

Separating semantic conflict and response conflict in the Stroop task: A functional MRI study

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Attentive behavior requires the ability to perform in the face of distraction. Distracting information can cause conflict at any level along the information processing stream. However, it is not yet known whether the brain has distinct subsystems dedicated to detecting and resolving these different forms of distraction. Although previous studies have localized brain activity during semantic and response conflict, no prior study has specifically determined whether these activations occur in distinct or overlapping regions. We used a modified version of the Stroop color-word task, by which we were able to separate semantic from response conflict. Behavioral data indicate that these two kinds of conflict both contribute to the overall Stroop interference effect, while fMRI data indicate that they elicit non-overlapping activation in anterior cingulate, prefrontal, and parietal brain regions. These results suggest that the brain has distinct but parallel attentional mechanisms for resolving these different forms of cognitive interference.

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Introduction

One of the central purposes of our attentional systems is to overcome interference caused by distracting information. The Stroop task (Stroop, 1935) is among the most frequently used tasks in cognitive psychology, clinical neuropsychology, and cognitive neuroscience to study interference and attention (e.g., Kornblum et al., 1999; MacLeod, 1991; MacLeod and MacDonald, 2000; Pardo et al., 1990; Stuss et al., 2001). In this task, participants have to

name the ink color of a word that spells a color name. When the color and the word are congruent (e.g., the word “blue” in blue letters), the task is easy; when the color and the word are incongruent (e.g., the word “red” in blue letters), people experience interference. This is thought to occur because word reading is a more practiced and more automatic skill than is the naming of colors, so attentional control is required to overcome the tendency to respond to the word instead of to the color (Cohen et al., 1990; MacLeod, 1991).

Most neuroimaging studies that have investigated the neural basis of these attentional systems by studying the Stroop or Stroop-like tasks have identified the dorsolateral prefrontal cortex (PFC), anterior cingulate cortex (ACC), and posterior parietal cortex (PPC) as being central to overcoming interference (Banich et al., 2000a,b; Barch et al., 2001; Bush et al., 1998; Carter et al., 1995, 2000; Fan et al., 2003; MacDonald et al., 2000; Milham et al., 2001, 2003; Pardo et al., 1990). The dorsolateral PFC is most often thought to select the relevant information by imposing an attentional set, or biasing information in posterior cortices by representing context (Banich et al., 2000a; Miller and Cohen, 2001). The ACC is often thought to detect the presence of conflict and alert other systems to exert control (Botvinick et al., 2001; Van Veen and Carter, 2002a), while the PPC is often thought to represent task-relevant stimulus-response mappings or stimulus-response transformations or to be involved in the visuospatial selection of relevant stimuli (Bunge et al., 2002; Casey et al., 2000; Rushworth et al., 2001).

For decades, it has been debated at which level of processing the conflict that causes Stroop RT interference occurs. While it has been suggested that conflict occurs at the response level (e.g., Cohen et al., 1990; Duncan-Johnson and Kopell, 1981; MacLeod, 1991), it has also been argued that conflict additionally occurs between representations at the level of semantic or conceptual encoding (e.g., Brown and Besner, 2001; Luo, 1999; Seymour, 1977; Treisman and Fearnley, 1969; Zhang and Kornblum, 1998) or conceptual (lemma) selection (Roelofs, 2003). Evidence for the contribution of semantic conflict to Stroop interference comes from

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various sources; examples include studies that have shown greater RT interference when the word is semantically closer to the color (e.g., Brown and Besner, 2001; Fox et al., 1971; Klein, 1964; Klopfer, 1996) and studies that have shown an interference effect when color and word are incongruent even when the task is simply to note whether color and words are the same or not (e.g., Luo, 1999; Treisman and Fearnley, 1969; Zysset et al., 2001). In contrast, supportive evidence for a contribution of response conflict to Stroop interference comes, among others, from the finding that the latency of the P300 (a component of the event-related potential sometimes assumed to index stimulus-related processing) does not differ between congruent and incongruent stimuli (Duncan-Johnson and Kopell, 1981), and from the finding that interference is larger when the incongruent color word is part of the response set than when it is not (e.g., Milham et al., 2001; West et al., 2004).

Several studies have shown evidence for both kinds of conflict contributing to the Stroop interference effect within the same experiment. First, there have been studies that have manipulated response eligibility by using incongruent color words that either were (“eligible”) or were not (“ineligible”) part of the response set, and compared these to the effects of neutral, non-color words (e.g., Milham et al., 2001, 2003; West et al., 2004). These studies have found longer RTs for incongruent-ineligible trials compared to neutral trials, presumably reflecting semantic conflict, and still longer RTs for incongruent-eligible trials, presumably reflecting response conflict. Milham et al. (2001) found response conflict activity in ACC and right PFC and non-response conflict activity in left PFC and PPC. In a subsequent study, Milham et al. (2003) used a similar design but presented incongruent-eligible and incongruent-ineligible trials in only a small proportion of trials, a manipulation that usually increases interference (Logan, 1985; Tzelgov et al., 1992) and ACC activity (Carter et al., 2000). In addition, Milham et al. used oddball neutral trials, in which the irrelevant neutral word occurred as infrequently as did the color words of the incongruent trials. In this study, semantic conflict engaged bilateral superior parietal cortex, bilateral inferior and dorsolateral PFC, a small area of the ACC, and other regions; response conflict engaged bilateral inferior and dorsolateral PFC, ACC, and inferior parietal cortex. Note that in this study, semantic conflict only activated a small area of the ACC, whereas response conflict engaged a much larger area of this structure, encompassing the semantic conflict area. A similar study using ERPs yielded slightly different results. West et al. (2004) used a numeric version of the Stroop task with neutral, incongruent-eligible and incongruent-ineligible trials, and found that the N450 of the event-related potential was enhanced to both types of conflict but did not differ between incongruent-eligible and incongruent-ineligible trials. They modeled this component as having ACC and right PFC generators, suggesting that these regions responded to semantic conflict but did not distinguish between response eligibility.

A different behavioral study that showed evidence that both forms of conflict contribute to the Stroop interference effect was conducted by De Houwer (2003). Based on the dimensional overlap model of Kornblum and colleagues (e.g., Kornblum et al., 1990, 1999; Zhang et al., 1999), De Houwer used a two-choice button-press version of the paradigm, with two colors associated with each response hand. This manipulation allowed for stimuli to be either congruent (CO; word and color are the same), incongruent at only the semantic level (SI; word and color are

different, but mapped onto the same response hand), or incongruent at both semantic and response levels (RI; word and color are different and mapped onto opposite response hands). De Houwer (2003) showed that, with this version of the Stroop task, RTs are longest to the RI condition, somewhat faster to the SI condition, and fastest to the CO condition. Note that this design assumes “subtractive” logic; the RI condition is assumed to contain both semantic and response conflict, the SI condition only semantic conflict, and the CO condition neither. Therefore, the RI–SI comparison should reflect the effects of response conflict, and the SI–CO comparison should reflect the effects of semantic conflict.

In determining how the brain processes and deals with these two different kinds of conflict, a study based on the experimental design used by De Houwer (2003) might have an advantage over studies manipulating response eligibility. In each trial type of De Houwer’s design, the distracting word is part of the response set, thus controlling for response eligibility. In the studies manipulating response eligibility, the distracting word stimuli were not always part of the target set, and it is possible that this might have biased the results. There is some evidence suggesting that stimuli that are not part of the target set are processed differently in the brain. For instance, event-related potential studies of the Stroop task have shown that the brain distinguishes neutral from congruent and incongruent stimuli before it distinguishes congruent from incongruent stimuli (West and Alain, 1999). This might suggest that the brain attenuates the processing of such task-irrelevant stimuli quite early in the processing stream. Another study has found that congruent words, compared to neutral words, elicit increased activation in bilateral PPC and PFC (Milham et al., 2002). It is possible that color word stimuli elicit competition between entire task sets (i.e., color naming versus words reading), and neutral words that are not part of the target set might do less so (cf. Monsell et al., 2001; Posner and DiGirolamo, 1998). In the design of the present study, the distracter is always part of the target set for each trial type, thereby eliminating such possible confounds.

Therefore, in the present study, we used this version of the Stroop task to investigate what brain networks underlie the detection and resolution of these two different forms of conflict in the Stroop task, and to what degree these networks might overlap. Areas selective to the detection and resolution of semantic conflict should display greater activity for SI and RI than for CO, but not differ between SI and RI. Areas selective to response conflict should display similar activity to the CO and SI conditions, and be increased only to the RI condition. Finally, areas involved in general difficulty or the detection and resolution of general conflict (i.e., conflict regardless of its nature or source) should display a stepwise increase in activity; activity should be greater to the SI than to the CO condition, and greater still to the RI condition.

If we were to find different areas of the PFC to be engaged by semantic and response conflict, this finding would provide partial support for an “organization-by-material” view of the PFC, according to which different subregions of this area are involved with controlling different representational domains (e.g., Smith and Jonides, 1999). Although research on this area has focused mostly on different stimulus or working memory domains, such as verbal versus spatial, it has recently been suggested that more dorsal areas of the PFC are more sensitive to the stimulus demands of a task, whereas more ventral areas are more sensitive to the response demands (Casey et al., 2001). Thus, this view would predict that the SI–CO contrast would result in more dorsal activation in the PFC, whereas the RI–SI contrast would result in more ventral

activation. In contrast, it is also possible that the SI–CO contrast would result in activation of the left ventrolateral PFC (BA 47/45), as this area has repeatedly been implicated in selecting between competing alternatives from semantic memory or the control of semantic retrieval (e.g., Badre and Wagner, 2002; Kan and Thompson-Schill, 2004; Thompson-Schill et al., 1997; Wagner et al., 2001). And, if the findings by Milham et al. (2001) were to replicate, we would find left-lateralized activation with semantic conflict and right-lateralized activation with response conflict.

In addition, since the PPC has often been implied in stimulus-response mapping (e.g., Bunge et al., 2002), we expect it to be engaged by the SI–CO contrast. The ACC has often been associated with response conflict (e.g., Milham et al., 2001; Van Veen et al., 2001) so we expect it to be engaged by the RI–SI contrast; however, it has sometimes been associated with conflict between semantic or stimulus representations (e.g., Milham et al., 2003; Weissman et al., 2003; Zysset et al., 2001) and it is therefore possible that it will be engaged by the SI–CO contrast.

Materials and methods

Research participants and task

Informed consent was obtained from 14 right-handed participants (6 women, 8 men) with an age range of 19–28 years old ($M = 21.4$, $SD = 2.2$). They were instructed to make a left index finger button press if the color of the presented word was red or yellow, or a right index finger button press when the color of the word was blue or green. For congruent stimuli (CO), color and word were the same (e.g., “red” printed in red); for semantically incongruent stimuli (SI), color and word were different but mapped onto the same finger (e.g., “red” in yellow); and for response-incongruent stimuli (RI), color and word were mapped onto opposite response fingers (e.g., “red” in blue). Participants performed 3 blocks of 124 trials each. Blocks started and ended with 4 CO trials; for the rest, stimuli were presented in random order with 50% being CO trials, 25% SI and 25% RI. Instructions were to respond fast but accurately. Stimuli were presented using E-Prime (Psychological Software Tools, Pittsburgh, PA). Each stimulus lasted 300 ms and was followed by a 2700-ms fixation point (note that a 3000-ms stimulus onset asynchrony was also used in another Stroop study from our laboratory; see Kerns et al., 2004).

Image acquisition and analysis

MR images were acquired using a 3.0-T scanner (General Electric Company) with a standard head coil, using a spiral pulse sequence ($TR = 1.5$ s; $TE = 181$ ms; $FOV = 20$ cm; flip angle = 70°); we acquired 28 functional images parallel to the AC–PC line, with the 23rd slice from the top through the middle of the AC. Data analysis was performed using BrainVoyager (Brain Innovation, Maastricht, the Netherlands). Functional data were preprocessed using 3D motion correction, interscan slice time correction, 3D Gaussian spatial filtering ($FWHM = 8$ mm), and high-pass filtering (low cutoff: 3 cycles/block, or 0.0078125 Hz). For each subject, three-dimensional images (SPGRs) were acquired; functional data were aligned to these and then transformed into Talairach space. Using subject as a random factor, analyses were then performed using a general linear approach using four predictors: three predictors accounted for each of the different trial types (CO, SI,

and RI; correct responses only) and one for error trials. These predictors were obtained using a model of the hemodynamic response locked to the onset of each trial type. The contrasts of interest were SI vs. CO, reflecting semantic conflict, and RI vs. SI, reflecting response conflict.

We used a statistical threshold of $P < 0.005$, with a cluster contiguity threshold of 250 mm^3 (corresponding to 8 voxels). The filter width of the estimated smoothness of the statistical maps, calculated in 2D, was less than 1.5 voxels. Correcting for the number of slices examined that contained activations and for the per-voxel alpha and clustering threshold, this resulted in a corrected image-wise threshold of $P < 0.05$, based on the criteria of Forman et al. (1995).

A conjunction analysis was also performed. This analysis identified voxels that were active in both contrasts and was thus able to identify regions that increased monotonically ($CO < SI < RI$). Because we wanted to investigate possible overlap between neural systems responding to semantic and response conflict, we wanted to avoid a type 2 error; we wanted to avoid identifying brain areas that respond to one type of conflict while failing to identify its response to the other type of conflict. For this reason, both contrasts were thresholded at $P < 0.071$ for this analysis, so that the overall threshold of the conjunction analysis corresponded to $0.071 \times 0.071 = 0.005$.

Finally, post-hoc tests were performed to verify whether the regions identified by one of the contrasts were indeed responsive to only that contrast. These tests were performed as follows. We identified each region identified by the SI–CO and the RI–SI contrasts as a region of interest (ROI), and calculated the mean time course of each ROI by averaging the time courses of all individual voxels in each ROI. We then applied the GLM to these mean time courses to obtain beta weights for the CO, SI, RI, and error predictors for each ROI, and tested the RI–SI and the SI–CO contrasts on these beta weights for each ROI, using participants as a random factor, and a threshold of $P < 0.05$. To avoid an overly conservative bias in favor of a negative result, this uncorrected threshold was used for the tests to see whether areas activated by the RI–SI contrast also showed activity for the SI–CO contrast and vice versa. In contrast, Bonferroni correction for multiple comparisons (adjusted threshold corresponding to $P < 0.00192$) was used for the RI–SI post hoc contrast tested on areas that were identified with the RI–SI contrast, and for the SI–CO contrast tested on areas that were identified with the SI–CO contrast.

Results

Performance data

Average performance data are summarized in Fig. 1. Mean RTs for the CO, SI, and RI conditions were 598 ms ($SD = 146$), 643 ms ($SD = 164$), and 719 ms ($SD = 203$), respectively, which were significantly different ($F(2,13) = 38.98$, $P < 0.001$). Planned contrasts indicated that RTs to SI trials were slower than to CO trials ($F(1,13) = 25.64$, $P < 0.001$), and RTs to RI trials were again slower than to SI trials ($F(1,13) = 39.82$, $P < 0.001$). Erroneous responses tended to be fast ($M = 570$ ms, $SD = 188$); planned contrasts indicated error RTs to be significantly faster than RTs during RI trials ($F(1,13) = 10.21$, $P < 0.01$). Mean accuracy for the CO, SI, and RI conditions was 92.5% ($SD = 6.9$), 92.6% ($SD =$

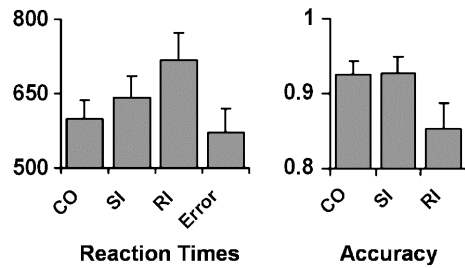


Fig. 1. Behavioral performance as a function of trial type (CO: congruent; SI: semantically incongruent; RI: response-incongruent). Left: reaction times in millisecond. Right: accuracy in proportion of correct trials.

8.6), and 85.4% (SD = 12.5), respectively. These also differed significantly between the three trial types ($\chi^2(2, N = 14) = 7.09, P < 0.05$). Wilcoxon signed ranks revealed that accuracy did not differ between CO and SI trials but was reduced to RI trials ($Z = 2.39-2.61, P < 0.05$).

fMRI data

Functional MRI results showed that different regions of the brain were responsive to the two different kinds of conflict (see Table 1). Both forms of conflict elicited activity in DLPFC and ACC; the SI–CO contrast also elicited activity in the inferior parietal cortex, whereas the RI–SI contrast also elicited activity in the superior temporal cortex and thalamus (ventral lateral nucleus). Importantly, there was no overlap in activation between these two contrasts (see Fig. 2); the conjunction analysis of SI–CO and RI–SI, which looked at voxels that activated to both semantic and response conflict, did not result in any activation. Post hoc comparisons also converged on the finding that areas that were activated to semantic conflict were not engaged by response conflict, and vice versa: every area identified by one of the two contrasts was also post hoc significant for that same contrast, and not the other (see Table 1). Note that these survive Bonferroni correction for multiple comparisons (threshold corresponding to $P = 0.00192$). Whereas a region in the insula and transverse temporal gyrus, identified in the RI–SI contrast, showed a trend towards significance in the SI–CO contrast, this would not have survived correction for multiple comparisons.

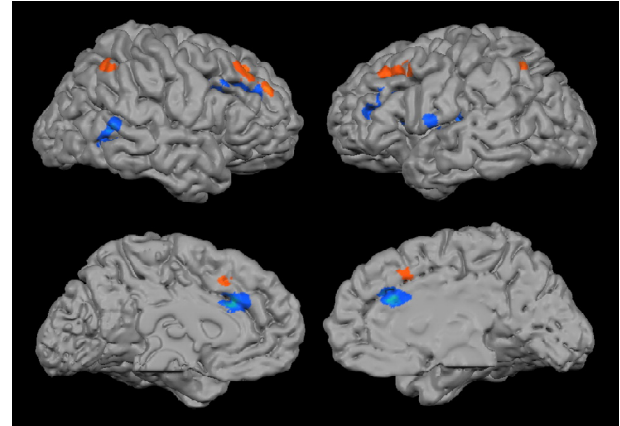


Fig. 2. Functional magnetic resonance imaging activation elicited by semantic conflict (orange) and response conflict (blue). Left, top: right hemisphere, lateral view. Right, top: left hemisphere, lateral view. Left, bottom: left hemisphere, medial view. Right, bottom: right hemisphere, medial view.

Calculating the RI–CO contrast, the “classical” Stroop effect, resulted in activation throughout the expected frontoparietal network, at the threshold of $P < 0.005$, and encompassed all areas identified by the RI–SI and SI–CO contrasts. The RI–CO post hoc contrast was significant for all of these regions, t range = 2.559–5.812, all $P < 0.05$. It should however be noted that although most of these regions survived the correction for multiple comparisons for this contrast, the two parietal regions identified in the SI–CO contrast did not, t range = 2.559–2.816, P range = 0.023–0.014.

Discussion

The performance data replicated those by De Houwer (2003): RT increases with SI compared to CO, reflecting a contribution of semantic conflict (without response conflict), and increases again with RI compared to SI, indicating response conflict. This provides strong evidence for a contribution of both kinds of conflict to the overall Stroop effect (cf. Brown and Besner, 2001; Luo, 1999;

Table 1
Activated areas in response to semantic conflict and response conflict

Region	BA	mm ³	x	y	z	SI–CO	RI–SI
SI–CO							
R. middle frontal gyrus	8	1655	35	32	43	$t = 4.404, P = 0.000685$	$t = 0.439, P = 0.668$
R. superior frontal gyrus	9	590	37	49	34	$t = 4.58, P = 0.000516$	$t = -0.19, P = 0.852$
L. middle frontal gyrus	8/9	1332	-34	26	41	$t = 4.83, P = 0.000329$	$t = 0.535, P = 0.6021$
Anterior cingulate cortex	32/6	293	7	18	42	$t = 4.425, P = 0.000685$	$t = 1.645, P = 0.124$
R. inferior parietal lobule	40	547	50	-54	46	$t = 4.444, P = 0.000662$	$t = -0.151, P = 0.882$
L. inferior parietal lobule	40	284	-45	-56	47	$t = 4.023, P = 0.001448$	$t = -0.021, P = 0.984$
RI–SI							
R. middle/inferior frontal gyrus	9/44/46/45	2218	37	25	30	$t = 0.666, P = 0.517$	$t = 5.013, P = 0.000237$
L. middle/inferior frontal gyrus/insula	9/44/46/45	2118	-34	24	18	$t = 1.073, P = 0.303$	$t = 6.134, P = 0.000036$
L. precentral gyrus	6	325	-59	3	12	$t = -0.819, P = 0.428$	$t = 4.345, P = 0.000795$
Anterior cingulate cortex	24/32	1751	1	26	28	$t = -1.51, P = 0.154$	$t = 5.653, P = 0.000079$
R. middle temporal gyrus	21/37	696	59	-52	5	$t = -0.405, P = 0.692$	$t = 6.172, P = 0.000034$
L. insula/transverse temporal gyrus	41/43	579	-41	-16	14	$t = -2.123, P = 0.054$	$t = 4.225, P = 0.000992$
L. thalamus: ventral lateral nucleus		259	-16	-12	17	$t = -1.121, P = 0.283$	$t = 5.442, P = 0.000113$

Talairach coordinates refer to centers of mass.

Milham et al., 2001; Roelofs, 2003; Seymour, 1977; Zhang and Kornblum, 1998). In addition, accuracy was analyzed because increased response conflict during interference tasks usually manifests itself as an increase in action slips, i.e., fast erroneous responses based on incomplete stimulus processing. Accuracy was similar for CO and SI stimuli, but reduced for RI stimuli; thus, the accuracy data indicated that response conflict was indeed similar for CO and SI trials and enhanced for RI trials.

This interpretation of our results is based upon the assumption that the SI condition and CO condition have equivalent amounts of response conflict. We believe that this is a reasonable assumption based on what we know about response conflict in interference tasks, as resulting from fast response activation in reaction to the irrelevant, distracting stimulus dimension (from squeeze force studies, lateralized readiness potential studies, and so forth (e.g., Coles et al., 1985; Gratton et al., 1988, 1992; Kopp et al., 1996), and on the fact that we do not see a difference in error rates between these two conditions. The relevant and irrelevant stimulus dimensions were mapped onto the same response in both the SI and the CO conditions. Therefore, we see no theoretical or empirical reason to assume that these two conditions elicited differential amounts of response conflict (cf. De Houwer, 2003; Kornblum et al., 1999; Zhang et al., 1999).

The logic used in a lot of cognitive psychophysiology is that if two manipulations affect two different physiological measures, this provides evidence that these manipulations affect (at least partially) different cognitive processes. No overlap of activation was found in the RI–SI and SI–CO contrasts of the fMRI data. This strongly suggests that these contrasts are relatively “pure” measures of semantic and response conflict in the Stroop task, and do not reflect “difficulty”, processing time, or any other general processes common to both contrasts. The activation of these structures in these contrasts most likely reflects conflict, the detection of that conflict, and the allocation of attentional resources to overcome this conflict. Although our design does not allow us to make inferences about the specific role of each individual area within this process, previous studies suggest an interpretation of the role of the prefrontal, parietal, and cingulate cortices. Specifically, conflict detection is believed to be carried out by the ACC (Botvinick et al., 2001; Casey et al., 2000; Gruber and Goschke, 2004; MacDonald et al., 2000; Van Veen and Carter, 2002a). The allocation of attentional resources necessary to resolve conflict is thought to be dependent on prefrontal and parietal cortices (Bunge et al., 2002; Casey et al., 2000; Gruber and Goschke, 2004; Kerns et al., 2004; MacDonald et al., 2000; Rowe et al., 2000). The present findings indicate that the brain has distinct but analogous mechanisms to deal with conflict occurring at different levels of processing, ensuring allocation of the appropriate attentional resources to overcome the conflict, depending on the nature of it. Thus, we suggest that separate areas of the PFC can resolve semantic or intermediate-level conflict and response conflict. Separate regions in the ACC detecting these different types of conflict would then allow for them to alert the appropriate area of the PFC to overcome that particular kind of conflict.

These results are somewhat different from the results of other studies that have compared semantic and response conflict in this task, discussed earlier (Milham et al., 2001, 2003; West et al., 2004). Specifically, we did not replicate the data by Milham et al. (2001) that suggested that response conflict engages right DLPFC

and semantic conflict engages left DLPFC; instead, we found that semantic conflict engages relatively more superior DLPFC areas, while response conflict engages relatively more inferior areas. As discussed, these prior studies have used neutral conditions with non-color words, incongruent-ineligible conditions with color words not part of the response set, and incongruent-eligible conditions with color words that are part of the response set. It is possible that the brain processes distracting stimuli that are not part of the target set very differently than distracting stimuli that are part of the target set; therefore, semantic conflict in those studies might have been less than semantic conflict induced in the present experiment. If this is the case, and semantic conflict in the response-ineligible condition is not as great as it is in the SI condition of the present study, it is possible that the incongruent-eligible–incongruent-ineligible contrast does not isolate response conflict but instead reflects both response conflict plus a small degree of semantic conflict. This possibility needs to be tested further in future empirical studies.

Noteworthy of the activation patterns is the ACC activity to semantic conflict. This was located more posterior and more dorsal to the area of the ACC engaged by response conflict. The more anterior location of the ACC region that was activated to response conflict is consistent with the location of ACC activation in other studies eliciting response conflict (Botvinick et al., 1999; Bunge et al., 2002; Casey et al., 2000; Van Veen et al., 2001). This area of the ACC was also engaged by errors, consistent with the conflict hypothesis of this brain structure; this analysis was presented elsewhere (Van Veen et al., 2004). The finding that the ACC can be engaged by semantic/conceptual conflict is also in agreement with previous findings; activity in cingulate area 32, overlapping with the present activation in the SI–CO contrast, has been observed in a “semantic matching” version of the Stroop task which presumably does not involve response conflict (Norris et al., 2002; Zysset et al., 2001), in a study that compared incoherent to coherent narratives in which there was no response requirement (Robertson et al., 2000), and to sentences that end with a semantically anomalous word (Kiehl et al., 2002; Ni et al., 2000). In addition, other studies have shown ACC activation to non-response conflict as well (Badre and Wagner, 2004; Weissman et al., 2003). Furthermore, Milham et al. (2003) observed ACC activity to the incongruent-ineligible condition; one possible difference between this study and their previous one (Milham et al., 2001) that can possibly account for this difference is the fact that the incongruent-ineligible trials were more infrequent in the latter study, a manipulation that is known to enhance conflict and ACC activation (Carter et al., 2000). Although some earlier findings (Van Veen and Carter, 2002b; Van Veen et al., 2001) based on the Eriksen flanker task suggested that the ACC is selectively activated to response conflict rather than non-response conflict, non-response conflict in that task takes place at the stimulus (input) level rather than at a semantic (intermediate) level; words and colors do not share any stimulus features. Therefore, the present findings might not contradict these earlier findings. Alternatively, Weissman et al. (2003), who found the ACC to be engaged by stimulus conflict induced by global distracters during the “local” part of a global/local task, suggested that the stimulus presentation in our earlier study (Van Veen et al., 2001) might have been too slow. They noted that slow presentation rates might have reduced overall attentional demands and ACC activity (cf. Bench et al., 1993). In sum, the precise conditions under which the ACC responds to

conflict between representations other than response tendencies have yet to be determined.

Activation of the posterior parietal cortex to semantic conflict is also consistent with earlier reports. It has been found to be active in earlier Stroop experiments in both RI–neutral (Milham et al., 2001) and RI–CO (Carter et al., 2000) comparisons, as well as in a comparison between non-color and color neutral words (Milham et al., 2001). This area has been suggested to contribute to executive control by maintaining task-relevant response mappings (Bunge et al., 2002), and our findings are consistent with this interpretation.

Dorsolateral PFC activation has also often been found in Stroop neuroimaging studies (e.g., Banich et al., 2000a,b; Kerns et al., 2004; Milham et al., 2001, 2002). Note that although MacDonald et al. (2000) did not find conflict-related PFC activation, this may have been because of the slow presentation rate used in that study, or more likely because that study used a slightly different version of the Stroop paradigm (cue-probe) in which the participants were allowed to prepare to overcome the conflict. Since, in their task, the PFC was already engaged to a considerable extent before the conflict stimulus was presented, the responsiveness of this region was therefore most likely limited. In the present study, activation in the DLPFC was more dorsal in the SI–CO contrast than in the RI–SI contrast. This is consistent with the recent proposal that relatively more dorsal areas in the PFC are involved in representation of the stimulus demands of the task, while relatively more ventral areas are involved in the representation of the response demands (Casey et al., 2001). We speculate that in the present task, these areas might be involved in relatively early (semantic) versus relatively late (response) aspects of a late selection process that biases greater attention toward task-relevant processing as a means for overcoming interference. The relatively more inferior location of the response conflict-foci is consistent with studies that have shown that area 46 and surrounding areas are associated with control processes related to response selection (Rowe et al., 2000). A left inferior PFC region, absent in the semantic conflict contrast, has often been implicated in semantic processing in picture naming studies and related paradigms (Wagner et al., 2001). It is thought that this area is involved in selection between competing alternatives in semantic memory (Kan and Thompson-Schill, 2004; Thompson-Schill et al., 1997). Although the fact that we did not find this area in the semantic conflict condition might appear inconsistent with this proposal, one possible difference between those studies and the present design that might account for this difference is the fact that in picture naming studies, semantic conflict is elicited by a single stimulus whereas in the present Stroop task, semantic conflict is elicited by different stimulus dimensions. It should be noted, however, that activation of the (more superior) middle frontal gyrus has often been observed in word generation tasks in tandem with the more inferior lateral prefrontal areas (Petersen et al., 1988; Thompson-Schill et al., 1997). Furthermore, this area of the middle frontal gyrus has been shown to be related to generating color names to object pictures (Martin et al., 1995) and to semantic conflict in a “matching” version of the Stroop task that does not involve response conflict (Zysset et al., 2001). More studies are therefore needed to explain the relative roles of the inferior and middle frontal gyri in semantic conflict and selection.

Lastly, the response conflict contrast resulted in activity in an area in the left premotor cortex, and in an area of the left

thalamus that most likely corresponds to the ventral lateral nucleus. This area of the thalamus projects to the motor cortices (Jones, 2001; Rausell et al., 1992), consistent with the interpretation of increased response activation in this contrast but not in the semantic contrast.

It is not surprising that different sources of conflict are dealt with by different neural substrates, and the present findings are not unprecedented. For instance, producing speech is a complex form of action planning involving multiple processing levels, but nevertheless it can be broken down as depending on two major independent systems: a semantic/conceptual system and a phonological/phonetic system (Levelt, 2001), which might correspond to the systems identified in the current study. Although we did not use verbal responses, it might be the case that the two components described in the current task overlap with these two systems: a semantic/conceptual and an output system. However, more research is needed to investigate whether this analogy holds.

In conclusion, conflict monitoring is thought to be a mechanism by which we are able to detect potential “trouble” during task performance prior to making errors, and to allocate resources to maintain performance in a task appropriate manner. Having separate but analogous mechanisms implemented at the neural level to deal with different kinds of representational conflict may enhance the allocation of the appropriate attentional resources to overcome specific forms of conflict.

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