 34 neuroimaging publications, which reveals that conflict-related activity is reliably reported in anterior cingulate cortex and bilaterally in lateral prefrontal cortex, anterior insula, and the parietal lobe. In the second part, we further explore these candidate ‘conflict’ regions through a novel fMRI experiment in which the same group of subjects perform related visual and auditory Stroop tasks. By carefully controlling for the same task (Stroop), the same to-be-ignored stimulus dimension (word meaning), and by separating out inhibitory processes from those of facilitation, we attempt to minimise the potential differences between the two tasks. The results provide converging evidence that the regions identified by the systematic review are reliably engaged in conflict processing. Despite carefully matching the Stroop tasks, some regions of differential activity remained, particularly in the parietal cortex. We discuss some of the task-specific processes which might account for this finding.

Introduction

The ability to process conflicting information and respond appropriately is critical to cognitive control. Many laboratory tasks have been devised to test conflict processing, and these generally require subjects to suppress the tendency to make an automatic or natural response in favour of an alternative stimulus-response mapping. The colour-word Stroop task is a classic conflict paradigm of this type. In this task, subjects are required to name the colour of a printed word, whilst ignoring the meaning of the word. In congruent trials, the print colour and word meaning are compatible, while in incongruent trials they are not (e.g. ‘RED’ printed in blue ink). Incongruent trials reliably lead to performance costs in both reaction times (RTs) and accuracy, reflecting the need to inhibit the irrelevant stimulus feature and its corresponding inappropriate response. Other conflict tasks include i) the flanker task (Eriksen & Eriksen, 1974) where flanking arrows interfere with judgments about the direction of a central target arrow, ii) spatial conflict or ‘Simon’ tasks where stimulus-response incompatibility is generated by, for example, requiring a right-handed response to a left-sided stimulus (Lu & Proctor, 1995; Simon, 1990; Simon & Berbaum, 1990) and iii) the ‘go/no-go’ task where subjects must withhold a response to a non-target stimulus (see Buchsbaum, Greer, Chang, & Berman (2005) for a review).

Neuroimaging studies have used these different tasks to identify the neural substrates of conflict processing. These studies typically identify a bilateral anterior network comprising the anterior cingulate cortex (ACC) and lateral prefrontal cortex (LPFC) (Buchsbaum et al., 2005; MacDonald, Cohen, Stenger, & Carter, 2000; Milham, Banich, & Barad, 2003; Smith & Jonides, 1999; Wager et al., 2005), with many studies also noting involvement of the parietal lobe (Buchsbaum et al., 2005; Bush et al., 1998; Carter, Mintun, & Cohen, 1995; George et al., 1994; Hazeltine, Poldrack, & Gabrieli, 2000; Milham et al., 2002). Across different tasks, the fronto-parietal pattern appears to differ somewhat in terms of its regional specificity and hemispheric symmetry (Buchsbaum et al., 2005). Nevertheless, these regions are more consistently reported to be engaged in conflict processing than other cortical areas, such as the inferior temporal gyrus (Bush et al., 1998; Carter et al., 1995; Fan, Flombaum, McCandliss, Thomas, & Posner, 2003; Peterson et al., 2002), fusiform gyrus (Ruff, Woodward, Laurens, & Liddle, 2001; Ullsperger & von Cramon, 2001), middle occipital gyrus (Bush et al., 1999; Compton et al., 2003; Ullsperger & von Cramon, 2001) and posterior cingulate (Paus, Petrides, Evans, & Meyer, 1993; Wager et al., 2005). Differences across studies are typically attributed to individual biases at the perceptual, cognitive or response levels that are unique to each task. For example, any task-related activity could differ according to whether the conflict is associated with irrelevant stimulus features, response selection, response execution, and/or response mapping. Additionally, task-specific strategies may be employed to overcome conflict, such as selectively attending to the central arrow in the flanker task (Casey et al., 2000).

In the first part of this paper, we examine the strength of evidence for the fronto-parietal network (ACC, LPFC and parietal lobe) engaged during conflict processing, by reporting a systematic review of published neuroimaging studies on this topic. It is perhaps surprising that such evidence is not more readily available, although at least two meta-analyses were reported in 2005. One was concerned only with reports of the ‘go/no-go’ task: a distinctive task that requires withholding a prepotent response, rather than producing a competing response (Buchsbaum et al., 2005). In this meta-analysis of 18 go/no-go studies, inhibition was reliably associated with activation in bilateral (but predominantly right-hemisphere) LPFC and inferior parietal lobe (IPL), and unilateral cingulate, fusiform gyrus, putamen, and thalamus. Another meta-analysis combined studies of ‘go/no-go’, flanker and spatial conflict tasks (Wager et al., 2005), although details such as the number of studies are not provided. They found a more lateralised pattern of common activation including dorsolateral PFC (DLPFC, BA 9 & 46), medial prefrontal and angular gyrus on the right side, anterior insula on the left side and anterior cingulate on the midline. Consistent with the Buchsbaum study, the right-hemisphere bias was largely driven by the results from go/no-go studies. Here, we present a systematic review which combines data from 40 neuroimaging studies of conflict tasks. We excluded go/no-go tasks, to include only studies which required subjects to process conflicting information and make an unnatural or competing response. The review should therefore identify regions of the fronto-parietal network, and elsewhere, which are reliably engaged by these processes.

While meta-analyses and reviews can identify consistent patterns of activation, interpretations about common functional anatomy are somewhat limited by their low spatial resolution and limited power. For a number of reasons (Brett, Johnsrude, & Owen, 2002), stereotaxic co-ordinates can be difficult to compare across subject groups and across studies. At the individual level, participants’ brains vary in size and shape. Differences are also introduced during normalisation due to variations in normalisation templates and the contrast or signal-to-noise of structural images. Finally, researchers employ different analysis techniques and reporting conventions. To circumvent these problems, a few studies have presented different conflict tasks to the same group of individuals, enabling direct statistical comparisons to be applied (Fan et al., 2003; Peterson et al., 2002; Wager et al., 2005).

In the second part of this paper, we adopt this approach by examining the degree to which two closely related conflict tasks engage common cortical areas in the same group of participants. We then relate these findings to the candidate regions defined by the systematic review in Part 1. We were struck by the widespread differences in the patterns of conflict-related activity reported by Fan et al. (2003). Fan et al. report activation associated with conflict processing on three different tasks: the colour-word Stroop task; the flanker task; and a spatial conflict task. ACC and PFC were active during conflict processing on all three tasks, but a number of additional areas were engaged during conflict processing on only one or two of the tasks. In fact, in this study, the differences appear to far exceed the commonalities. Our imaging experiment explores Fan et al.'s (2003) claim that regions of differential activation are engaged in task-specific operations to resolve the conflict. Unlike Fan et al's study, and other previous studies (Peterson et al., 2002; Wager et al., 2005), our fMRI experiment takes the same basic conflict task (the Stroop task) and presents it in different sensory modalities (vision and audition). Thus, we are able to control for the same task (Stroop), the same to-be-ignored stimulus dimension (word meaning) and hence the same conflict-resolution operations (i.e. suppression of the irrelevant stimulus dimension and competing response selection). This general approach has been used previously to identify regions of common and task-specific activation (Banich et al., 2000a; Banich et al., 2000b). In the first of these studies (Banich et al., 2000a) subjects were presented with incongruent or neutral colour-word stimuli and colour-object stimuli, and asked to monitor for an atypical item (either a colour, word, or object). On both tasks, right prefrontal cortex was more active for incongruent stimuli than for neutral stimuli when subjects monitored the more attentionally-demanding stimulus dimension (colour in the colour-word task, and object in the colour-object task). However, additional regions of frontal cortex were active for the colour-word stimuli only, and neither task produced conflict-related activation in ACC or parietal lobe, suggesting that monitoring for an atypical item does not produce strong conflict-related activation. The second paper (Banich et al., 2000b), compared activation associated with conflict on colour-word and spatial-word Stroop tasks (Experiment 1). Both tasks revealed activation associated with conflict processing in the dorsolateral prefrontal cortex and left inferior parietal cortex. Unfortunately this paper focused on dissociations between activation on the two tasks, and did not report a conjunction analysis. As with previous studies, the analysis revealed a number of regions which were more active during conflict processing on one task than the other, including subdivisions of prefrontal cortex, cingulate cortex, supplementary motor area, and parietal cortex.

Interpretative leverage is gained when behavioural data (RTs and accuracy) are also acquired during the imaging session. Significant correlations between behavioural measures of interference would validate the claim that different conflict tasks probe common cognitive processes. However, some studies have failed to find correlations between behavioural measures from different conflict tasks, despite showing common fronto-parietal activation (Fan et al., 2003; Wager et al., 2005). In a previous study of 40 participants (Roberts, Hall, & Summerfield, 2004; see also Roberts, Summerfield, & Hall, 2006), we reported that RT interference costs were positively correlated across the two Stroop tasks presented in our fMRI study, strengthening our claim that they are well-matched in terms of their capacity to elicit cognitive conflict. Another novel feature of our fMRI experiment is that we exclude the effects of facilitation from those of inhibition. Previous studies which have compared activation associated with conflict from different tasks (Fan et al., 2003; Peterson et al., 2002; Wager et al., 2005) have contrasted activation on incongruent and congruent trials. However, this contrast includes components relating to both inhibitory and facilitatory processes. By including a neutral condition (in which the irrelevant dimension does not indicate a possible response), it is possible to separately evaluate interference generated by conflicting information, and facilitation generated when both stimulus dimensions indicate the same response. This may be important, since facilitation benefits are smaller (MacLeod, 1991) and more variable (Fan et al., 2003) than interference costs. Arguably, some of the reported differences in conflict-related activity across tasks could reflect this variability in facilitatory effects, rather than differences in conflict processing.

Part 1 : Systematic review of the conflict network

The systematic review identified cortical regions consistently associated with conflict processing. Neuroimaging (fMRI and PET) studies including the keywords ‘Stroop’, ‘Simon’ or ‘flanker’ were identified through searches of ScienceDirect, Ingenta, PsycINFO, and the Proceedings of the National Academy of Sciences (PNAS) in August 2004. Five additional papers were identified through citation searches of recent review articles (Barch et al., 2001; Bush et al., 1998; Cabeza & Nyberg, 2000; Duncan & Owen, 2000; Nee, Jonides, & Wager, 2004). Studies from the resulting list of 80 papers were included if they satisfied five criteria: i) reported a conflictgenerating task, ii) analysed data using comparisons between incongruent trials and either neutral or congruent trials, iii) reported results for normal adult participants, including studies which reported separate results for control and patient groups, iv) reported a whole-brain analysis (not a region of interest analysis), and v) reported stereotaxic co-ordinates of peak activity. Thirty-four papers, reporting a total of 40 experiments, met these criteria. Of these, 24 used a neutral baseline, while 16 used the congruent condition as a baseline. Details of these papers are listed in Appendix 1. Those peak co-ordinates reported in Talairach space (Talairach & Tournoux, 1988) were converted into MNI space using objectively-defined transformation parameters (Brett, Christoff, Cusack, & Lancaster, 2001). To account for residual variability in the precise location of the peak co-ordinate, we extended each peak for 5 mm in 3-dimensions to form a cubic activation volume of 11 mm^3. This size approximates the typical smoothing kernel applied to image data for group analysis. A separate binary map was generated for each of the 40 experiments and the binary maps were then summed together to produce probability maps (Figure 1, column 1). An advantage of this procedure is that it reduces any weighting bias due to those studies that report multiple peaks in the same region, although we acknowledge that it does underestimate the typical extent of activation around each peak.

-- Figure 1 --

The probability map revealed a broad scatter of peak co-ordinates throughout the brain. Table 1 summarises the most *typical* pattern by reporting the locations of those centres of activation identified by at least five studies. Activation was most reliably reported in the left inferior frontal gyrus (IFG), part of the LPFC. In this region, nine studies reported peaks located around the central co-ordinate. The right IFG was also commonly engaged by conflict processing. Other centres of common activation included ACC, bilateral parietal lobes and anterior insula cortices. We acknowledge that this approach adopts a rather stringent criterion, since it excludes those studies which might also report activation in the vicinity of these regions, but whose peak co-ordinates are located more than 10 mm away from the centre of activation. Nevertheless, the review was successful in confirming the proposed fronto-parietal model of conflict processing. It also raises interesting questions about the role of the anterior insula in conflict processing. The role of the insula is not well-defined, but it has been associated with error processing, failed inhibition in go/no-go studies, and response to oddball stimuli (Ramautar et al., 2006).

-- Table 1 --

To investigate whether some of the study-to-study variability might be reliably associated with the different types of conflict task, we further divided the 40 experiments into two groups: those using a traditional colour-word Stroop task (n=21) and those using a different type of Stroop or other conflict task (n=19). Separate probability maps were created using the same procedure as before and are shown in Figure 1 for comparison (columns 2 and 3). Of the nine studies which contributed to the centre of activation in left IFG, seven were colour-word Stroop tasks. The remaining two were adapted colour-word Stroop tasks (Norris, Zysset, Mildner, & Wiggins, 2002; Zysset, Müller, Lohrmann, & von Cramon, 2001) in which subjects were shown two rows of letters and decided whether the ink colour on the top row corresponded to the colour name on the bottom row. Although this task differs from the colour-word Stroop task, it is the only other conflict task in the systematic review which requires the subject to inhibit a prepotent response generated by fast and automatic colour-word reading. A greater number of colour-word Stroop studies also contributed to the conjoint activation in the bilateral insula cortex (six out of seven studies in the left hemisphere and four out of five studies in the right). The remaining study was a speeded flanker task (Ullsperger & von Cramon, 2001). Activation in the other cortical regions showed no clear differentiation across the types of task. We anticipated more consistency in the ‘colour-word Stroop’ group than in the ‘other conflict task’ group, as the latter is contributed to by numerous different tasks. However, we were still struck by the degree to which activation from the two groups was segregated, particularly in left IFG.

The systematic review confirms that IFG, ACC, parietal lobe, and insula cortex are reliably engaged during conflict processing. Furthermore, the pattern of results suggests that conflict tasks of the same type are more likely to generate activation in the same portion of these regions, since maximum overlap occurred for the colour-word Stroop tasks in left IFG and anterior insula. One interpretation might be that the colour-word Stroop elicits a specific set of task-related processes. Although one can only speculate from these results, it is perhaps the linguistic nature of the conflict that determines the left-sided emphasis in IFG (Bookheimer, 2002).

Part 2 : An fMRI study of visual and auditory Stroop tasks

This study explores behavioural and neural correlates of two Stroop tasks. We examine the effect of interference on both behavioural performance and the pattern of cortical activation, and compare these effects across the two tasks. The results of the systematic review generated *a priori* predictions about the location of conflict-related activation and informed our approach for statistical inference.

Participants

Sixteen healthy volunteers participated in this study. The mean age of the group was 24.3 years (range 16-42) and nine were male. Participants were all right-handed native English speakers, with normal or corrected-to-normal visual acuity and normal hearing thresholds (< 25 dB HL between 250 Hz and 8000 Hz). Participants gave informed consent prior to the study and were paid for their time. Six additional participants were scanned whilst performing the Stroop tasks, but their data had to be rejected because head movement exceeded 6 mm during one of the tasks.

Stimuli and presentation methods

All participants were first exposed to Stroop conflict as part of a larger (n = 40) behavioural study (Roberts et al., 2006). In the behavioural study the auditory Stroop task was presented in the context of a spatial cueing paradigm, where target words were preceded by cues, and stimuli were presented in a random order. As part of this study subjects also performed a simple (uncued) colour-word Stroop task, with stimuli presented in counterbalanced order, with every condition following every other condition equally often (Roberts et al., 2004). Sixteen of the subjects from the behavioural study returned to take part in the neuroimaging study. Target stimuli were identical in the behavioural and fMRI studies, but for the fMRI study we presented both tasks without cues, and optimised the detectability of conflict-related activation by presenting trials in blocks of the same trial type. Blocks were of 24 s duration and contained a sequence of 14 trials. The imaging study also included a baseline condition in which subjects either saw a black cross or heard a 1 kHz tone, presented at the same rate as the words. Visual Stroop stimuli were generated following Fan et al. (2003). Target words (RED, BLUE, GREEN, YELLOW, LOT, SHIP, KNIFE, FLOWER) were presented in one of four colours (red, blue, green, or yellow). Different colour-word combinations produced congruent, incongruent, and neutral conditions. These stimuli were first presented to a flat-screen monitor in a sound-attenuated testing room. A single letter of the colour-word Stroop stimuli subtended 0.58° of visual angle in height and 0.49° in width. The gap between letters subtended 0.08° of visual angle. During the fMRI study, these stimuli were back-projected onto a screen placed at the end of the scanner bed and were viewed by participants through prism goggles. The size of the stimuli was adjusted to match the visual angle of the behavioural study. Stimuli used in the auditory Stroop task were words (HIGH, LOW, DAY) spoken on a high- and low-pitch and recorded in a high-quality digital format (sampling rate = 44,100 Hz). Three exemplars of each stimulus were selected to provide overall similarity in average duration (457 ms), pitch (high $F_0 = 290$ Hz; low $F_0 = 112$ Hz), and amplitude (RMS = -20.26 dB re: full scale). Again, different pitch-word combinations produced congruent, incongruent, and neutral conditions. Spoken words were presented via Sennheisser HD 480II headphones in the sound booth, and specially-modified electrostatic transducers in the MR scanner (Palmer, Bullock, & Chambers, 1998). The speech was clearly audible above the background scanner noise. For each visual trial, participants were required to identify the ink colour and respond by pressing the corresponding button on a four button response box. For each auditory trial, participants discriminated the pitch by pressing one of two buttons. In-house software was used for stimulus presentation and response logging. Responses were only logged if executed within 1.5 seconds of stimulus onset. For each task 11 blocks of each condition were presented in a counterbalanced order, giving a total of 154 trials per condition.

Imaging protocol

Scanning was performed on a dedicated echo-planar imaging 3-Tesla MR system with purpose-built head gradient coils (Bowtell & Peters, 1999) and a TEM head coil (Nova Medical Inc.). A total of 354 functional scans were acquired during each Stroop task. These scans were collected using a T2*-weighted sequence (flip angle 90°; in-plane resolution = 3 x 3 mm; 128 x 64 matrix; TR = 3 s, TE = 36 ms). Each scan contained 22 coronal slices, 8 mm thick with no slice gap. For the majority of participants, the field of view covered the whole head, but for some it excluded the occipital pole. Thus, an additional whole-head 64-slice T2*-weighted image at 4 mm slice thickness was acquired to facilitate post-processing.

Image analysis

Image analysis was performed on a Sun Ultra 2 computer (Sun Microsystems) using SPM99 software (Friston, Holmes et al., 1995: http://www.fil.ion.ucl.ac.uk/spm) running in MATLAB v6.5 (Mathworks Inc., Natick, MA, USA). The first two scans were discarded to allow for steady-state saturation and the remaining scans were realigned to account for head movement (Friston, Ashburner et al., 1995). By selecting reference scans as the final scan in the first time series and the first scan in the second time series, we were able to minimise the effects of motion that occurred between the two tasks. All scans were transformed into a standard brain space using an amended version of the EPI template available in SPM99 (for details see Hall, Fussell, and Summerfield (2005)). Transformation was achieved using a nine-parameter affine procedure, with non-linear deformations using discrete cosine transform basis functions to match the 64-slice scan to the template using a least-squares algorithm (Friston, Ashburner et al., 1995).

Normalised data were up-sampled to a resolution of 3 x 3 x 4 mm and spatially smoothed using a Gaussian kernel of 10 mm full-width-at-half-maximum. Data were modelled separately for each participant in a first-level analysis. The three Stroop task conditions were modelled using box-car functions, convolved with a 6-s delayed haemodynamic response function. Six additional regressors modelled estimates of the signal related to head movement and rotation. Cyclical variations in signal intensity, which could be associated with aliased respiratory and cardiac effects, were treated by high-pass filtering the time series using cosine basis functions up to a maximum frequency of 0.2 cycles per minute. T contrasts specified the difference between the incongruent and the neutral condition and the difference between the congruent and the neutral condition. Individual contrast images were then entered into a second-level, random-effects analysis. One sample t tests were performed on the group data to separately determine the effects of interference and facilitation. In addition, to identify regions of common activation across the two tasks, we computed a conjunction analysis using SPM2 software (Nichols, Brett, Andersson, Wager, & Poline, 2005). This analysis properly assesses the conjunction using the null hypothesis to identify regions that reach statistical significance in *both* contrasts. Unless otherwise stated, we specified a significance threshold of $p<0.001$ (uncorrected) to find all voxels displaying a higher magnitude of activation on one condition relative to another ($z = 3.09$). In order to reduce Type 1 error (false positive error for one in every 1000 voxels), we took only those areas which comprised at least 12 suprathreshold voxels. This extent threshold approximates to the expected number of voxels per cluster (<k>) for the chosen height threshold.

Results

Behavioural performance

Behavioural performance during the fMRI study was highly accurate. Overall, subjects failed to respond during the 1.5-second response window on 2.25% of trials on the auditory Stroop task, and 2.81% of trials on the visual Stroop task. In addition, subjects responded incorrectly on 3.21% of auditory trials, and 3.95% of visual trials. For each participant, median correct RTs were calculated for each trial type. Group averaged RTs and error rates are shown in Table 2.

-- Table 2 --

ANOVA analyses revealed that RTs were significantly ($p<0.001$) influenced by trial type for both visual ($F_{2,30} = 68.1$) and auditory ($F_{1.2,18.4} = 23.2$) Stroop tasks. Where the assumption of sphericity is violated a Greenhouse-Geisser correction has been applied. Both visual and auditory Stroop tasks elicited a significant ($p<0.01$)

interference effect ($t_{15} = 5.5$ and $t_{15} = 4.4$, respectively), as well as a significant effect of facilitation ($t_{15} = 6.1$ and $t_{15} = 3.8$). In both tasks, the interference cost was greater than the facilitation benefit (visual Stroop, 62 and 46 ms; auditory Stroop, 59 and 23 ms, respectively). Performance accuracy was also strongly influenced by trial type (visual Stroop, $F_{2,30} = 14.1$; auditory Stroop, $F_{2,30} = 8.1$, $p<0.01$). Planned contrasts revealed that this effect was due to an interference cost (visual Stroop: $t_{15} = 3.1$; auditory Stroop: $t_{15} = 2.5$, $p<0.05$) in both tasks, but a facilitation effect only in the visual task ($t_{15} = 1.6$, $p<0.05$) (auditory task: $t_{15} = 1.0$).

Prior to the fMRI study, all participants had been exposed to the Stroop tasks as part of a larger behavioural study (Roberts et al., 2004; Roberts et al., 2006). In the behavioural study, the auditory Stroop task was presented in the context of a cueing paradigm. Measures of interference and facilitation were obtained by collapsing the data across the different cueing conditions. The pattern of results found in the behavioural study was similar to that found in the imaging study, for the same set of participants (Table 2). The main difference was that participants responded more slowly to the auditory trials during the behavioural study than during the scanning session. This is most likely to be a consequence of the cueing protocol, since no comparable difference in overall response times was observed for the visual Stroop task, which was uncued in both studies.

RT measures of interference were correlated (0.28, $p = 0.08$) across the visual and auditory Stroop tasks presented in the behavioural study ($n = 40$) (Roberts et al., 2004). This result confirms that the two tasks were well-matched in terms of their capacity to elicit cognitive conflict. The facilitation effect was not correlated across tasks (0.04, p = 0.8). Behavioural measures of interference and facilitation obtained during the fMRI study were not significantly correlated between the two Stroop tasks. However, with only 16 participants it is difficult to interpret non-significant correlations.

Activation patterns

Interference

To isolate those regions associated with conflict processing we used a directional hypothesis in which activation during neutral blocks was subtracted from that during incongruent blocks. This approach circumvents concerns about defining interference as the subtraction of congruent from incongruent trials (Fan et al., 2003; Peterson et al., 2002; Wager et al., 2005). The result revealed activity in widespread regions of the brain, which were broadly similar for the visual and auditory Stroop tasks. Common activation included bilateral frontal and left parietal regions and the anterior cingulate cortex (see Table 3). In the visual Stroop task, additional regions of activation included the IFG (extending up to the anterior insula) and parietal lobe on the right side.

-- Table 3 --

To evaluate the consistency with which our experimental results matched the outcome of the systematic review we overlaid the two sets of results (Figure 2). The white outlines depict the border of the principal regions identified by the systematic review

(Table1), excluding regions reported by only one study. Regions which were commonly engaged by visual and auditory Stroop conflict are shown in blue. The overlay reveals a high degree of coincidence. Activation within the bilateral frontal cortex (Figure 2; panels A and B), anterior cingulate (C) and left parietal lobe (D), for both visual and auditory Stroop conflict, coincided with the regions that had been identified by the systematic review. The right parietal activation was distant from the peak region identified by the review, but close to another region where three studies reported peaks (E). The right-sided IFG/insula activation observed during visual conflict was also close to the region defined by the systematic review (F). Given that the review had revealed the involvement of the *bilateral* anterior insula in conflict processing, we explored our experimental results again using a less stringent height threshold ($p<0.01$). Although not precisely coincident, the experimental data are generally supportive of this claim. For both tasks we found some support for left hemisphere involvement of the anterior insula (G). The visual analysis showed a cluster of 17 voxels with a peak location at -45 18 -4 mm and a voxel-level Z value of 2.87 ($P=0.002$), while for the auditory task the large frontal cluster extended to include the anterior insula, with a local peak at -33, 21, 0 ($z = 3.14$, $p=0.001$). In addition, the lower threshold revealed common activation in right IPL, coincident with the region identified by the systematic review (H).

-- Figure 2 --

Correlations between behavioural performance and the strength of activation in the above regions would strengthen the evidence for a supramodal network engaged in conflict processing. For each subject, we extracted an index of the response magnitude within each of the clusters identified by the conjunction analysis. The response magnitude was based on the beta weights from the individual-level contrast between the incongruent and neutral conditions. These values were then correlated with RT and accuracy measures of conflict. When both tasks were combined, activation in left LPFC was broadly and positively correlated with accuracy costs (r=0.304, p=0.09). On the auditory task, RT and accuracy interference costs were correlated with the strength of activation in left LPFC (r=0.462, p=0.07) and ACC (r=0.466, p=0.07), respectively. No correlations were found for the visual task alone. Correlations from only 16 subjects should not be given too much weight, but these results are certainly consistent with the involvement of left PFC and ACC in conflict processing.

Task-specific conflict processing

A paired t-test showed two regions which were significantly more active during auditory Stroop conflict (incongruent – neutral) than during visual conflict. One region (30 voxels; peaks at -48, 42, 0 and -54, 24, 0) is part of the left LPFC region and appears to result simply from more extensive activation of LPFC during auditory conflict than during visual conflict. The other region (18 voxels; peaks at -63, -24, -4, and -63, -33, -4) is located in the superior temporal sulcus (STS), at the lower boundary of the auditory cortex. This region was not identified by the incongruent vs. neutral contrast. Only one area was significantly more active during visual conflict than auditory conflict: an area of 17 voxels in the right IFG (BA 11), with a peak at 27, 30, -16 mm. This peak is immediately adjacent to peak in IFG for the colour-word Stroop task (24, 30, -16).

While the SPM paired t test did not identify any task-specific activation in the parietal lobe, subdivisions within this region appeared to be differentially engaged by visual and auditory conflict (see Figure 2, panel D). Common activation was found around the intraparietal sulcus (IPS), but activation then extended downwards: anteriorly and laterally for auditory conflict, and posteriorly and medially for visual conflict. Two different underlying patterns could give rise to this effect. First, activation could be centred on a common region for both visual and auditory contrasts, with the spread of activation extending in different directions. Second, interference could activate two separate regions, which intersect due to the spatial smoothness of the data. Figure 3 plots the activation responses in an alternative format which has previously been used to address questions of this sort (Hall et al., 2002). Responses were obtained for points along a curved section ($z = -0.1111y^2 - 13.598y -367.76$) of left-hemisphere cortex passing through the maximal peaks for visual and auditory conflict; located in the superior parietal lobe (SPL, at -30, -72, 36, $z = 5.21$)) and IPL (at -39, -51, 36, $z = 4.78$) respectively. The curve was also constrained to pass through another significant peak of activity for auditory conflict located in SPL (at -33, -66, 44, $z=3.87$). Each response value was based on the beta weight from the group-level contrast between incongruent and neutral conditions, for the visual and auditory tasks separately. Values for points along this curve were obtained for sagittal slices between $x = -63$ mm and -9 mm (in 3 mm steps), and were then plotted in 3D mesh graphs (Figure 3). The graphs for both modalities show a ridge of activation across the IPS (illustrated by the black line). However, the peak of the visual Stroop contrast is clearly shifted in position relative to that for the auditory Stroop task. This shift across the axis of the IPS indicates functional segregation, suggesting that the peak of the conjunction reflects the intersection of the spread of activation from two separate regions, rather than a common core region within the IPS. To statistically evaluate this hypothesis we entered the incongruent – neutral activation values into a two-way task (auditory, visual) by location (auditory peak, visual peak) ANOVA. We selected the most robust peak of conflict-related activation within left parietal lobe for the auditory (IPL: -36, -51, 36) and visual (SPL: -30, -72, 36) tasks. As hypothesised, the results reveal a significant interaction ($F(1,15) = 5.443$, $p<0.05$) but no significant main effects. A graph of the interaction can be seen in Figure 3.

Facilitation

Subtracting congruent from neutral trials revealed activation in bilateral fusiform gyrus for the visual Stroop task (Table 3), but no significant effects for the auditory Stroop task. Thus, in line with behavioural evidence, the neural correlates of facilitation appear to be markedly less than those of interference.

Discussion

Neuroimaging studies implicate a range of cortical regions in conflict processing. Here, we report a systematic review which confirms that conflict processing is reliably associated with activation in ACC, and bilaterally in IFG, anterior insula, and the parietal lobe. Since comparing activation patterns across different studies has limited sensitivity, we also conducted a novel fMRI study to directly compare conflict-related activation on two different tasks: a visual colour-word Stroop task, and an auditory pitch-word Stroop task. These related tasks again confirmed common activation in ACC, bilateral PFC, and left SPL, which coincided with the regions identified by the systematic review. In addition, activation associated with visual Stroop conflict was located close the systematic review region in the right anterior insula. A less conservative threshold revealed common activation in left anterior insula and right IPL, again coincident with the regions identified by the systematic review. These findings provide support for a supramodal fronto-parietal network engaged during conflict processing.

To determine whether these cortical regions were directly involved in conflict processing, we additionally examined whether activation in these regions covaried with the extent of behavioural interference. The results indicate a link between increased interference costs and increased activity in LPFC and ACC. In other studies, practice-related reductions in interference costs have been associated with decreases in DLPFC activity, suggesting a specific role of DLPFC in implementing attentional control (Milham, Banich, Claus, & Cohen, 2003). Similarly, Wager et al. (2005) have shown that activation in bilateral anterior insula is positively correlated with behavioural measures of interference on three different conflict tasks, suggesting that the insula has a generic role in conflict processing.

We used a blocked design to optimise detectability of conflict-related activation. However, it is important to note that subjects may have engaged different strategies on this task than on an event-related task in which stimuli are presented in random order. Leung et al. (2000) compared patterns of conflict-related activity on blocked (Peterson et al., 1999) and event-related (Leung et al., 2000) Stroop tasks conducted in their laboratory. They found that the patterns of activation were broadly similar in terms of which regions were strongly activated. However, the distribution of insula and inferior frontal activation was more extensive in the event-related design. In addition, activation in middle frontal gyrus and the parietal lobe was bilateral in the event-related study but predominantly left-sided in the blocked design. The results from our fMRI study are consistent with this finding, and we would suggest that the left-hemisphere bias in our findings might reflect strategic preparatory processes which are present in blocked designs but might not be evident in event-related designs. One important drawback to the blocked design is that, in the congruent condition, it is not possible to determine whether subjects were complying with the task instructions and attending to the colour or pitch of the word or instead were simply attending to the word itself. As a result, one cannot confirm that the visual facilitation effect observed in the fusiform gyrus reflects different trial types. Instead, it may reflect different task strategies, such as those related to word reading. For this reason, a functional interpretation of the 'facilitation' effects must be viewed with caution. It is interesting to note that when directly contrasting incongruent and congruent conditions, Peterson et al. (2002) reported conflict-related activation in bilateral inferior temporal gyrus, close to the regions that we found to be activated in the contrast between neutral and congruent conditions. These findings underscore the importance of including a neutral condition to allow the effects of interference to be isolated.

Turning back to the conflict-related activity, in addition to finding strong support for a fronto-parietal network engaged in conflict processing, the results of the systematic review and fMRI study indicate regions which might be engaged in task-specific operations. In the next part of this section we consider this task-specific activation, and suggest some possible explanations for these findings.

We chose to present the same task (Stroop) in different perceptual modalities (vision and audition) in the hope that any regions which were not commonly engaged would be easily ascribed to differences in task modality, rather than differences in conflict processing. Three regions were reliably activated by conflict processing on the visual task, but not the auditory task: right IFG, left premotor cortex, and the precuneus. Of these, only right IFG activity significantly differed across modalities. It is not clear how these regions might be attributed to differences in task modality. Instead they may relate to specific strategies used to overcome conflict on the two tasks. Activity in these regions could also be influenced by the different types of response required: for the visual task subjects made an arbitrary four-button stimulus-response mapping, while for the auditory task a more intuitive two-button mapping was required (high = upper button; low = lower button). In particular, this might account for the lack of reliable auditory conflict-related activation in the premotor cortex, since this region is involved in motor planning.

We also observed evidence for a dissociation of activation across the parietal lobe. While there were no significant differences between the amount of conflict-related activation on the two tasks, analysis of variance revealed a significant interaction between the type of conflict (auditory or visual) and the location of the activation (auditory peak within IPL or the visual peak within SPL). We identify two possible explanations for this task-related shift in the pattern of parietal activity. As with the other regions engaged by only one of the tasks, it could relate to task-specific strategies for overcoming conflict. This explanation is particularly applicable to the parietal lobe, since it has been shown to play a role in selective attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000). Selective attention can be employed in task-specific ways to reduce conflict: for example, an effective strategy for overcoming colour-word Stroop conflict is to selectively attend to a small section of the word. To differentiate between selective-attention and conflict-resolution processes, Casey et al. (2000) varied the probability of an incongruent trial being presented on a flanker task. They hypothesised that if an incongruent trial was highly probable, an efficient strategy would be to selectively attend to the target item in the array, suppressing the flankers. However, this strategy might prove less efficient when incongruent trials were less probable, and would therefore be less likely to be engaged. The results showed different patterns of activation for the two probabilities, and were consistent with an anterior system involved in conflict resolution, incorporating ACC and DLPFC, and a posterior system involved in selective attention, including SPL. Our finding of common conflict-related activation in ACC and PFC, and task-specific activation in the parietal lobe, is also consistent with these functional roles. An alternative explanation for the pattern of activity in the left parietal lobe is that it reflects the flow of information between sensory and higher-order areas. Task-specific activation appears to spread from IPS towards the respective sensory cortex (anterior and lateral to auditory cortex; and posterior and medial to visual cortex), along well-specified anatomical pathways linking the sensory cortices to the parietal lobe (e.g. Mishkin, Ungerleider, & Macko, 1983; e.g. Romanski et al., 1999). In addition, modality-specific activation has been reported in the parietal lobe during auditory and visual spatial localisation tasks (Bushara et al., 1999) and oddball tasks (Nishitani, Nagamine, & Shibasaki, 1998). While the pattern of activation in these studies does not precisely match that found in this study, they nevertheless provide further support for modality-specific processing in the parietal lobe.

While the fMRI study revealed common activation in lateral PFC and anterior insula, there was some suggestion of task-specificity when the systematic review studies were divided into colour-word Stroop tasks and other types of conflict task. One simple explanation for this pattern of results is that these regions are engaged in processes which were common to both visual and auditory Stroop tasks, but which differ across other types of conflict task. Unfortunately our data do not allow us to address this issue fully, and so questions such as which specific processes are involved, and whether other tasks might activate nearby areas of the same functional regions, remain open.

Conclusions

We present converging evidence for a supramodal fronto-parietal network engaged during conflict processing. A systematic review of 34 published neuroimaging studies revealed that ACC, and bilateral IFG, parietal lobe, and anterior insula, are reliably engaged during conflict processing. An fMRI study of related visual and auditory Stroop tasks confirmed the involvement of these candidate regions, even when we contrasted incongruent with neutral trials (thereby removing any potential effects of facilitation from the conflict network). Regions of task-specific processing were also identified, and are discussed in terms of flow of activation from sensory areas, selective attention strategies for overcoming conflict, and task-specific stimulus-response mappings.

References

Barch, D. M., Braver, T. S., Akbudak, E., Conturo, T., Ollinger, J., & Snyder, A. (2001). Anterior cingulate cortex and response conflict: effects of response modality and processing domain. *Cerebral Cortex, 11*, 837-848.

Bookheimer, S. (2002). Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience, 25*, 151-188.

Bowtell, R., & Peters, A. (1999). Analytic approach to the design of transverse gradient coils with co-axial return paths. *Magnetic Resonance in Medicine, 41*, 600-608.

Brett, M., Christoff, K., Cusack, R., & Lancaster, J. (2001). Using the Talairach atlas with the MNI template. *NeuroImage, 13*(6), S85.

Brett, M., Johnsrude, I. S., & Owen, A. M. (2002). The problem of functional localization in the human brain. *Nature Reviews: Neuroscience, 3*, 243-249.

Buchsbaum, B. R., Greer, S., Chang, W.-L., & Berman, K. F. (2005). Meta-analysis of neuroimaging studies of the Wisconsin Card-Sorting task and component processes. *Human Brain Mapping, 25*(1), 35-45.

Bush, G., Frazier, J. A., Rauch, S. L., Seidman, L. J., Whalen, P. J., Jenike, M. A., et al. (1999). Anterior cingulate cortex dysfunction in attention-deficit/hyperactivity disorder revealed by fMRI and the counting Stroop. *Biological Psychiatry, 45*, 1542-1552.

Bush, G., Whalen, P. J., Rosen, B. R., Jenike, M. A., McInerney, S. C., & Rauch, S. L. (1998). The counting Stroop: An interference task specialised for functional neuroimaging - validation study with functional MRI. *Human Brain Mapping, 6*, 270-282.

Bushara, K. O., Weeks, R. A., Ishii, K., Catalan, M.-J., Tian, B., Rauschecker, J. P., et al. (1999). Modality-specific frontal and parietal areas for auditory and visual spatial localisation in humans. *Nature Neuroscience, 2*(8), 759-766.

Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience, 12*(1), 1-47.

Carter, C. S., Mintun, M., & Cohen, J. D. (1995). Interference and facilitation effects during selective attention: An $H_{20}{}^{15}O$ PET study of Stroop task performance. *NeuroImage, 2*, 264-272.

Casey, B. J., Thomas, K. M., Welsh, T. F., Badgaiyan, R. D., Eccard, C. H., Jennings, J. R., et al. (2000). Dissociation of response conflict, attentional selection, and expectancy with functional magnetic resonance imaging. *PNAS, 97*(15), 8728-8733.

Compton, R. J., Banich, M. T., Mohanty, A., Milham, M. P., Herrington, J., Miller, G. A., et al. (2003). Paying attention to emotion: An fMRI investigation of cognitive and emotional Stroop tasks. *Cognitive, Affective, & Behavioral Neuroscience, 3*(2), 81-96.

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience, 3*(3), 292-297.

Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences, 23*, 475-483.

Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & Psychophysics, 16*(1), 143-149.

Fan, J., Flombaum, J. I., McCandliss, B. D., Thomas, K. M., & Posner, M. I. (2003). Cognitive and brain consequences of conflict. *NeuroImage, 18,* 42-57.

Friston, K. J., Ashburner, J., Frith, C. D., Poline, J.-B., Heather, J. D., & Frackowiak, R. S. J. (1995). Spatial registration and normalization of images. *Human Brain Mapping, 3*, 165-189.

Friston, K. J., Holmes, A. P., Poline, J.-B., Grasby, P. J., Williams, S. C. R., Frackowiak, R. S. J., et al. (1995). Analysis of fMRI time-series revisited. *NeuroImage, 2,* 45-53.

George, M. S., Ketter, T. A., Parekh, P. I., Rosinsky, N., Ring, H., Casey, B. J., et al. (1994). Regional brain activity when selecting a response despite interference: An H215O PET study of the Stroop and an emotional Stroop. *Human Brain Mapping, 1*, 194-209.

Hall, D. A., Fussell, C., & Summerfield, A. Q. (2005). Reading fluent speech from talking faces: Typical brain networks and individual differences. *Journal of Cognitive Neuroscience, 17*(6), 939-953.

Hall, D. A., Johnsrude, I. S., Haggard, M. P., Palmer, A. R., Akeroyd, M. A., & Summerfield, A. Q. (2002). Spectral and temporal processing in human auditory cortex. *Cerebral Cortex, 12*, 140-149.

Hazeltine, E., Poldrack, R., & Gabrieli, J. D. E. (2000). Neural activation during response competition. *Journal of Cognitive Neuroscience, 12*(Supplement 2), 118-129.

Lu, C. H., & Proctor, R. W. (1995). The influence of irrelevant location information on performance - a review of the Simon and spatial Stroop effects. *Psychonomic Bulletin & Review, 2*(2), 174-207.

MacDonald, A. W., Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science, 288,* 1835-1838.

MacLeod, C. M. (1991). Half a century of research on the Stroop effect: An integrative review. *Psychological Bulletin, 109*(2), 163-203.

Milham, M. P., Banich, M. T., & Barad, V. (2003). Competition for priority in processing increases prefrontal cortex's involvement in top-down control: an event related fMRI study of the Stroop task. *Cognitive Brain Research, 17,* 212-222.

Milham, M. P., Banich, M. T., Claus, E. D., & Cohen, N. J. (2003). Practice-related effects demonstrate complementary roles of anterior cingulate and prefrontal cortices in attentional control. *NeuroImage, 18,* 483-493.

Milham, M. P., Erickson, K. I., Banich, M. T., Kramer, A. F., Webb, A., Wszalek, T., et al. (2002). Attentional control in the aging brain: insights from an fMRI study of the Stroop task. *Brain and Cognition, 49*, 277-296.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences, 6,* 414-417.

Nee, D. E., Jonides, J., & Wager, T. D. (2004). *A meta-analysis of interference-resolution tasks.* Paper presented at the Meeting of the Cognitive Neuroscience Society.

Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J.-B. (2005). Valid conjunction inference with the minimum statistic. *NeuroImage, 25*, 653-660.

Nishitani, N., Nagamine, T., & Shibasaki, H. (1998). Modality-specific subregions in human inferior parietal lobule: A magnetoencephalographic study during cognitive tasks. *Neuroscience Letters, 252*, 79-82.

Norris, D. G., Zysset, S., Mildner, T., & Wiggins, C. J. (2002). An investigation of the value of spin-echo-based fMRI using a Stroop color-word matching task and EPI at 3T. *NeuroImage, 15*, 719-726.

Palmer, A. R., Bullock, D. C., & Chambers, J. D. (1998). A high-output, high-quality sound system for use in auditory fMRI. *NeuroImage, 7*, S359.

Paus, T., Petrides, M., Evans, A. C., & Meyer, E. (1993). Role of the human anterior cingulate cortex in the control of oculomotor, manual, and speech responses: A positron emission tomography study. *Journal of Neurophysiology, 70*(2), 453-469.

Peterson, B. S., Kane, M. J., Alexander, G. M., Lacadi, C., Skudlarski, P., Leung, H.-C., et al. (2002). An event-related functional MRI study comparing interference effects in the Simon and Stroop tasks. *Cognitive Brain Research, 13*, 427-440.

Roberts, K. L., Hall, D. A., & Summerfield, A. Q. (2004). Conflict resolution in vision and audition: Behavioural and neuroimaging data. *NeuroImage, 22*(Suppl. 1), e2103-e2105.

Roberts, K. L., Summerfield, A. Q., & Hall, D. A. (2006). Presentation modality influences behavioural measures of alerting, orienting, and executive control. *Journal of the International Neuropsychological Society, in press*.

Romanski, L. M., Tian, B., Fritz, J., Mishkin, M., Goldman-Rakic, P. S., & Rauschecker, J. P. (1999). Dual streams of auditory afferents target multiple domains in the primate prefrontal cortex. *Nature Neuroscience, 2*(12), 1131-1136.

Ruff, C. C., Woodward, T. S., Laurens, K. R., & Liddle, P. F. (2001). The role of the anterior cingulate cortex in conflict processing: evidence from reverse Stroop interference. *NeuroImage, 14*, 1150-1158.

Simon, J. R. (1990). The effect of an irrelevant directional cue on human information processing. In R. W. Proctor & T. G. Reeve (Eds.), *Stimulus-response compatibility: An integrated perspective* (pp. 31-88). Amsterdam: Elsevier.

Simon, J. R., & Berbaum, K. (1990). Effect of conflicting cues on information processing: the 'Stroop effect' vs. the 'Simon effect'. *Acta Psychologica, 73,* 159-170.

Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science, 283*, 1657-1661.

Talairach, J., & Tournoux, P. (1988). *Co-Planar stereotaxic atlas of the human brain*. New York: Thieme.

Ullsperger, M., & von Cramon, D. Y. (2001). Subprocesses of performance monitoring: a dissociation of error processing and response competition revealed by event-related fMRI and ERPs. *NeuroImage, 14*, 1387-1401.

Wager, T. D., Sylvester, C.-Y. C., Lacey, S. C., Nee, D. E., Franklin, M., & Jonides, J. (2005). Common and unique components of response inhibition revealed by fMRI. *NeuroImage, 27*, 323-340.

Zysset, S., Müller, K., Lohrmann, G., & von Cramon, D. Y. (2001). Color-word matching Stroop task: Separating interference and response conflict. *NeuroImage, 13*, 29-36.

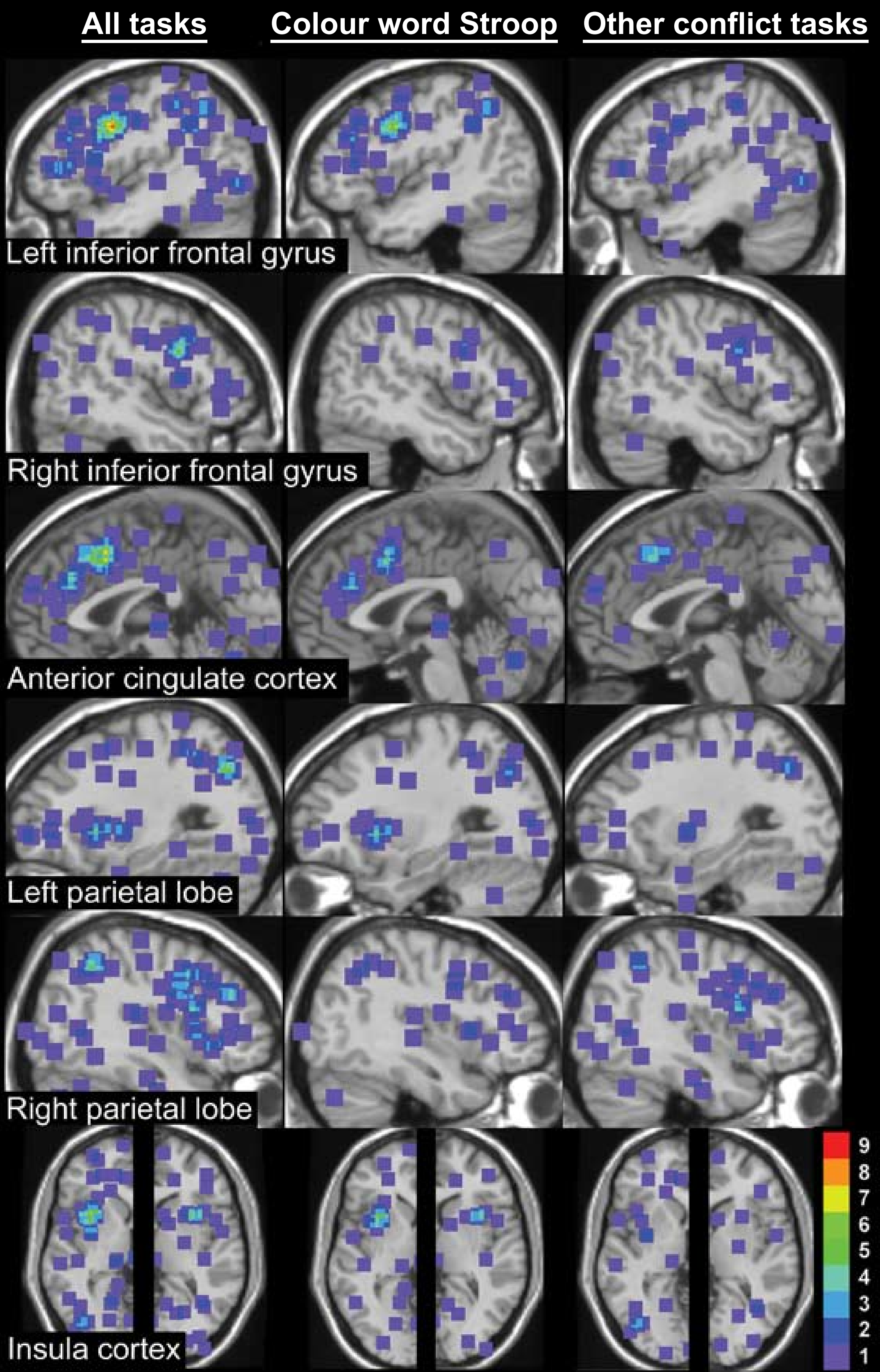
Figure Captions

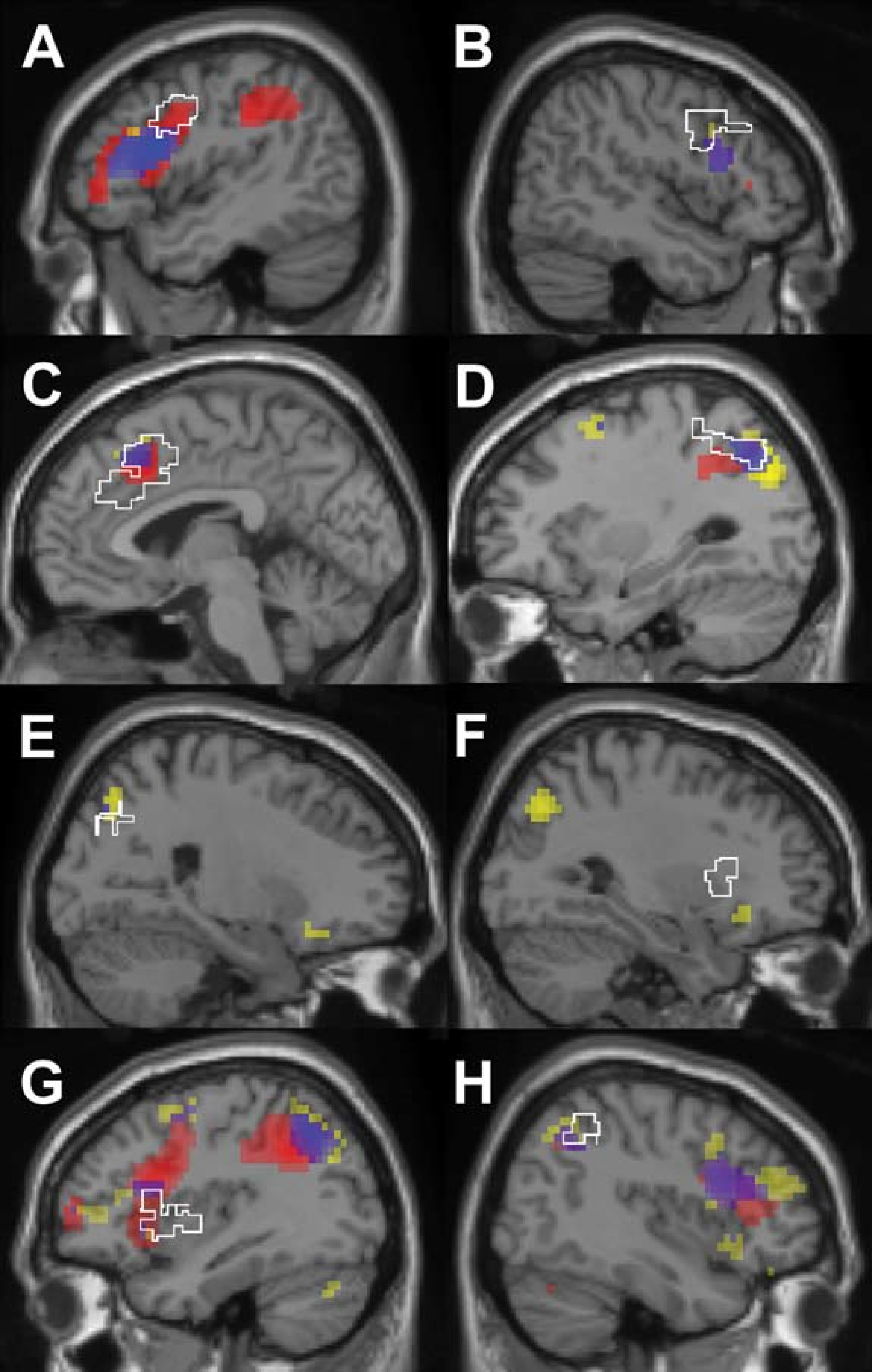
Figure 1: Probability maps showing the distribution of previously-reported peaks of conflict-related activation, overlaid onto a canonical brain. The first column of images reports the outcome of the complete meta-analysis. For each brain region, sagittal slices are displayed through the peak co-ordinates reported in Table 1. The insula cortex is presented on axial slices, again taken through the peak co-ordinates. The two additional columns of images illustrate the contribution of the 21 traditional colour-word Stroop tasks (second column) and the 19 other studies of conflict processing (third column) to the overall pattern of activity reported in the first column. The colour scale shows the number of studies reporting peaks in each region.

Figure 2: Interference-related activation on the auditory (red) and visual (yellow) Stroop tasks, and from a conjunction of the two (blue). Regions identified by the meta-analysis are outlined in white. Panels are as follows (coordinates in MNI space). A: L PFC, x=-45. B: R PFC, x=48; C: ACC, x=-3; D: L SPL, x=-30; E: R SPL, x=24 (region identified by only 3 meta-analysis studies); F: R IFG / ant. ins., x=30 (visual Stroop only); G: L IFG / ant. ins., x=-36, $p<0.01$; H: R IPL, x=41, $p<0.01$.

Figure 3: Magnitude of conflict-related activation (incongruent - neutral) in the left parietal lobe resulting from the two Stroop tasks. The red and yellow dots indicate the location of the peak of activation for the auditory and visual tasks, respectively, while the blue dot shows the peak of the conjunction. SPL denotes the superior parietal lobe and IPL denotes the inferior parietal lobe. The black line shows the approximate location of the intraparietal sulcus. The example sagittal slice is at x = -36 mm; the

white line shows the shape and location (in y and z) of the curve. The middle inset shows the significant interaction between the type of conflict (auditory or visual) and spatial location (auditory or visual activation peak). The solid line represents the size of the auditory conflict effect at the two spatial locations. The dotted line represents the visual conflict effect.


All tasks
Colour word Stroop
Other conflict tasks
Left inferior frontal gyrus
Right inferior frontal gyrus
Anterior cingulate cortex
Left parietal lobe
Right parietal lobe
Insula cortex
9
8
7
6
5
4
3
2
1


A
B
C
D
E
F
G
H

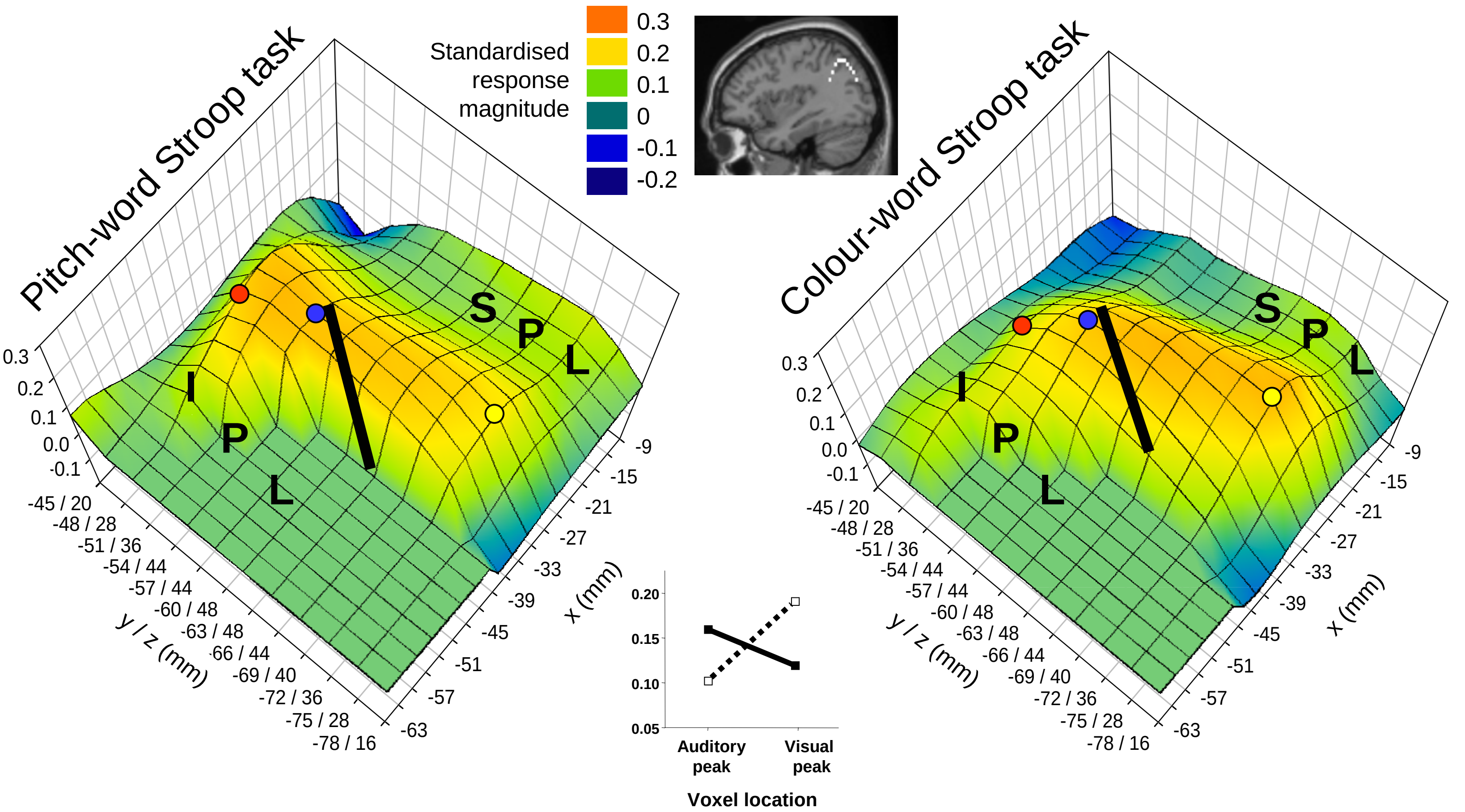

Pitch-word Stroop task
Colour-word Stroop task
Standardised response magnitude
0.3
0.2
0.1
0
-0.1
-0.2
S
P
L
I
P
L
0.3
0.2
0.1
0.0
-0.1
-45 / 20
-48 / 28
-51 / 36
-54 / 44
-57 / 44
-60 / 48
-63 / 48
-66 / 44
-69 / 40
-72 / 36
-75 / 28
-78 / 16
y / z (mm)
-9
-15
-21
-27
-33
-39
-45
-51
-57
-63
x (mm)
0.20
0.15
0.10
0.05
Auditory peak
Visual peak
Voxel location

Table 1: Regions of activation reliably reported in studies of conflict processing. This table reports those co-ordinates which were identified in five or more studies. Co-ordinates are reported in MNI space.

Region	BA	Max. Overlap	Approx. Centre			Extent in X	Extent in Y	Extent in Z
L IFG	44	9	-43	5	35	-51:-37	-3:14	28:41
R IFG	44	5	48	10	31	46:51	8:12	27:35
ACC	32	7	1	12	47	-8:5	11:27	35:52
L SPL	7	6	-28	-67	40	-31:-25	-71:-65	39:45
R IPL	40	5	41	-51	46	41:42	-53:-50	46:47
L Ant. Ins.		7	-31	14	1	-36:-26	6:16	0:5
R Ant. Ins.		5	31	13	5	31:31	10:16	0:5

IFG: inferior frontal gyrus; ACC: anterior cingulate cortex; SPL: superior parietal lobe; IPL: inferior parietal lobe; Ant. Ins.: anterior insula cortex.

Table 2: Overall reaction times (RTs) and error rates for the different trial types within the Stroop task (n=16 participants). The first value in each cell relates to performance measured during fMRI scanning using a blocked-trial design. The second value (in parentheses) relates to performance for the same set of participants using a randomised-trial design, measured in a quiet laboratory.

Task	Incongruent	Neutral	Congruent
Reaction time (ms)			
Visual Stroop	723 (737)	661 (662)	615 (633)
Auditory Stroop	578 (729)	518 (619)	495 (590)
Error rates (%)			
Visual Stroop	7.0 (7.2)	5.0 (8.9)	3.9 (6.8)
Auditory Stroop	6.1 (8.9)	3.2 (2.8)	2.4 (1.0)

Table 3: Areas of activity associated with interference (incongruent - neutral) and facilitation (congruent vs. neutral) for the visual and auditory Stroop tasks (p<0.001, extent > 12 voxels). The size of the activation cluster is given by the number of suprathreshold voxels and the cluster level significance is indicated by ***p<0.001, **p<0.01 and *p<0.05. All peak co-ordinates are reported in MNI space and peak locations are estimated using the Brodmann atlas.

		Visual Stroop		Auditory Stroop		Conjunction	
Region	BA	# voxels	Peak	# voxels	Peak	# voxels	Peak
Incongruent - Neutral							
L lateral PFC	44/45	197***	-45 27 20	460***	-45 12 24	185	-48 15 20
			-48 18 20		-54 21 20		
					-51 18 4		
R lateral PFC	44	29	48 15 24	99**	45 15 24	53	45 15 24
	8		45 12 40		48 30 8		
ACC	32	48*	-6 30 48	107**	-3 21 44	40	-3 24 48
L Premotor	6	21	-30 9 56			3	-30 6 56
			-39 0 56				
L SPL	7	174***	-30 -72 36	297***	-33 -66 44	90	-36 -57 48
	7		-12 -78 48				
L IPL	40			[297***]	-39 -51 36		
					-45 -30 36		
R SPL	7	92**	30 -72 40			3	24 -75 44
Precuneus	7	[92**]	6 -72 44				
R IFG / ant. ins.		22	24 30 -16				
Neutral - Congruent							
L fusiform	37	40*	-42 -51 -20				
R fusiform	37	27	39 -66 -20				
			39 -54 -20				
Congruent - Neutral							
L MOG	19	20	-45 -75 16				

PFC: prefrontal cortex; ACC: anterior cingulate cortex; SPL: superior parietal lobe; IPL: inferior parietal lobe; IFG: inferior frontal gyrus; ant. ins.: anterior insula cortex; MOG: middle occipital gyrus.

Appendix 1: List of studies entered into the meta-analysis, including date published, type of conflict task, number of participants and number of activation foci. For some studies, multiple foci were reported within a single cluster of activation. Where the same incongruent-trial activation was compared against different baseline conditions we selected the neutral-word baseline (Bench et al., 1993; Taylor et al., 1997) or neutral-trial baseline (Carter et al., 1995; Mead et al., 2002; Zysset et al., 2001).

Author	Year	Task	Participants (N)	Foci (N)
Colour-word Stroop Task				
Adleman et al.	2002	Colour-word Stroop	11	3
Banich et al.	2000	Colour-word Stroop	10	4
Bench et al.	1993	Colour-word Stroop	6	2
Bench et al.	1993	Colour-word Stroop	6	5
Brown et al.	1999	Colour-word Stroop	7	4
Carter et al.	1995	Colour-word Stroop	15	6
Compton et al.	2003	Colour-word Stroop	12	5
Fan et al.	2003	Colour-word Stroop	12	13
George et al.	1994	Colour-word Stroop	21	10
George et al.	1997	Colour-word Stroop	11	3
Mead et al.	2002	Colour-word Stroop	18	1
Milham et al.	2001	Colour-word Stroop	16	7
Milham et al.	2002	Colour-word Stroop	12	14
Pardo et al.	1990	Colour-word Stroop	8	13
Peterson et al.	1999	Colour-word Stroop	34	40
Potenza et al.	2003	Colour-word Stroop	11	10
Ruff et al.	2001	Colour-word Stroop	12	10
Steel et al.	2001	Colour-word Stroop	7	26
Taylor et al.	1997	Colour-word Stroop	12	10
Taylor et al.	1997	Colour-word Stroop	6	10
Videbach et al.	2004	Colour-word Stroop	46	13

Author	Year	Task	Participants (N)	Foci (N)
Other types of Conflict Task				
Banich et al.	2000	Colour-object Stroop	10	3
Brass et al.	2001	Inhibition of imitative responses	10	5
Bunge et al.	2002	Flanker (inc. go/no-go)	16	11
Bush et al.	1998	Counting Stroop	9	7
Bush et al.	1999	Counting Stroop	8	7
de Zubicaray et al.	2001	Picture-word conflict	8	9
Fan et al.	2003	Flanker	12	14
Fan et al.	2003	Spatial conflict	12	11
Hazeltine et al.	2000	Flanker	8	4
Liu et al.	2004	Simon task	11	34
Liu et al.	2004	Spatial Stroop	11	15
Maclin et al.	2001	Spatial conflict	8	5
Matthews et al.	2004	Counting Stroop	18	5
Norris et al.	2002	Adapted colour-word Stroop	7	10
Tamm et al.	2002	Counting Stroop	14	3
Taylor et al.	1994	S-R compatibility	8	3
Ullsperger et al.	2001	Flanker	9	34
van Veen et al.	2001	Flanker	12	8
Zysset et al.	2001	Adapted colour-word Stroop	9	9