

Research report

Competition for priority in processing increases prefrontal cortex's involvement in top-down control: an event-related fMRI study of the stroop task

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Abstract

Prior work indicates that various aspects of task-irrelevant information (e.g. its salience, task-relatedness, emotionality) can increase the involvement of prefrontal cortex (PFC) in top-down attentional control. In light of these findings, we hypothesize that PFC's involvement increases when task-irrelevant information competes for priority in processing. In an event-related fMRI study using an oddball variant of the Stroop task, we examine the generality of this hypothesis using three manipulations designed to increase the ability of task-irrelevant information to compete for priority in processing. First, we investigated how the frequency of occurrence of task-irrelevant information affects PFC activity. Second, we examined whether conflicting color information (i.e. incongruent trials) increases activity in regions of PFC that are similar to or distinct from those sensitive to infrequently occurring task-irrelevant information. Finally, we examined the impact of the number of levels at which conflict could occur (e.g. non-response only, non-response and response). Activity in posterior–dorsolateral and posterior–inferior PFC increased for infrequently occurring task-irrelevant information, being largest when the task-irrelevant information contained conflicting color-information. In contrast, increases in mid-dorsolateral prefrontal cortex's activity were only noted when conflicting color information was present, being largest when conflict occurred at multiple levels. The anterior cingulate was primarily sensitive to the occurrence of conflict at the response level with only a small sub-region exhibiting sensitivity to non-response conflict as well. From these findings we suggest that posterior DLPFC and PIPFC are involved in biasing processing in posterior processing systems, mid-DLPFC is involved in biasing the processing of the contents of working memory, and ACC is primarily involved in response-related processes.

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1. Introduction

The ability to select between task-relevant and task-irrelevant information is a basic aspect of attentional function. Neuropsychological and neuroimaging studies indicate a role for prefrontal cortex in this process, as it

provides a top-down bias that favors the selection of task-relevant information (e.g. [2,22,29,33,38]). Here we argue that such a bias is especially important for exerting attentional control when task-irrelevant information can effectively compete with task-relevant information for priority in processing.

As discussed by Frith [17] and others (e.g. [15]), the perceptually-related properties of a task-irrelevant stimulus (e.g. brightness) can increase its salience relative to a task-relevant stimulus, thereby favoring its processing and allowing associated representations to effectively compete for priority in processing. Top-down control by prefrontal

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cortex is required to overcome such a bias [25]. Another situation in which top-down control is required because task-irrelevant information can effectively compete for priority in processing occurs when task-irrelevant information is processed relatively automatically. In such cases, task-irrelevant representations and/or associated responses are activated to a high degree [12]. A classic example is provided by the Stroop task, in which an individual must identify a word's ink color while ignoring its identity. Since word-reading is a relatively automatic process, the word activates task-irrelevant information (i.e. semantic and phonological representations as well as their associated responses) to a high degree, despite attempts to ignore it. Because processing of this task-irrelevant information occurs to a high degree, it is extremely effective at interfering with the processing of task-relevant information. As a result, there is an increased need for top-down control by PFC to select the correct information that should be used to guide performance, as demonstrated in numerous studies of the Stroop task and its variants [2,31,32]. Finally, other attributes of task-irrelevant information, such as its emotional value, can sometimes increase its ability to compete. For example, emotionally laden information, especially when arousing or negative, is effective at capturing attention [51,53], leading to an increased need for top-down control by PFC [51,53].

Two recent studies in our laboratory support the idea that PFC's involvement in top-down control increases when task-irrelevant information can effectively compete for priority in processing. In one study [31], we found greater PFC activity when task-irrelevant information is *related* to the task at hand than when it is not. More specifically, in the color-word Stroop task, we found increases in PFC's activity when the task-irrelevant information introduced by the word was color-related (relative to neutral words), regardless of whether or not it conflicted with task-relevant color information. Thus, we observed greater PFC activity for both congruent (e.g. the word 'red' in red ink) and incongruent (the word 'blue' in red ink) color-word trials relative to neutral-word trials (e.g. the word 'bond' in red ink). The task-irrelevant information introduced by the word is better able to compete for priority in processing on both congruent and incongruent color-word trials than on neutral-word trials, as it is related to the task concept (color). We observed additional PFC activity for incongruent trials relative to congruent and neutral-word trials, probably due to their ability to compromise selection of the correct response.

The findings of a second study by our laboratory are also consistent with our hypothesis, as they suggest that activity within PFC increases with the number of levels at which a stimulus can compete for priority in processing [32]. Using a manual version of the color-word Stroop task, we examined increases in neural activity associated with two different types of incongruent trials (response-eligible, response-ineligible) relative to that associated with

neutral trials. On response-eligible incongruent trials, the incongruent color-word names a possible response (e.g. the word 'blue' in yellow ink, when blue, yellow, and green are the possible ink colors). For these trials, task-irrelevant information is present and can compete for priority in processing at both the response and non-response levels. On response-ineligible trials, the incongruent color-word does not name a possible response (e.g. the word 'purple' in yellow ink, when blue, yellow, and green are the possible ink colors), and hence can only compete at non-response levels. Consistent with our hypothesis, DLPFC activity was greater, relative to neutral trials, for response-eligible trials, which could introduce competing information at both response and non-response levels of processing, than for response-ineligible trials, which introduce competing information at just non-response levels. Interestingly, we noted increases in activity (relative to neutral trials) within anterior cingulate cortex only for response-eligible incongruent trials, not response-ineligible trials, implicating this prefrontal structure in response-related processes, not top-down control (see [31,37], and [36] for additional evidence of the cingulate's activity being linked specifically to response-related processes).

Here, we further explore the possibility that PFC's involvement in control is dependent upon the ability of task-irrelevant information to compete for priority by examining another variable, frequency of occurrence. Although fMRI studies using priming and oddball paradigms have consistently demonstrated greater neural activity in prefrontal regions for the processing of relatively novel or infrequently occurring information when it is task-relevant, such investigations have not focused on information that is task-irrelevant. When task-irrelevant information occurs infrequently it should be better able to compete for priority in processing, as it is relatively novel and hence more salient [7].

To test our hypothesis that PFC's involvement in control increases in response to the ability of task-irrelevant information to compete for priority in processing, we determined if PFC's activity is greater for infrequently occurring task-irrelevant information than frequently occurring task-irrelevant information. To accomplish this, we employed an oddball variant of the Stroop task that made use of two sets of neutral words—the first was baseline neutral trials, which comprised the majority of trials (86%), and the second was oddball neutral trials, which occurred with a much lower frequency. If as we suggested, PFC's involvement in top-down control is dependent upon the ability of task-irrelevant information to compete for priority in processing, increases in activity should be noted for oddball neutral trials relative to baseline neutral trials.

The second goal of the present study was to determine if the subregions of PFC sensitive to infrequently occurring task-irrelevant information overlap with those engaged when task-irrelevant information conflicts with task-relevant information, as on incongruent trials in the Stroop

task. To accomplish this, we included oddball incongruent trials as well as oddball neutral trials. Task-irrelevant information introduced by incongruent color-words has a unique ability to compete for priority in processing, as it is both related to the task at hand and able to interfere with selecting the correct representation on which a response should be based. Hence, we examined whether the additional ability of task-irrelevant information to compete with task-relevant information on incongruent trials leads to further increases in activity within the same regions of PFC as activated by neutral oddball trials, or whether activation is observed in additional and distinct subregions of the PFC.

The third goal of our study was to re-examine the impact of response eligibility on increases in neural activity within prefrontal regions. A prior study in our laboratory [32] indicated that the ACC was impervious to the occurrence of conflict at non-response levels. Not only did we find that it exhibited greater activity during response-eligible than response-ineligible trials, but we found no significant difference in activity for response-ineligible and neutral trials. Thus, as long as the word did not name a possible response, no ACC activity was noted. However, other studies have indicated that the ACC is most responsive to novel or infrequent events [8,54]. Thus, we reasoned that if the ACC has *any* sensitivity to non-response related conflict, it might be detectable with an oddball design in which the trial types of interest occur with low frequency.

To review, we made use of an oddball design, in which the majority of trials were neutral trials (referred to as baseline neutrals), with oddball trials occurring once every six to eight trials. Three oddball trial types were included: (1) neutral word trials; (2) response-ineligible incongruent trials; and (3) response-eligible incongruent trials. While we expected that all three oddball types would produce increases in neural activity due to their low frequency of occurrence, we expected activations to be more extensive for interference trials, due to their ability to activate representations of conflicting color information, which would provide them with a greater ability to compete for priority in processing. Finally, we expected response-eligible trials to produce greater increases in neural activity than response-ineligible trials, as they can compete with task-relevant information at more levels of processing.

2. Materials and methods

2.1. Stimuli/design

The Stroop task was programmed using Mel V2.0 and presented using an IBM-PC compatible computer. We made use of an oddball design, in which participants were presented a series of neutral word trials, with an oddball trial occurring every six to eight trials. Three types of

oddball trials were included: incongruent-eligible, incongruent-ineligible, and neutral.

The stimuli consisted of words presented in one of three colors: blue, green and yellow. The word set for incongruent-eligible trials consisted of the words 'BLUE', 'GREEN' and 'YELLOW' printed in an incongruent color (e.g. the word 'blue' in green ink) while that for incongruent-ineligible trials consisted of the words 'RED', 'ORANGE' and 'BROWN' (e.g. the word 'red' in blue ink). For the oddball neutral trials, we made use of a word set consisting of three semantically related words ('MILE', 'YARD', 'METER') that have no association with color. For the intervening baseline neutral trials, the word set consisted of six color-neutral words, unrelated to the oddball neutrals. It is important to note each baseline neutral word appeared with a frequency of one in every seven trials, while each oddball word appeared with a frequency of one in every 42 trials. Thus, baseline neutral words appeared six times as frequently as oddball words (neutral, incongruent-ineligible, incongruent-eligible).

Each scanning session consisted of four runs, consisting of 257 trials per run presented at a rate of one trial every 2 s (36 oddball trials were presented per run in a random order—we ensured that each oddball trial type occurred 12 times per run). Each trial consisted of a 300-ms fixation cross followed by a 1200-ms presentation of the word and 500-ms inter-trial interval.

2.2. Procedure

Participants were instructed to identify the ink color in which each word was presented, while ignoring the word's identity. Responses were acquired using a three-button response pad.

2.3. Data acquisition

A GE Signa (1.5 T) magnetic resonance imaging system equipped for echo-planar imaging (EPI) was used for data acquisition. Sixteen right-handed native English-speaking participants were included in our study. For each run, a total of 261 EPI images was acquired (TR=2000 ms, TE=40 ms, flip angle=90°), each consisting of 10 contiguous slices (thickness=8 mm, in-plane resolution=3.75 mm), parallel to the AC-PC line. A high-resolution 3D anatomical set (T1-weighted three-dimensional spoiled gradient echo images) was collected for each participant, as well as T1-weighted images of our functional acquisition slices. The head coil was fitted with a bite bar to minimize head motion during the session. Stimuli were presented on a goggle system designed by Magnetic Resonance Technologies.

2.4. Image processing

Within-subject statistical analyses were carried out using

FEAT, the FMRIB Easy Analysis Tool (<http://www.fmrib.ox.ac.uk/fsl>). The first five volumes of each run's time series were discarded to allow the MR signal to reach steady state. Prior to statistical tests, images were motion corrected using MCFLIRT ([24]). The following pre-statistical processing was applied: (1) spatial smoothing using a Gaussian kernel of FWHM 8 mm; (2) mean-based intensity normalization of all volumes by the same factor; (3) non-linear high-pass temporal filtering (Gaussian-weighted LSF straight line fitting, with $\sigma=35.0s$); and (4) Gaussian low-pass temporal filtering (HWHM 2.8s.)

2.5. Statistical analyses

Statistical analysis was carried out for each participant using FILM (FMRIB's Improved Linear Model) with local autocorrelation correction ([24]). Event-related responses were modeled using the SPM 99 hemodynamic response. In our model, we included three predictors: (1) FREQUENCY OF OCCURENCE, responses associated with all oddball trials relative to the baseline neutral trials; (2) STROOP INTERFERENCE TRIALS, responses associated only with incongruent trial types (greater for both incongruent trial types relative to oddball neutral trials); and (3) RESPONSE CONFLICT DURING STROOP INTERFERENCE TRIALS, responses specific to incongruent-eligible trial types (incongruent-eligible > incongruent-ineligible). Temporal derivatives for each predictor were included in the model.

Parameter estimate (PE) maps for each participant for each predictor were transformed into a common stereotaxic space [47] using MedX 3.4 (landmark-based image registration, polynomial transformation, trilinear interpolation) (<http://medx.sensor.com>). The parameter estimates for each predictor were then entered into a random effects group analysis, in which we tested if the parameter estimates across all participants were significantly greater than 0. We used a significance level of $P<0.001$ to threshold our statistical maps. In order to protect against false positives due to multiple comparisons, a contiguity threshold (minimum spatial extent) of 10 voxels was employed [16]. In order to differentiate between regions within an active cluster, we used a peak detection algorithm to identify peak activations within a cluster [34]. For each cluster, we report the center of intensity and peak activation(s).

2.6. Confirmatory analysis

In order to confirm that the increases in neural activity identified when contrasting oddball trial types (neutral, incongruent-ineligible, incongruent-eligible) with baseline neutral trials reflected increases in activity for all three oddball trial types (as opposed to only incongruent trial types, for example), we examined each of the oddball trial

types individually relative to baseline neutrals and conducted a conjunction analysis. More specifically, for each region (cluster) identified as active, we calculated the mean parameter estimate (across voxels within the region) for each oddball trial type for each participant. Then for each region, we tested for the presence of increases in neural activity relative to neutral trials for the oddball trial type individually at a level of $P<0.05$. In order to pass the conjunction test, a region had to pass for all three conditions, providing a conjunction probability of $P<0.000125$. For regions in which multiple peaks were identified, rather than testing the region as whole, we carried out a conjunction test at each peak, using the mean signal for a sphere defined around each peak (diameter = five voxels). The same approach was employed to verify that increases in neural activity associated with conflicting task-relevant color information (incongruent-ineligible and incongruent-eligible > neutral) were not driven by a single trial type.

3. Results

3.1. Regions sensitive to the frequency of irrelevant information

The first goal of our analysis was to identify regions sensitive to the frequency with which task-irrelevant materials were presented (see Fig. 1A and Table 1). Regression analyses revealed increases in activity throughout left dorsolateral prefrontal cortex (primarily posterior) and posterior inferior prefrontal cortex common to all three oddball trial types (neutral, incongruent-ineligible, incongruent-eligible) relative to baseline neutrals. Our confirmatory conjunction analysis verified that these increases in activity relative to baseline neutral trials are present for all three oddball trial types when compared to baseline neutrals, although as can be seen in Fig. 1B not necessarily to an equal degree. Of most importance is the finding that the oddball neutral trials yielded significantly greater activity in these regions than did baseline neutral trials, indicating that activity in these regions reflects the greater ability of infrequently occurring (i.e. novel) task-irrelevant information to compete with task-relevant information for priority in processing and thereby increase the need for top-down control.

The regions identified in this analysis are the same regions implicated in implementing attentional control across a variety of other manipulations that increase the need for top-down control [2,22,29,31]. Thus, the present findings support the idea that these regions are responding to the ability of task-irrelevant information to compete with task-relevant information, regardless of the specific manipulations employed to vary this ability (e.g. infrequent events, conflict).

Consistent with prior studies demonstrating the exist-

ODDBALL > BASELINE

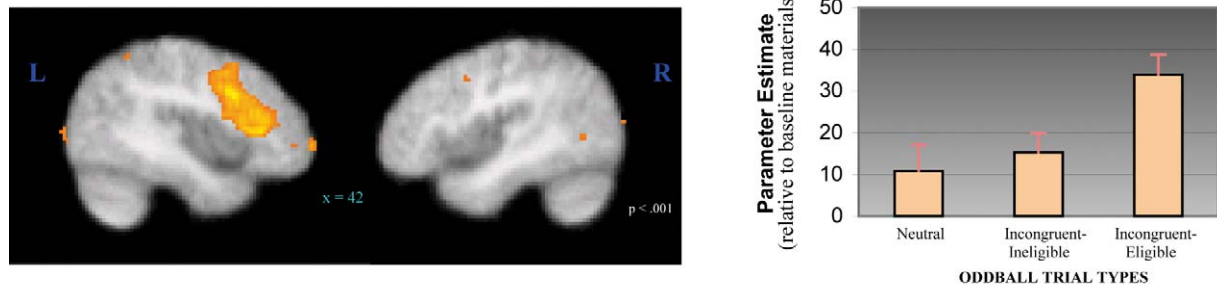


Fig. 1. Regions sensitive to infrequently occurring task-irrelevant information. (A) All three oddball trial types produced increases in neural activity within left prefrontal cortex (center of intensity: $x=-40$; $y=18$; $z=24$; see Table 1), including posterior dorsolateral prefrontal cortex (BA 6/9) and posterior inferior prefrontal cortex (BA 44). (B) Results of the confirmatory analysis indicating that the parameter estimates for all three types of oddball trials (relative to baseline neutral trials) were significant.

ence of a fronto-parietal circuit underlying attentional control, this contrast also revealed increases in parietal activity in response to infrequently occurring task-irrelevant information. More specifically, we noted bilateral activity within the anterior inferior parietal sulcus (AIPS) and nearby regions of the inferior parietal lobule. These regions are highly similar to those reported in studies of attentional function employing other paradigms and manipulations (e.g. [18,31,52]). Recent work has suggested that these activations in parietal cortex may reflect generation of a top-down signal that modulates processing in extrastriate regions (see [14] for a review). Given its connectivity with posterior DLPFC [42], it is possible that PFC may rely upon its interactions with parietal cortex (at least to some degree) in order to implement top-down influences. Consistent with this notion, across participants, left PFC activity was significantly correlated with activity

within the left AIPS ($r=0.78$, $P<4\times 10^{-4}$) and right AIPS ($r=0.66$, $P<6\times 10^{-3}$). However, some caution needs to be taken with respect to these findings concerning parietal regions, as they failed to pass our confirmatory conjunction analysis due to variability in the response to oddball neutral trials across individuals.

Finally, increases in activity were noted in the superior frontal gyrus (SFG), adjacent to anterior cingulate cortex. This activation is similar to that noted by Hopfinger et al. [22] when using a cueing paradigm to identify regions involved in top-down control. Thus, consistent with prior suggestions, the medial wall does appear to be involved in attentional control to some degree, but primarily the superior frontal gyrus, not the cingulate region as postulated by some models of attention [45].

In sum, the presentation of infrequently occurring task-irrelevant information produced increases in activity

Table 1
Regions sensitive to the frequency of irrelevant information (oddball trials)

Regions	BA	Cluster size	x^a	y	z	Max sig ^b	Mean sig ^b
L. middle occipital gyrus ^c	19	464	-28	-92	10	4.87	3.4
L. inferior occipital gyrus	19		-34	-80	-6	3.46	
L. middle occipital gyrus ^d	18/19		-18	-94	14	4.28	
L. orbital gyrus	19		-32	-84	24	4.87	
R. middle occipital gyrus ^c	19	318	32	-92	16	4.61	3.51
R. middle occipital gyrus ^d	18/19		24	-100	12	3.83	
R. middle temporal gyrus ^d	19		38	-90	18	4.61	
L. superior frontal gyrus	10	11	-28	58	22	3.44	3.19
L. inferior frontal gyrus ^c	44	1843	-40	18	24	5.62	3.81
L. inferior frontal gyrus ^d	44		-44	16	16	5.62	
L. middle frontal gyrus ^d	6/9		-44	8	44	4.99	
L. middle frontal gyrus	10	78	-36	56	0	4.14	3.38
R. inferior frontal gyrus	44	12	42	8	36	3.29	3.14
R. medial frontal gyrus	8	52	4	34	38	3.86	3.29
L. inferior parietal lobule	7	536	-30	-60	46	5.04	3.53
R. inferior parietal lobule	7	17	34	-58	46	3.25	3.09

^a x , y , z coordinates specify the Talairach coordinates for each cluster's center of intensity.

^b Significance levels reported in terms of $-\log(\text{probability})$.

^c Clusters in which more than one peak activation was detected [34].

^d Passed confirmatory analysis.

Table 2

Regions sensitive to Stroop interference regardless of the level at which conflict occurs (incongruent-eligible and incongruent-ineligible > neutral)

Region	BA	Cluster size	x^a	y	z	Max sig ^b	Mean sig ^b
L. inferior frontal gyrus ^d	44	492	-34	14	18	6.49	3.86
R. inferior frontal gyrus ^d	44	129	32	16	16	5	3.67
L. middle frontal gyrus ^d	46/9	20	-46	40	24	3.77	3.26
R. middle frontal gyrus ^c	46/9	214	48	38	24	5.65	3.53
R. middle frontal gyrus ^d	46		50	34	26	5.65	
R. middle frontal gyrus ^d	46/9		40	50	26	3.27	
R. pre-central gyrus	6	20	44	2	16	3.68	3.28
R. cingulate gyrus (ACC) ^d	32	134	8	30	28	3.76	3.3
R. inferior frontal gyrus	44	126	60	10	32	4.06	3.33
L. precuneus cortex ^d	7	19	-12	-62	38	3.55	3.22
R. inferior parietal lobule ^d	7	42	56	-56	48	3.89	3.27
L. superior parietal lobule ^d	7	28	-28	-50	46	3.49	3.26
R. superior parietal lobule ^d	7	39	36	-70	52	3.47	3.21
R. precuneus cortex ^d	7	34	2	-72	56	3.54	3.16
L. cuneus gyrus	18	10	-6	-82	16	3.65	3.27
L. lingual gyrus ^d	19	10	-22	-70	18	3.51	3.15

^a x , y , z coordinates specify the talairach coordinates for each cluster's center of intensity.^b Significance levels reported in terms of $-\log(\text{probability})$.^c Clusters in which more than one peak activation was detected [21].^d Passed confirmatory analysis.

throughout a distributed network of regions, including DLPFC, posterior inferior frontal cortex, IFC, the anterior interparietal sulcus, superior parietal lobule and superior frontal cortex, regardless of whether or not this information conflicted with the task-relevant information.

3.2. Regions sensitive to Stroop interference regardless of the levels at which conflict can occur (incongruent-eligible and incongruent-ineligible > oddball neutral)

The introduction of conflicting color information by an incongruent color-word produced further increases in PFC activity, regardless of whether or not the word named a possible response (Table 2). Not only did both incongruent trial types produce more widespread activity within L. PIPFC (relative to oddball neutral trials), but they also produced increases in activity within R. PIPFC as well,

leading to a more bilateral pattern of activation. Our confirmatory analyses verified these increases in neural activity. In one of our prior studies of the Stroop task, we found that such increases in PIPFC activity were also associated with congruent trials [31]. In tandem, these findings suggest that PIPFC is responding to the fact that the task-irrelevant information is related to the task concept (i.e. the task-irrelevant information is related to color when the task is color identification) [31].

Although the posterior DLPFC was activated by all oddball trials (with incongruent-eligible trials producing the largest activations), only incongruent oddball trials produced significant increases in activity within mid-DLPFC (BA 46/9) (See Fig. 2A). Given models suggesting that mid-DLPFC is involved in monitoring and manipulating information in working memory [42], this activity probably reflects the need to select between color-

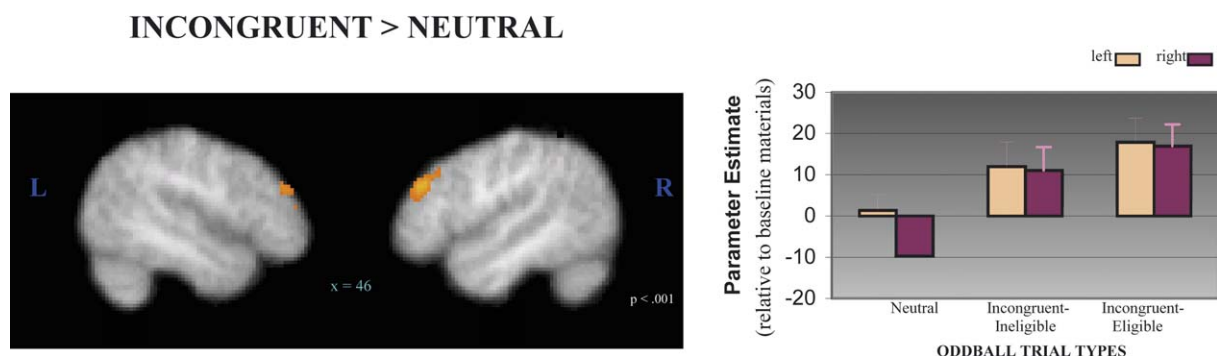


Fig. 2. Regions sensitive to stroop interference. (A) Both incongruent trial types produced increases in neural activity within mid-DLPFC (BA 46/9) bilaterally [centers of intensity: (L): $x = -46$; $y = 40$; $z = 24$; (R): $x = 48$; $y = 38$; $z = 24$, see Table 2]. (B) Results of the confirmatory analysis indicating that only the parameters estimates for incongruent trials (both eligible and ineligible) were significant relative to neutral baseline trials. Thus these regions only showed increases in neural activity for incongruent trial types (relative to baseline).

representations in working memory that are task-relevant (i.e. those related to ink color) and task-irrelevant (i.e. those related to the color word). Supporting such a conclusion, the increases in mid-DLPFC activity were accompanied by increases in activity within precuneus cortex (across subjects, L. DLPFC and precuneus were significantly correlated: $r=0.59$, $P<0.02$), a region which has recently been demonstrated to be more sensitive to working memory than attentional demands [27]. Confirmatory analyses indicated that activity was significantly increased in both response-eligible and response-ineligible trials in mid-DLPFC relative to oddball neutral trials. Fig. 2B shows the parameter estimates for each of the oddball trial types relative to baseline neutral trials. Notice that activation in this region is specific to incongruent trial types, as there was no increase in neural activity for oddball neutral trials relative to baseline neutral trials (i.e. the parameter estimates for oddball neutral trials were not significantly greater than zero).

The introduction of conflicting task-irrelevant color information produced increases in activity within regions of parietal cortex as well. More specifically, increases in activity were noted bilaterally within the superior parietal lobule. While early studies of attentional control noted activity within the superior parietal lobule for tasks involving spatial attention (e.g. [13]), several studies have reported activity in superior parietal lobule for non-spatial

tasks as well [4,31,32,52], often in tandem with the AIPS. Finally, increases in activity were also noted with the lateral inferior parietal lobule, a region that has been implicated in non-spatial attention [52]. Overall, these data suggest that as the need for attentional resources increases, lateral inferior parietal and superior parietal are recruited in addition to AIPS.

3.3. Regions sensitive to the occurrence of response conflict during Stroop interference trials (incongruent-eligible>incongruent-ineligible)

Consistent with prior studies of response conflict and/or inhibition (e.g. [18,32]), the occurrence of conflict specifically at the level of response (incongruent-eligible>incongruent-ineligible) produced increased activity throughout a distributed network of structures (see Table 3). Relative to incongruent-ineligible trials, incongruent-eligible trials produced additional activations bilaterally throughout prefrontal cortex. Increases were observed in anterior inferior prefrontal cortex, consistent with prior studies of conflict resolution at the level of response (e.g. [18,48]). Increases in activity were also noted throughout DLPFC (posterior, middle, anterior) and PIPFC bilaterally, most likely reflecting the increased attentional and working memory demands associated with response conflict. Further recruitment of activity was noted within precuneus

Table 3
Regions sensitive to the occurrence of response conflict during Stroop interference trials (incongruent-eligible>incongruent-ineligible)

Region	BA	Cluster size	x^a	y	z	Max sig ^b	Mean sig ^b
L. middle frontal gyrus	46	11	-42	40	16	3.63	3.22
L. inferior frontal gyrus ^c	44/45	1293	-36	22	14	5.77	3.57
L. middle frontal gyrus	9		-34	10	36	4.74	
L. middle frontal gyrus	9		-38	24	32	3.91	
L. inferior frontal gyrus	47		-44	24	-2	4.68	
			-26	22	0	3.5	
R. inferior frontal gyrus ^c	45/46	1642	42	28	8	6.6	3.67
R. middle frontal gyrus	46		40	36	26	4.03	
R. middle frontal gyrus	46		44	42	16	5.06	
R. inferior frontal gyrus	44		52	14	18	4.5	
R. inferior frontal gyrus	47		34	26	0	6.6	
R. cingulate gyrus	32/9	831	4	38	22	6.99	4.05
R. cingulate gyrus	24	160	8	8	32	4	3.31
L. cingulate gyrus	23/24	11	-8	-14	26	3.21	3.08
R. cingulate gyrus	23/31	43	6	-28	34	3.57	3.19
L. cingulate gyrus	24	11	-22	-4	44	3.87	3.31
R. precentral gyrus	6	12	50	4	34	3.57	3.24
R. supramarginal gyrus ^c	39/40	1136	50	-52	30	4.54	3.49
R. supramarginal gyrus	40		56	-56	36	4.42	
R. inferior parietal lobule	40		40	-70	42	4.54	
R. inferior parietal lobule	40		46	-42	44	4.09	
R. precuneus cortex	31	99	10	-64	16	5	3.65
L. superior parietal lobule	7/19	20	-30	-60	42	3.49	3.21
Precuneus cortex	7	14	0	-64	54	3.52	3.19
L. inferior occipital gyrus	18	18	-42	-74	-2	3.49	3.21

^a x , y , z coordinates specify the talairach coordinates for each cluster's center of intensity.

^b Significance levels reported in terms of $-\log(\text{probability})$.

^c Clusters in which more than one peak activation was detected [34].

cortex as well, suggesting an even greater increase in working memory demands associated with the activation of competing response-related representations.

The presence of conflict at the level of response produced extensive patterns of activity throughout anterior cingulate cortex (ACC), a finding consistent with prior studies of the Stroop task [2–4,9,10,20,28,29,31,32,35,49] as well as various paradigms focusing on resolution of response conflict and/or competition (e.g. [37,48]). While activations within anterior cingulate cortex were most prominent, increases in activity were also noted within mid- and posterior cingulate cortex.

3.4. Behavioral results

Four participants were excluded from the analysis of behavioral measures due to technical difficulties with the response device. Mean reaction times for all oddball trial types were significantly longer than those for baseline neutrals ($P < 6 \times 10^{-6}$), indicating that infrequently occurring events led to more potent interference. We also found evidence of a Stroop interference effect, as the mean reaction time to incongruent oddball trial types were significantly longer than for neutral oddball trials ($P < 2 \times 10^{-3}$). Finally response-related conflict increases interference as mean reaction time for incongruent-eligible trials was longer than to incongruent-ineligible trials ($P < 2 \times 10^{-4}$). Overall, these behavioral findings are consistent with those of prior studies employing similar trial types [30], and indicate that we were able to differentiate increased attentional demands on the basis of frequency, Stroop interference, and whether conflict was present at both response- and non-response related levels or just at non-response levels.

4. Discussion

Our findings indicate that neural activity within DLPFC and PIPFC, two regions previously implicated in top-down control, is influenced by three factors: the frequency with which task-irrelevant information is presented, the ability of task-irrelevant information to introduce conflicting task-irrelevant information, and the number of levels at which such conflict or interference can occur. As such, our results are consistent with the hypothesis that top-down control by PFC increases in response to the ability of task-irrelevant information to compete for priority in processing. Increases in activity associated with infrequently presented task-irrelevant information were noted within posterior-DLPFC and posterior-IPFC, two regions that we have previously argued are involved in modulating activity within posterior processing regions to ensure task-appropriate performance [2–4,32]. The introduction of task-irrelevant information that conflicts with task-relevant information during incongruent trials produced further

increases of activity in posterior-DLPFC and posterior IPFC.

Although these regions of the fronto-parietal attentional network exhibited increases in activity anytime the ability of task-irrelevant information to compete for priority in processing was increased (i.e. due to frequency of occurrence or conflict at response and non-response levels), some subregions were only sensitive to conflict. More specifically, mid-DLPFC and anterior inferior prefrontal cortex only exhibited increases in activity when the word introduced color information that conflicted with task-relevant information (i.e. as on incongruent trials). These increases were largest when conflict could occur at both response and non-response levels. In addition, right-hemisphere involvement was only noted during incongruent trials. We posit that the activity within these regions reflects the increased attentional demands associated with incongruent trials, not necessarily the occurrence of ‘conflict’. This conclusion is based on the results of the present study in conjunction with our prior findings [31]. The regions that showed increased activity in response to incongruent trials in the current study were not identical to those that were specific to ‘conflict’ in our prior study in which we compared activation in incongruent as compared to congruent and neutral trials.

Of note, the differential activation of anterior and posterior inferior prefrontal cortices observed in the present work is consistent with a framework recently proposed by Wagner et al. [50] as part of effort to understand PFC’s involvement in working memory and executive control. More specifically, they proposed that AIPFC is specifically involved in conditions requiring controlled semantic retrieval (e.g. retrieval of weakly associated information as opposed to strongly associated information), whereas PIPFC is involved in retrieval and selection processes for a variety of stimulus types (e.g. phonological, non-phonological, early semantic). Consistent with their proposal, we found that PIPFC was sensitive to competing task-irrelevant information regardless of its semantic relatedness to task relevant information (i.e. oddball neutral, incongruent-ineligible, incongruent eligible), while AIPFC was uniquely responsive to trial types on which semantic conflict could occur (i.e. incongruent-ineligible, incongruent-eligible).

Overall, the data provide evidence that multiple regions of PFC (i.e. posterior dorsolateral and posterior inferior PFC) were sensitive to both low frequency of occurrence and the conflict/interference engendered by incongruent trials. Of note, some PFC sub-regions (i.e. mid-DLPFC) were primarily sensitive to the conflict/interference engendered by incongruent trials. We posit that this pattern of activation provides important information about the nature of mechanisms of attentional control in the PFC. In particular, as discussed next, we posit that mid-DLPFC and posterior-DLPFC are likely to play different roles in attentional control.

4.1. Differentiating mid- and posterior-DLPFC

We along with others have posited that PFC works to maintain proper task performance through two mechanisms (e.g. [31,50]): (1) the modulation of processing in posterior processing systems (i.e. amplifying neural activity within task-relevant processing systems); and (2) the biasing of selection processes within working memory. Though speculative, we posit that posterior DLPFC is primarily responsible for the modulation of processing in posterior perceptual processing systems, as it is a region that is repeatedly activated in studies of attentional control and is more highly interconnected with posterior visual processing regions than other portions of DLPFC ([5,43,44,23,1,46]; see [42] for a review). Consistent with this interpretation, all infrequent trial types, regardless of whether or not they contained conflicting information, produced increases in activity within posterior DLPFC. Furthermore, activity within these regions increased with attentional demands (i.e. baseline neutral < oddball neutral < incongruent-ineligible < incongruent-eligible).

In contrast, we posit that mid-DLPFC is responsible for biasing selection of task-relevant representations within working memory. Such a suggestion is consistent with animal and neuroimaging studies alike, that have shown that mid-DLPFC is responsible for monitoring and manipulating representations in working memory ([39–41]; see [42] for a review). Furthermore, this region lacks the direct connectivity with major portions of extrastriate and parietal regions, making a direct role in the modulation of neural activity within posterior perceptual processing regions less likely. Our data are consistent with such an idea, as only incongruent oddballs, not neutral oddballs, evoked significant increases in activity within mid-DLPFC. Incongruent color words are more capable of taxing working memory's resources because they activate representations of two colors, the word's ink color and the color named by the word. In contrast, neutral words only activate one representation of color, namely that of the ink color. Furthermore, our prior work revealed increases in activation of mid-DLPFC for congruent color words relative to neutral words, as they also contain two sources of color information, one in the ink color and one in the word [31].

Wagner et al. [50] made a proposal similar to the one suggested here, though they attributed the role of modulating neural activity within posterior processing regions to PIPFC (referred to as VLPFC in their work) rather than posterior DLPFC. While the two proposals may at first seem disharmonious, it is important to note that Petrides [42] argued that posterior DLPFC is highly interconnected with the dorsal (spatial) visual processing stream, while PIPFC (and inferior portions of VLPFC) is highly interconnected with the ventral (non-spatial) visual processing stream. Thus, posterior DLPFC may work to modulate neural activity within the dorsal (spatial) visual processing stream, while PIPFC may work to modulate neural activity

within the ventral (non-spatial) visual processing stream. Given that both processing streams have been noted to be involved in color [6] and word processing [26], it is not surprising to find both regions active for the color-word Stroop task. In fact, across our studies of the color-word Stroop task, these two prefrontal regions show highly similar patterns of activity.

4.2. ACC and response conflict

Consistent with the findings of our prior study [32] activity within the ACC is greatly increased for incongruent response-eligible trials compared to response-ineligible trials. Such findings once again implicate the ACC as playing a major role in response-related processes.

Although the findings of our prior study suggested that increases in ACC activity are specific to incongruent-eligible trial types, our primary and confirmatory analyses detected a region of ACC (towards BA 9) that exhibited increases in activity for both incongruent trial types (incongruent-ineligible and incongruent-eligible), though far greater for incongruent-eligible trial types (see Tables 2 and 3). A study by Braver et al. [8] may provide an explanation for these latter findings. They found that the ACC's activity is sensitive to the frequency of an event, exhibiting greater activity to infrequent events. While the ratio of incongruent trials (eligible or ineligible) to neutral trials in our prior study was 50:50, the ratio of incongruent trials (eligible or ineligible) to neutral trials in the present study was 2:21. This relatively low frequency of occurrence appears to have amplified activity in the ACC. In fact, even the activity specifically associated with incongruent-eligible trials (incongruent-eligible > incongruent-ineligible) is far greater in the present study than our prior study (see Table 3 and [32]). As such, the residual ACC activity associated with an incongruent-ineligible trial may have been amplified in the present study, making it more detectable. Hence, the present study's findings are compatible with our prior study's, as the ACC appears to be much more sensitive to occurrence of conflict at the response level than at the non-response level. However, under specific conditions, a sub-region of the ACC was capable of showing some degree of sensitivity to conflict at non-response levels.

Our findings have implications for the conflict monitoring theory [11,55], one of the more popular theories regarding the function of the ACC activity. The finding of increased activity within one subregion of the ACC for both response-eligible and response-ineligible trials suggests that it is possible that ACC monitors for the occurrence of conflict at both response and non-response levels of processing. However, this ability was restricted to a specific portion of the cingulate, towards BA 9. Furthermore, this effect was only observed when the task-irrelevant information occurred infrequently, thereby increasing its salience. Given the results of our prior study and the

extensive difference in ACC activations between incongruent-eligible and ineligible trials in the present study (see Table 3), we suggest that it is more likely that ACC does not directly monitor for conflict at the non-response level. Instead, we suggest that ACC's sensitivity to the occurrence of conflict at non-response level occurs through its interactions with other regions that are directly involved in processing at the non-response level, such as DLPFC [19].

5. Summary

In sum, the present study provided support for our hypothesis that PFC's involvement in attentional control increases with the ability of task-irrelevant information to compete for priority in processing. We found PFC's activity to be sensitive to each of three factors: the frequency with which task-irrelevant information is presented, the ability of task-irrelevant information to introduce conflicting color information, and the number of levels at which such conflict or interference could occur. A differential pattern of results was noted for posterior and mid-DLPFC, with posterior DLPFC showing increased activity anytime task-irrelevant information could compete for priority in processing, but mid-DLPFC only exhibiting activity during trial types that are better able to tax working memory processes (i.e. the incongruent trial types, which introduce two sources of color information, the word and the ink color). Based on anatomical and working memory studies, we suggested a possible explanation for this apparent differentiation, namely, that posterior DLPFC and PIPFC are involved in top-down biasing of processing in posterior processing systems to ensure that task-relevant information is selected, while mid-DLPFC is involved in biasing processing of the contents of working memory. Finally, our results indicate that relative to DLPFC, the ACC is much more sensitive to conflict at the response than non-response level.

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