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Material-dependent and material-independent selection processes in the frontal and parietal lobes: an event-related fMRI investigation of response competition

Eliot Hazeltine[a,*], Silvia A. Bunge[b,1], Michael D. Scanlon[c], John D.E. Gabrieli[b,c]

[a] NASA Ames Research Center, Mail Stop 262-4, Moffett Field, CA 94035, USA
[b] Neurosciences Program, Stanford University, Stanford, CA, USA
[c] Department of Psychology, Stanford University, Stanford, CA, USA

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Abstract

The present study used the flanker task [Percept. Psychophys. 16 (1974) 143] to identify neural structures that support response selection processes, and to determine which of these structures respond differently depending on the type of stimulus material associated with the response. Participants performed two versions of the flanker task while undergoing event-related functional magnetic resonance imaging (fMRI). Both versions of the task required participants to respond to a central stimulus regardless of the responses associated with simultaneously presented flanking stimuli, but one used colored circle stimuli and the other used letter stimuli. Competition-related activation was identified by comparing Incongruent trials, in which the flanker stimuli indicated a different response than the central stimulus, to Neutral stimuli, in which the flanker stimuli indicated no response. A region within the right inferior frontal gyrus exhibited significantly more competition-related activation for the color stimuli, whereas regions within the middle frontal gyri of both hemispheres exhibited more competition-related activation for the letter stimuli. The border of the right middle frontal and inferior frontal gyri and the anterior cingulate cortex (ACC) were significantly activated by competition for both types of stimulus materials. Posterior foci demonstrated a similar pattern: left inferior parietal cortex showed greater competition-related activation for the letters, whereas right parietal cortex was significantly activated by competition for both materials. These findings indicate that the resolution of response competition invokes both material-dependent and material-independent processes.
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Keywords: Flanker task; Response competition; Response selection; Executive control; Domain-specificity

1. Introduction

When individuals are confronted with multiple possible actions, a single response must be selected. This operation, termed response selection, is a basic component of cognition whose neural substrate remains poorly understood. Response selection has been studied using a variety of experimental tasks, including set-shifting, Stroop, and go/no-go tasks, all of which require participants to suppress undesirable responses and produce an appropriate one. It is often assumed that the selection operation is performed by a unitary process that is invoked regardless of the task domain. This assumption is critical for interpreting neuroimaging and neuropsychological results, and heavily constrains the cognitive architecture underlying performance across a wide range of tasks. The present study addresses the seldom-examined fundamental question: do distinct neural systems support response selection for different types of stimulus materials?

Evidence for a unitary selection process stems from a variety of sources. A substantial behavioral literature suggests that response selection processes for unrelated tasks using distinct stimulus materials appear to be implemented in a serial fashion (e.g. [1,2]; but see [3]). There is active debate over whether the costs to performance observed when two responses must be selected in immediate succession reflect a structural feature of the cognitive architecture or a strategic choice that can be overcome with the appropriate incentives and levels of practice (see [4–7]). Nonetheless, the available data suggest that in the absence of considerable task-specific practice, response selection occurs for a single task at a time, consistent with the proposal that a set of common processes are engaged across tasks.

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[*] Corresponding author. Tel.: +1-650-604-4508; fax: +1-650-604-3323.
E-mail address: ehazeltine@mail.arc.nasa.gov (E. Hazeltine).

[1] Co-corresponding author.

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Data from neuroimaging experiments are consistent with a unitary selection process hypothesis because they have identified brain structures that play a role in response selection in a variety of behavioral tasks. These studies have focused on the role of the frontal lobes in implementing response selection under conditions in which competing options must be inhibited. Neuroimaging studies using the flanker [8,9] and set-shifting tasks [10–12,51] have all reported foci of competition-related activity within 1 cm of the border between Brodmann areas (BA) 44 and 45 of the right frontal lobe. Nearby activations have also been associated with response inhibition during go/no-go tasks [13,14,51,52] and during Stroop interference [15,16]. The anterior cingulate cortex (ACC) is also frequently reported in studies of response competition, especially when the Stroop task is used (e.g. [17,53]). A meta-analysis of 15 neuroimaging studies found that response competition resulted in reliable activation of the ACC and right lateral prefrontal cortex [18].

There are, however, additional frontal regions for which activity is frequently associated with response competition. Specifically, some researchers have emphasized foci within left frontal cortex (e.g. [19,20]) or in bilateral prefrontal cortices (e.g. [14,15]). Integrating the existing findings is difficult, because the tasks used in the experiments differ along multiple dimensions. One possibility is that different stimulus materials engage distinct neural substrates. There is neurophysiological [21,22] and neuroimaging [23,24] evidence from working memory studies suggesting that prefrontal regions are organized in terms of their sensitivity to distinct stimulus domains. This proposal has received considerable attention, but no clear picture has emerged. Some direct tests have supported the segregation-by-material hypothesis (e.g. [25,26]), whereas others have found little or no difference in the activation regions of the prefrontal cortex for distinct stimulus materials (see [27–29]).

1.1. Material-specificity in the prefrontal cortex

The majority of imaging studies testing the segregation-by-material hypothesis have used working memory tasks (e.g. [25,29,30]). However, theorization about the computational role of the prefrontal cortex has emphasized its contribution to the selection of response alternatives, especially when incoming sensory information is ambiguous as to which response is most appropriate (e.g. [31–33]). Thus, response selection tasks may provide a particularly sensitive means of identifying material-dependent regions within the prefrontal cortex.

One neuroimaging study of response selection [16] investigated the attentional mechanisms that were specific to different stimulus-materials using a Stroop-like paradigm in which multiple stimulus dimensions were associated with the responses. Conflict activated left lateral prefrontal cortex (BA 9) when the relevant stimulus feature was either color or location. However, much of the observed activation depended on the task: when participants responded to the word's color, the conflicting meanings activated BA 44 and 46, bilaterally. When participants responded to the word's location, the conflicting meanings activated more superior bilateral prefrontal foci in the left middle frontal gyrus (BA 8 and 9). In the second experiment, the relevant stimulus feature was held constant (color) and the irrelevant feature was varied (word or shape). Here, both types activated foci within the left and right middle frontal gyri (BA 9 and 46), although different irrelevant features produced different patterns of activation in posterior brain regions.

Although these findings suggest that stimulus properties can determine which prefrontal structures subserve response selection, it is difficult to draw strong conclusions. First, in all conditions of the experiment, multiple stimulus dimensions activated the responses, making it difficult to assign specific features to brain regions. Second, the interference was based on long-term semantic associations. Such semantic associations may engage their own set of prefrontal regions or those that are engaged by verbal materials. Third, as pointed out by the authors, different forms of visual attention may be engaged to select the relevant stimulus properties for the different conditions, and these attentional mechanisms may be distinct from response selection processes.

While few neuroimaging studies have directly addressed whether distinct stimulus materials engage separate response selection processes, behavioral experiments have shed light on the question. Virzi and Egeth [34] assessed the effects on performance of two types of irrelevant information (verbal and spatial) on either vocal or manual responses. The magnitude of the slowing of reaction times was dependent on an interaction between the modality of the irrelevant information and the mode of responding: verbal information produced larger costs on vocal responses, and spatial information produced larger costs on manual responses (see also [35]). Similarly, Cohen and Shoup [36] used a flanker task in which stimuli indicated the appropriate response by either their color or orientation. Color flankers interfered only with color targets, and orientation flankers interfered only with orientation targets; thus, competition appeared to occur within but not between perceptual dimensions. Such findings can be accounted for by separate, domain-specific response selection mechanisms that operate on distinct stimulus materials.

The present experiment uses the flanker task, introduced by Eriksen and Eriksen [37], because it allows competing responses to be indicated by the same type of stimulus material. On each trial, a central target is presented simultaneously with two surrounding flankers. Participants respond to the target on the basis of previously learned stimulus–response (S–R) associations, regardless of the responses indicated by the flankers. The flankers can indicate the same response as the target (Congruent trials), a different response (Incongruent trials), or no response (Neutral trials). Incongruent trials are performed more slowly than Congruent or Neutral trials, even when all trials involve flankers that are physically different from the target.

Two versions of the flanker task, one using color stimuli and the other letter stimuli, were used to determine whether the stimulus materials affected the patterns of neural activation associated with response competition. Both the color and letter versions of the task required manual responses and involved highly similar task demands. The letters and colors were placed in the same locations of the visual field, so that when response conflict was induced by incongruent flankers, information from one region of the visual field had to be selected and information from surrounding regions had to be suppressed. Thus, attentional demands were held constant across the two tasks. Moreover, the irrelevant information did not possess an a priori correspondence to particular responses but instead depended on the same arbitrary stimulus–response associations as the relevant stimulus information. In this way, interference was restricted to the stimulus information in the display and not long-term associations in semantic memory as in most versions of the Stroop task. By comparing competition-related activation in the color and letter flanker tasks, we determined whether brain regions showed material-dependent activation (i.e. activation during competition between stimuli of one type but not the other) or material-independent activation (i.e. activation during competition between stimuli of both types).

2. Methods

2.1. Participants

Paid volunteers were recruited from Stanford University and around the Bay Area. The reported data are from 10 healthy right-handed volunteers (five males, five females; aged 18–44 years, $M = 27$). Three of thirteen participants who performed the tasks were excluded: one on the basis of poor performance (on average 53% correct across conditions), and two on the basis of poor normalization of the anatomical volumes to the standard template brain.

2.2. Tasks

Participants underwent two color flanker scans and two letter flanker scans during the acquisition of whole-brain fMRI. The tasks had the same basic structure but involved different types of stimuli. On each trial, a horizontal array of three stimuli—including a central stimulus and two identical flanking stimuli—was presented for 1500 ms. Each stimulus subtended 1.0° of visual angle and was separated from its nearest neighbors by 0.4°. Presentation of the stimulus array was followed by a fixation period, in which a crosshair was presented for 1300 ms, followed by a 200 ms blank screen. On Fixation trials, participants viewed a crosshair for 2800 ms and a blank screen for 200 ms.

Responses were made with the index and middle fingers of the right hand. For the color task, participants were pressed a left button if the central target was a red or green circle and a right button if it was a blue or yellow circle. For the letter task, they pressed the left button for ‘B’ or ‘H’ and the right button for ‘F’ or ‘T’. Participants were instructed to respond as quickly and accurately as possible.

Each scan included Congruent, Incongruent, and Neutral trials, along with Fixation trials. On Congruent trials, the flankers were associated with the same response as the central stimulus. However, the flanking stimuli were physically different from the target. For example, a green target might be surrounded by red flankers on a Congruent trial during the color task. On Incongruent trials, the flankers were associated with the opposite response from the target. On Neutral trials, the target was flanked by stimuli that were not associated with any response (e.g. grey circles or asterisks for the color and letter tasks, respectively).

The tasks followed a rapid event-related design with a 3 s intertrial interval. The trial order was specified according to a stochastic design in SPM99, in which the probability of each trial type varied sinusoidally over a 30 s period. There were 68 Incongruent, 68 Congruent, 71 Neutral, and 33 Fixation trials over the course of two scans of a given type. The same two lists specifying the order of presentation of different trial types were used for the color and letter scans. Five participants performed the color scans first, and five performed the letter scans first. Color and letter flanker tasks were performed in separate scans to minimize the number of S–R associations to be kept in mind at one time.

2.3. Testing procedure

Prior to the scan session, participants learned arbitrary stimulus–response associations for each task. They performed 10–20 trials of each flanker task prior to the start of the scan session. They then performed two hundred and forty 3 s trials over the course of two scans of a given type (color or letter). Psyscope was used to display stimuli and collect responses.

2.4. Imaging data acquisition

Whole-brain imaging data were acquired on a 3 Tesla MRI Signa LX Horizon Echospeed scanner (GE Medical Systems, 8.2.5 systems revision). T2-weighted flow-compensated spin-echo anatomical images (2000 ms TR; 85 ms TE) were acquired in 16 contiguous 7 mm axial slices. Functional images were acquired in the same set of slices using a T2*-sensitive gradient echo spiral pulse sequence (1500 ms TR, 30 ms TE, 60° flip angle, 24 cm field of view, 64 × 64 data acquisition matrix; see [54]).

2.5. Data analysis

Functional images were motion-corrected and normalized with SPM99 (Wellcome Department of Cognitive Neurology), interpolated to 2 mm × 2 mm × 2 mm voxels, spatially smoothed with a Gaussian filter (6 mm full width-half maximum) and temporally filtered (low-pass filter: 4 s Gaussian; high-pass: SPM default based on trial frequency). Hemodynamic responses to each trial type were modeled using the canonical HRF in SPM with separate baselines computed for each scan. Images were averaged to create one image of mean activity per trial type per participant. These images were globally scaled to a mean signal intensity of 100. The *t*-tests were performed on the average images to create a series of SPM{Z} maps depicting differences in activity between trial types. The coordinates of foci were transformed from MNI to Talairach space.

For the present purposes, we focus on changes in activation between Incongruent and Neutral trials, because this comparison provides the most straightforward measure of response competition. Unlike Neutral trials, Congruent trials involved displays that contained stimuli indicating additional (compatible) response codes. Although Congruent trials are usually responded to at least as quickly as Neutral trials and more quickly than Incongruent trials, how the activation of these additional codes affects response competition is unclear. Nonetheless, we report whether foci identified by the comparison between Incongruent and Neutral trials also showed changes in activation during Congruent trials compared to the Incongruent trials.

Material-dependent competition-related activations were defined as regions showing greater differences between Incongruent and Neutral trials for one stimulus material than the other. Separate Incompatible–Neutral (I–N) contrast images were created for each subject and stimulus material. Foci preferentially engaged by competition between letter stimuli were identified from the following contrast: Letter I–N > Color I–N ($P < 0.05$ uncorrected, extent threshold of 10 voxels), masked to include only regions engaged by Letter I–N (at $P < 0.001$ uncorrected). Similarly, foci preferentially engaged by color stimuli were identified by: Color I–N > Letter I–N ($P < 0.05$ uncorrected, extent threshold of 10 voxels), masked to include only regions engaged by Color I–N (at $P < 0.001$ uncorrected). Because the mask generated by the letter stimuli were larger than the mask for the color stimuli, the corrected *P*-values associated with these comparisons differed for the two stimulus materials ($P < 0.05$ corrected for the letters and <0.001 corrected for the colors). Thus, the height and extent thresholds were the same for both stimulus materials, and the probability of Type I error was kept at or below a conventional level. In sum, a region was classified as showing material-dependent competition-related activation if it exhibited a greater increase from Neutral to Incongruent trials for one type of stimulus than the other. Such a region may show I–N increases for both stimulus materials, but the increase must be significantly larger for one stimulus material compared to the other.

To identify competition-related regions that were material-independent, we performed a conjunction analysis using SPM99. This analysis identifies regions that exhibit a main effect of both manipulations, and excludes regions for which activation differs significantly between the two. A combined threshold of $P < 0.00001$ uncorrected was used for the conjunction analyses, corresponding to $P < 0.001$ for each contrast. Thus, the statistical threshold for activation of Incongruent trials compared to Neutral trials for each type of stimulus was the same as in the tests for material-dependent regions. Clusters consisting of 10 or more contiguous voxels were reported, matching the extent threshold applied in the material-dependent analyses.

Patterns of activation in material-dependent and material-independent foci were confirmed in subsequent regions-of-interest (ROI) analyses. An average parameter estimate of the fitted hemodynamic response was calculated for each condition within each ROI. These parameter estimates were computed for each participant and submitted to *t*-tests and correlational analyses.

3. Results

3.1. Behavioral results

The proportion of correct responses (0.97) did not differ for the two types of stimulus materials and there was no main effect of trial-type (Congruent, Incongruent, and Neutral). Reaction times for correct responses were analyzed with an ANOVA using trial-type and material as within-subjects factors (Fig. 1). The main effect of trial-type [$F(2, 18) = 21.11$; $P < 0.0001$; M.S.E. $= 681.68$] and the interaction between trial-type and material [$F(2, 18) = 7.61$; $P < 0.005$; M.S.E. $= 465.77$] were significant. Separate ANOVAs performed on the color and letter reaction times revealed significant effects of trial-type for both materials

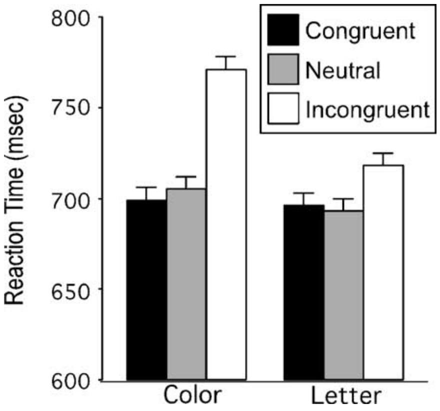

Fig. 1. Reaction times across the three trial-types for the two versions of the task. The error bars represent the within-subject standard error computed from the two-way (material × trial-type) ANOVA.

Table 1
Incongruent–Neutral, conjunction of Color and Letter

Volume	Z	x	y	z	Region frontal lobe		BA
408	5.99	44	23	28	R	Middle/inferior frontal gyrus[a]	9/44
544	5.89	14	24	43	R	Superior frontal/cingulate[a]	8/32
712	5.74	−26	3	61	L	Premotor cortex[a]	6
200	5.78	24	8	53	R	Premotor cortex[a]	6
160	5.32	−34	−21	51	L	Precentral	4
96	5.30	40	−40	52	R	Inferior parietal cortex	40

Height threshold: $Z = 3.61$, $P = 0.000001$; extent threshold: 10 voxels. Volume indicates the size of the focus in mm^3. Coordinates are reported in Talairach space.

[a] Significantly greater ($P < 0.05$) activation in the Incongruent trials compared to the Congruent trials for both types of stimuli.

[color: $F(2, 18) = 24.56$; $P < 0.0001$; M.S.E. $= 652.54$; letter: $F(2, 18) = 3.86$; $P < 0.05$; M.S.E. $= 494.91$] with Incongruent trials being slowest. Post hoc Bonferroni comparisons revealed similar patterns of findings for the color and letters, with significant differences between Incongruent and Neutral trials [color: difference $= 66$ ms; $P < 0.0001$; letter: difference $= 26$ ms; $P < 0.05$], but not between Congruent and Neutral trials [color: difference $= 6$ ms; $P > 0.05$; letter: difference $= -4$ ms; $P > 0.05$]. The interaction, therefore, reflects a greater slowing on Incongruent trials for the colors than for the letters.

3.2. Brain imaging results

3.2.1. Common activation

Regions demonstrating similar competition-related (Incongruent > Neutral) activation for the two stimulus types included the right inferior/middle frontal and superior frontal gyri and premotor, anterior cingulate, and inferior parietal cortices. In the left hemisphere, a large focus of activation in premotor cortex and a smaller focus in primary motor cortex (Table 1 and Fig. 2) were observed. Except for the precentral and parietal foci, these regions were more activated by Incongruent trials than Congruent trials for both stimulus types.

3.2.2. Color-specific activation

A region within the right inferior frontal gyrus demonstrated greater competition-related activity for the colors than for the letters (Table 2 and Fig. 3).

Table 2
Incongruent–Neutral, Color > Letter

Volume	T	x	y	z	Region		BA
96	3.06	44	4	28	R	Inferior frontal	44

Height threshold: $Z = 3.61$, $P = 0.001$; extent threshold: 10 voxels. Volume indicates the size of the focus in mm^3. Coordinates are reported in Talairach space. This region did not demonstrate significant differences between Incongruent and Congruent trials for either stimulus type.

3.2.3. Letter-specific activation

Regions that demonstrated greater competition-related activity for the letters than the colors included bilateral middle frontal gyri, the left inferior parietal cortex, and bilateral post-central gyrus (Table 3 and Fig. 3). Except for the left post-central gyrus, all of these regions were also significantly more activated by Incongruent letter trials than Congruent letter trials.

3.2.4. Correlational analyses

For each identified focus of activation, we performed correlations between the mean activation difference between Incongruent and Neutral trials and the mean reaction time difference between those trials, which ranged from −10 to 141 ms. The activation difference was based on the mean activation of the entire focus. Separate correlations were performed for the two stimulus materials. Only the activation in the right inferior frontal focus identified as being material-independent demonstrated a significant correlation with the RT difference between Incongruent and Neutral trials, and this was observed for the letter stimuli [$r = +0.65$;

Table 3
Incongruent–Neutral, Letter > Color

Volume	T	x	y	z	Region		BA
384	2.46	−52	10	36	L	Middle frontal gyrus[a]	9
240	2.98	34	22	42	R	Middle frontal gyrus[a]	8/9
88	2.30	−42	−22	42	L	Post-central gyrus	3/1/2
104	2.42	36	−30	66	R	Post-central gyrus[a]	3/1/2
224	3.17	−34	−60	34	L	Inferior parietal cortex[a]	39/40

Height threshold: $Z = 3.61$, $P = 0.001$; extent threshold: 10 voxels. Volume indicates the size of the focus in mm^3. Coordinates are reported in Talairach space.

[a] Significantly greater ($P < 0.05$) activation in the Incongruent compared to the Congruent trials with the letter stimuli. None of these regions demonstrated significant differences between Incongruent and Congruent trials with the color stimuli.

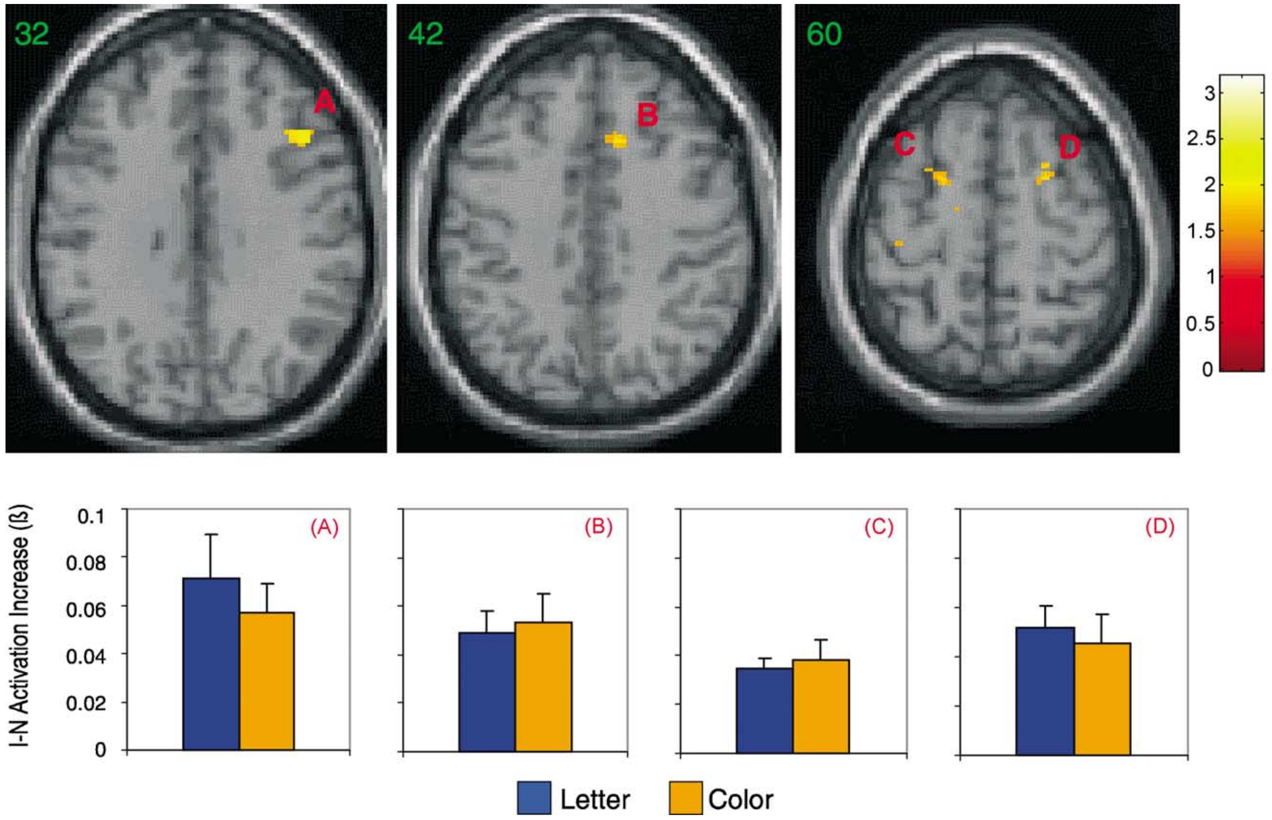

Fig. 2. Foci identified as material-independent shown on a canonical template brain along with their respective competition-related activations for the two stimulus materials. The *z*-coordinate for each slice is shown in the upper left corner; the left side of the figure corresponds to the left side of the brain. A represents right middle/inferior frontal gyrus, B the anterior cingulate, and C and D left and right premotor cortices, respectively. The color scale indicates *t*-values. For the bar charts, the increase in activation associated with Incongruent compared to Neutral trials is shown for each of the regions, with the increase for the letters shown in blue and the increase for the colors shown in orange. The increases were computed by subtracting the mean parameter estimate associated with the Neutral condition from the mean parameter estimate for the Incongruent condition for each subject. The error bars represent the standard error of the mean across subjects.

$F(1, 8) = 6.01$; $P < 0.05$] but not the color stimuli [$r = -0.16$; $F(1, 8) < 1$].

4. Discussion

For both types of stimulus materials, Incongruent trials were performed more slowly than Neutral trials, indicating the presence of response competition. As expected, response competition activated a distributed system of structures, predominantly in the frontal lobes, consistent with previous imaging studies of response competition (e.g. [8,9,13,38–40]). However, the activations were not identical across the two types of stimulus materials. Both material-dependent and material-independent activations were identified.

4.1. Material-independent regions in the prefrontal cortex

Several prefrontal structures were active during competition for both letter and color stimuli (Fig. 2). These regions included the border of right inferior and middle frontal gyri and the ACC—the same regions identified by Jonides et al. [18] in their meta-analysis of response competition studies. By demonstrating competition-related activation in these regions for different stimulus materials, the present study provides converging evidence that these two structures may play a generalized role in the resolution of response competition. Activation across a range of stimulus materials is consistent with the role of executive processes that control the flow of information to subcomponents that are specialized for particular stimulus materials.

MacDonald and Cohen [19] and colleagues have proposed a distinction between the role of lateral prefrontal cortex, which may maintain the cognitive set and attentional demands specific to the task, and the ACC, which may monitor response conflict (see also [41,50]). Given that much of the prefrontal activity in the present study was material-dependent, our findings support this hypothesis if it is assumed that cognitive control is implemented by material-specific modules whereas response conflict is monitored by a generic system. However, such an account ignores the material-independent focus identified on the border of the inferior and middle frontal gyri of the right cerebral

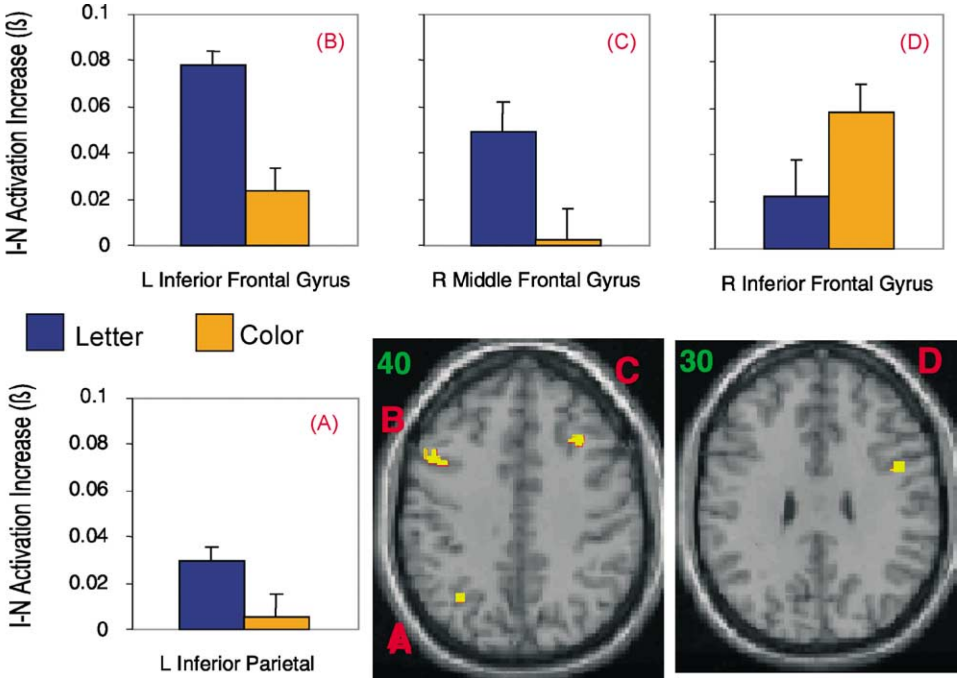

Fig. 3. Material-dependent prefrontal foci overlaid on a canonical template brain along with their respective competition-related activations for the two stimulus materials. The z-coordinate for each slice is shown in green in the upper left corner; the left side of the figure corresponds to the left side of the brain. A represents the left inferior parietal cortex, B the left inferior frontal gyrus, C the right middle frontal gyrus, and D the right inferior frontal gyrus. Foci A–C exhibited more competition-related activation for letters than colors; focus D exhibited the reverse pattern. The error bars represent the standard error of the mean across subjects.

hemisphere. We propose that right ventrolateral prefrontal cortex, along with the ACC, supports generalized selection processes that are invoked by response competition. This hypothesis is supported by the fact that increases are observed in these regions in the comparisons between Incongruent and Congruent trials.

4.2. Other material-independent regions

Bilateral activation within premotor cortex was associated with response competition for both types of stimulus materials. Several experiments have reported activation in this region associated with response competition (e.g. [14,15]). That these regions were more active during Incongruent trials than Congruent trials suggests that the representations are largely response-based, because the two trial types were equivalent in terms of stimulus conflict, but only in the Incongruent trials were two competing responses indicated.

Left sensorimotor and right parietal cortex were also activated by response competition regardless of the stimulus material. In contrast to the premotor foci, neither region exhibited significant differences between Congruent and Incongruent trials, suggesting that their roles may be more closely related to S–R mappings than response-based codes. The similarity in activation between Congruent and Incongruent trials suggests that the representations here are stimulus-based, because stimulus conflict, not response conflict, was equivalent for the two trial types. This conclusion is somewhat unexpected for the sensorimotor cortex and founded on a null result, so such an interpretation is speculative.

Activation of parietal cortex has been reported in several studies of response competition (e.g. [13,51]). Based in part on anatomical connectivity between prefrontal and parietal cortices [55,56], we suggest that sensitivity to competition in parietal cortex results from bias signals arising in prefrontal cortex (see [42]). That is, material-independent activation of right inferior prefrontal cortex due to response competition may arise from interactions with the material-independent region in right parietal cortex. However, unlike the prefrontal foci, activation in this region is equivalent for Congruent and Incongruent stimuli, suggesting that the representations here are less dependent on the indicated response.

4.3. Material-dependent regions

Material-dependent regions were defined as areas that showed greater increases in activation during Incongruent trials compared to Neutral trials for one type of stimulus material compared to another type. Therefore, these regions were material-dependent in terms of competition-related activation and not differences between the processing of color and letter stimuli.

The largest material-dependent foci were observed in the lateral prefrontal cortex (Fig. 3). This finding is consistent with the proposal that material-specific information is gated to distinct regions within prefrontal cortex. As noted above, neurophysiological and neuroimaging studies of working memory have provided evidence both for (e.g. [30,43]) and against (e.g. [27,29]) the proposal that different stimulus materials are represented by different regions within the human prefrontal cortex. The present results were derived from a response competition task rather than a working memory task and suggest a middle ground: much of the prefrontal cortex appears to increase activation during response conflict in a material-independent fashion, but some regions respond preferentially to conflict between particular stimulus materials.

Two material-dependent foci were observed in right lateral prefrontal cortex. One focus, centered in the inferior frontal gyrus, was more active during competition between color stimuli. This focus is very near to the one reported by Hazeltine et al. [8] in an fMRI study comparing activation during blocks of Incongruent trials to blocks of Congruent trials using color stimuli similar to those in the present study. The present results indicate that increased activation here is dependent on stimulus type; only modest, non-significant, increases were observed in this region when the task used letter stimuli.

The second focus, located in the right middle frontal gyrus, was more active during competition between letter stimuli. This site was accompanied by a similar focus in the homologous region of the left hemisphere, which was also active during response competition when the letter stimuli were used. There are few reports of activation in this left hemispheric region during non-verbal interference tasks, but it is frequently identified in studies of Stroop interference (e.g. [15,19]) when word meanings must be suppressed in favor of color identities and in go/no-go tasks when letter stimuli are used (e.g. [14,52]). The left prefrontal focus observed in the present study is near a region associated with the processing of proactive interference in working memory tasks involving letter stimuli [27,44].

The behavioral data offer an alternative interpretation of the material-dependent foci. Reaction times for the Neutral trials were similar across the two stimulus materials, indicating that decoding the stimuli into the appropriate responses did not differ in difficulty between the tasks. However, the Incongruent trials with color stimuli produced significantly greater slowing of responses than those with letter stimuli. Despite the greater behavioral interference generated by the color stimuli, we observed more competition-related activity with the letter stimuli. Greater prefrontal activation has been associated previously with a reduction of behavioral interference [39]. Given that the letters showed less behavioral interference than the colors, such a result is consistent with the greater number of prefrontal foci observed for the letters. However, even if one assumes that the additional prefrontal foci are responsible for the reduction in the magnitude of the flanker effect, it remains an open question what task conditions allow for these extra regions to be engaged. The present findings, along with those of Jonides et al. [18], indicate that the right inferior frontal and anterior cingulate cortices play a primary role in resolving response conflict, and that additional structures are recruited based on the nature of the competing information.

Only a small focus of activity in the right inferior prefrontal cortex was more active during competition between color stimuli compared to competition between letter stimuli. It is possible that this right inferior focus represents an expansion of this material-independent focus rather than a true material-dependent one. That is, the increased competition induced by the colors may require additional control processes, leading to competition-related activity within the right inferior frontal gyrus that was not present for the letters. This explanation is plausible, although the absence in this region of a significant correlation [$r = 0.02$; $F(1, 8) < 1$] between behavioral interference and competition-related activation on the color trials does not support it.

In sum, the findings are consistent with the conclusion that left prefrontal regions are recruited during competition between verbally-mediated response codes whereas right ventrolateral cortex is less material-dependent. The result parallels those obtained from memory tasks (e.g. [23,24,43]). Experiments using non-verbal conflict tasks, such as the flanker task [8,9,38] (the go/no-go task [13,51]) and tasks involving perceptual conflict [45,46], have reported increases near this right frontal region without corresponding foci in the left hemisphere. In contrast, set-shifting tasks almost always elicit bilateral prefrontal activation (e.g. [10–12]; but see [47]), as was observed with the letter stimuli in the present study. At present, we speculate that participants employ verbal codes while performing set-shifting tasks because the stimuli are not uniquely associated with particular responses.

What does material-dependence indicate about a region's role in resolving response competition? A region that is more active for one type of stimulus material compared to another must operate on representations that are not strictly response-related, because a structure suppressing unwanted output should not be affected by the stimulus material. The presence of such regions provides empirical support for accounts of stimulus-specific interference in behavioral studies (e.g. [34,36]). Moreover, the presence of both material-dependent and material-independent foci suggests that response selection occurs at multiple levels of representation, some that are largely stimulus-based and others that incorporate more abstract codes. These findings are consistent with behavioral data from dual-task studies demonstrating that responses can interfere generically, that is, independent of the particular response and, additionally, in a content-dependent way, in which interference is determined by the similarity or dissimilarity between the abstract responses of the two tasks [48,49].

4.4. Summary

Response competition evoked different patterns of activation depending on the type of stimulus information that had to be inhibited, indicating that competition is resolved by processes whose functions are not limited to the control of motor output. Within prefrontal cortex, activation in the right inferior frontal gyrus was observed during conflict between color stimuli and bilateral activation in the middle frontal gyrus was observed during conflict between letter stimuli. These findings are consistent with observations across a range of studies, suggesting that much of the prefrontal activation associated with competition is specific to the type of stimulus materials impinging on selection processes.

Along with the material-dependent foci of activation, several regions were active to near-equivalent degrees for the two types of stimulus materials. These regions included the ACC and the border of the middle and inferior frontal gyri of the right hemisphere. The predominance of these regions throughout the response competition literature may reflect their roles in response selection across a range of task domains. Together, the presence of both material-dependent and material-independent foci suggests that response selection is performed by two sets of processes, those operating on domain-specific representations and those operating on more abstract codes.

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