Neural basis of the Stroop interference task: Response competition or selective attention?

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Abstract

Previous neuroimaging studies of the Stroop task have postulated that the anterior cingulate cortex (ACC) plays a critical role in resolution of the Stroop interference condition. However, activation of the ACC is not invariably seen and appears to depend on a variety of methodological factors, including the degree of response conflict and response expectancies. The present functional MRI study was designed to identify those brain areas critically involved in the interference condition. Healthy subjects underwent a blocked-trial design fMRI experiment while responding to 1 of 3 stimulus conditions: (1) incongruent color words, (2) congruent color words, and (3) color-neutral words. Subjects responded to the printed color of the word *via* a manual response. Compared to the congruent and neutral conditions, the incongruent condition produced significant activation within the left inferior precentral sulcus (IpreCS) located on the border between the inferior frontal gyrus, pars opercularis (BA 44) and the ventral premotor region (BA 6). Significant deactivations in the rostral component of the ACC and the posterior cingulate gyrus were also observed. Selective activation of the left IpreCS is compatible with findings from previous neuroimaging, lesion, electrophysiological, and behavioral studies and is presumably related to the mediation of competing articulatory demands during the interference condition. (*JINS*, 2002, *8*, 735–742.)

Keywords: Stroop, fMRI, Inferior frontal gyrus, Anterior cingulate gyrus

INTRODUCTION

In 1935, Stroop demonstrated that naming is slowed when subjects are asked to name the ink color of an incongruous color word (e.g., the word "BLUE" printed in red ink). This interference effect has been the subject of extensive study in the experimental, clinical, and functional neuroimaging literatures. In a review of this vast literature, MacLeod (1991) presented various theoretical models to account for the Stroop effect, with two contrasting theories accounting for most of the empirical findings. The first, referred to as the "relative speed of processing" or "response selection" model, posits that the interference effect occurs because words are read faster than colors are named. The time cost of this response competition is thought to be the source of the interference effect. Thus, this model emphasizes that interference occurs at the output stage, presumably during articulatory processing of the verbal stimuli. The second, referred to as the "automaticity" or "selective visual attention" model, assumes that color naming requires more attentional resources than reading, which is considered to be a more automatic and obligatory process. Thus, the interference effect is thought to occur at the perceptual stage as a function of selective visual attention.

Experimental studies of the Stroop effect have provided empirical support for both theories without coming to resolution. Functional neuroimaging techniques have provided a greater understanding of the neuronal circuitry involved in response selection and selective visual attention and hold the promise of testing these contrasting theories. In the first PET study of the Stroop effect, Pardo et al. (1990) found greater activation in the incongruent than congruent condition in the right anterior cingulate cortex (ACC). These results were interpreted in support of the selective attention model, in light of the role of the ACC in spatial attention (Posner & Petersen, 1990). This study, however,

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had a methodological flaw in that the congruent condition was always presented prior to the incongruent condition, introducing the possibility that their findings may be accounted for by nonspecific time-dependent changes.

This possibility was essentially confirmed in a PET study by Bench et al. (1993). In the first of two experiments, three types of stimuli were used: incongruent words, neutral (colorunrelated) words, and colored crosses. Comparisons of the incongruent condition to the two control conditions resulted in completely different areas of activation. The nonverbal control revealed activation in right orbitofrontal cortex, right cingulate, and bilateral inferior parietal regions, whereas the neutral word control revealed activation of left inferior parietal and right superior parietal regions. In addition, they reported significant time-related increases in PET counts in numerous brain regions, including the ACC. In the second experiment, Bench et al. replicated all aspects of Pardo et al.'s (1990) experimental protocol using a counterbalanced design and again found highly significant time-related increases in the ACC. However, comparison of the incongruent condition to the congruent condition revealed no significant areas of activation.

This inconsistency in demonstrating activation of the ACC during Stroop interference has also characterized subsequent studies, and appears to depend on a variety of methodological factors. All experiments that compared incongruent color words to nonlexical stimuli such as color blocks, hatches, or crosses, have reported ACC activation (Bench et al., 1993; Brown et al., 1999; George et al., 1994, 1997; McKeown et al., 1998). However, these comparisons are confounded by highly disparate stimulus parameters and do not allow a precise delineation of the role of the ACC in the interference condition. In contrast, use of lexical control stimuli, such as congruent words, neutral words, or taboo words, results in less frequent activation of the ACC (Bench et al., 1993; Carter et al., 2000; Taylor et al., 1997; cf. Peterson et al., 1999). Interestingly, Carter et al. (2000) reported that ACC activation during the interference condition was dependent on the degree of conflict experienced during the task. When conflict between expectations and task demands was low (e.g., expected incongruent trial, received incongruent trial), activation of the ACC did not differ between incongruent and congruent conditions; when conflict was high (e.g., expected congruent trial, received incongruent trial), the ACC was differentially activated in the incongruent condition. Thus, increasing evidence suggests that activity in this brain region depends on the details of the experimental protocol, and the notion that it plays a specific, immutable role in the Stroop interference task is no longer tenable.

Another brain region that has received attention in the Stroop neuroimaging literature is the left inferior frontal lobe. For example, Taylor et al. (1997), using both lexical and nonlexical control stimuli in a PET study, reported that only the left inferior frontal gyrus was consistently activated during the interference condition. In a recent functional MRI (fMRI) study, the left pars opercularis was identified as one of the regions consistently activated by Stroop stimuli in comparison to both color block and reading control conditions (Brown et al., 1999). Selective activation of the left inferior frontal area, namely, Broca's area, would suggest that the Stroop interference effect is due to response selection competition involving speech articulatory processes. This is supported by the fact that focal lesions in Broca's aphasics have been shown to produce an abnormally large interference effect (Perret, 1974).

The present study was designed to further examine the neural mechanisms underlying the Stroop effect using wholebrain fMRI. Two different verbal control conditions were used, in an attempt to account for as many non-specific aspects of the interference condition as possible. The tasks were designed to isolate areas of activation that are highly specific to the interference aspect of the condition rather than to differences in the nature of the stimuli or the task parameters. In this way, we hoped that our results would allow us to draw stronger conclusions about which brain regions are critically involved in the Stroop interference condition and how these may relate to current cognitive theories of the task.

This study also served as the first neuroimaging experiment to examine the Stroop effect using a manual response. A review of the literature (MacLeod, 1991) indicates that manual responses are associated with significant Stroop interference, but to a somewhat lesser degree than with overt vocal responses. The cognitive/neural basis of this phenomenon is not well understood and response mode remains an important variable in neuroimaging studies of the Stroop task.

METHODS

Research Participants

Eighteen subjects (8 men; 10 women) ranging in age from 18 to 46 years (M = 26.7) participated in the study. All were right-handed on the Edinburgh Handedness Inventory (mean laterality quotient = 83; range = 41–100; Oldfield, 1971). Two additional subjects were excluded due to poor performance (<80% correct; chance = 25%) on the experimental (incongruent) condition. Potential subjects were excluded if they had a history of neurologic disease, a major psychiatric disturbance, substance abuse, or if they were taking psychoactive prescription medications. Participants provided informed consent according to institutional guide-lines established by the Medical College of Wisconsin Human Subjects Review Committee, and were compensated for their time.

Stroop Conditions

Subjects performed a series of three consecutive activation conditions that were preceded and followed by a baseline rest period. In each condition, stimuli were comprised of single words printed in one of four colors (red, blue, green, or yellow). In the congruent (C) condition, the stimuli were four color words ("red," "blue," "green," and "yellow") presented in the color denoted by the word (e.g., "red" shown in red). In the incongruent (I) condition, color words were presented in one of the three colors not denoted by the word (e.g., "red" shown in yellow). In the neutral (N) condition, four color-neutral words ("hat," "vest," "scarf," and "jacket") were printed in any one of the four colors. Stimuli were presented centrally at the rate of 1 trial every 2 s (1250 ms on; 750 ms off). For each condition, the subject's task was to respond to the printed color of the stimulus, ignoring the word. Subjects responded by pressing (with the index, middle, ring, or little fingers of the right hand) one of four buttons corresponding to the four possible print colors. To ensure accuracy of response mapping, the color names (in white type) were presented in the lower visual field in the order in which they mapped to the response buttons. These remained in view at all times, including during rest periods.

Functional MR Imaging

Whole-brain functional MRI was conducted on a commercial 1.5 T scanner (Signa, General Electric Medical Systems, Milwaukee) equipped with a prototype 30.5 cm i.d. three-axis local gradient head coil and an elliptical endcapped quadrature radiofrequency coil (Wong et al., 1992a, 1992b). Echo-planar images were collected using a singleshot, blipped, gradient-echo echo-planar pulse sequence [TE (echo time) = 40 ms; FOV (field of view) = 24 cm; matrixsize = 64×64 ; Bandettini et al., 1992]. Twenty-two contiguous sagittal 6-mm thick slices were selected to provide coverage of the entire brain (voxel size: $3.75 \times 3.75 \times$ 6 mm). Prior to functional imaging, high resolution, 3D spoiled gradient-recalled at steady-state (SPGR) anatomic images were collected [TE = 5 ms; TR = 24 ms; 40° flip angle; number of excitations (NEX) = 1; slice thickness = 1.2 or 1.3 mm; FOV = 24 cm; resolution = 256×192]. Foam padding was used to limit head motion within the coil. A nonferrous keypress device made from forcesensing resistors was used to record response times and accuracy.

Subjects underwent six functional imaging series. During each imaging series 104 sequential echo-planar images were collected with an interscan interval (TR) of 4 s (total scanning duration = 6 min, 56 s). The first two images of each image series were discarded to allow the spin lattice to reach stabilization. A series consisted of four cycles of rest and activation, with each cycle beginning and ending with a 24-s rest (R) period. Activation periods consisted of three consecutive 24 s (12 trial) epochs, during which subjects performed the C, I, and N conditions in a blocked trial format. Order of presentation of the three conditions was fully counterbalanced within subjects. A typical imaging series might have the following condition order: $R_1-C_1 N_1-I_1-R_2-I_2-C_2-N_2-R_3-N_3-I_3-C_3-R_4-C_4-I_4-N_4-R_5$. Words were computer-generated and rear-projected onto the center of an opaque screen located at the subject's feet (viewing distance = 200 cm). Subjects viewed the screen in a darkened room through prism glasses and corrective lenses, if necessary. Subjects briefly practiced the three conditions prior to scanning.

Image Processing and Statistical Analysis

Minor anatomic distortions in the EP images due to local field inhomogeneities were corrected using a field map generated by increasing the TE by 1 ms on the last two images of the time series (Jezzard & Balaban, 1995). Each image time series was spatially registered in-plane to reduce the effects of head motion using an iterative linear least squares method.

Functional images were created by generating statistical parametric maps (SPMs) of t-deviates reflecting differences in MR signal intensity between the activation conditions (I vs. C, I vs. N, C vs. N) and between each activation condition and the rest baseline (I vs. R, C vs. R, N vs. R) on a voxel-wise basis for each subject. The first two images (total of 8 s) in each of the three activation conditions and the rest periods were discarded from analysis due to the rise and fall time of the hemodynamic response (Bandettini et al., 1992). The first stage of the analysis (Rao et al., 1997) involved averaging the remaining four images for each rest and activation epoch. Difference images were created comparing the three activation conditions with each other and with rest. In all, 24 difference images (4 cycles/image series \times 6 image series/session) were generated per subject. Thus, the incongruent-congruent difference images would be calculated in the following manner: $D_{IC1} = I_1 - C_1$, $D_{IC2} = I_2 - C_2, \dots, D_{IC24} = I_{24} - C_{24}$. Difference images were also generated comparing each activation condition (I, C, N) with rest [e.g., $D_{IR1} = I_1 - (R_1 + R_2/2), D_{IR2} =$ $I_2 - (R_2 + R_3/2), \dots, D_{IR24} = I_{24} - (R_{24} + R_{25}/2)].$ Mean difference values were then compared on a voxelwise basis against a hypothetical mean of zero using pooledvariance Student t tests.

Individual SPGR anatomical scans and SPMs were linearly interpolated to volumes with 1 mm³ voxels, coregistered, and transformed into standard stereotaxic space (Talairach & Tournoux, 1988) using the "MCW-AFNI" software package (Cox, 1996). To compensate for normal variation in anatomy across subjects (Thompson et al., 1996), the stereotaxically resampled 3D SPMs were subjected to a Gaussian blur at each voxel over a sphere of radius 3 mm. The SPMs for each comparison were averaged across the 18 subjects on a voxel-wise basis. Thus each voxel in the resulting averaged SPM contains an averaged t statistic. The procedure of averaging statistics was chosen to guard against nonequal MR signal variances between subjects. A threshold was then applied to the averaged t statistics to identify voxels in which the mean change in MR signal between activation conditions and between the activation conditions and rest was unlikely to be zero. The average of a set of t deviates is not a tabulated distribution. Therefore, the Cornish-Fisher expansion of the inverse distribution of a sum of random deviates (Fisher and Cornish, 1960) was used to calculate probability values associated with average t deviates.

In addition to a t-deviate threshold, a minimum cluster size threshold of 200 μ l was applied to minimize false positives in the brain maps (Forman et al., 1995). A randomization procedure that involves relabeling activation conditions (Arndt et al., 1986; Bullmore et al., 1996; Holmes et al., 1996) was applied to select the appropriate *t*-deviate threshold to minimize the possibility that differences in MR signal were due to chance. This threshold was determined by reassigning the difference images to one of three random conditions (I_r, C_r, N_r) . Thus, each of the random conditions was comprised equally of the three experimental conditions. The random conditions were then subjected to the identical statistical analysis procedure described above. A histogram of t deviates was used to compare real and randomized analyses. This technique yielded a threshold of t =0.48 (p < .05), which effectively eliminated false positive clusters from the functional maps. Activated regions were overlayed onto a single representative brain for anatomical reference.

RESULTS

Behavioral Findings

Figure 1 displays the reaction time (RT) and accuracy results for each of the three experimental conditions. Median RTs (Figure 1A) were averaged across subjects for each condition and subjected to a one-way ANOVA. This analysis revealed a significant main effect of condition [F(2,34) =43.61, p < .001]. Post-hoc comparisons indicated significant differences between all three conditions (p < .001) such that RTs were fastest for congruent stimuli (673 \pm 20 ms; $M \pm SEM$), slower for neutral stimuli (725 ± 23 ms), and slowest for incongruent stimuli (781 \pm 29 ms). Analyses of accuracy (Figure 1B) levels also revealed a significant main effect of condition [F(2,34) = 5.75, p = .007]. High levels of accuracy were obtained for all conditions, but the pattern of performance was identical to that seen in the RT data; accuracy was highest for the congruent condition (97.6% \pm .46%), slightly lower for the neutral condition (96.6% \pm .57%), and lowest for the incongruent condition (95.3% \pm .88%). Post-hoc comparisons revealed a significant difference between congruent and incongruent conditions [t(17) = 3.43, p < .004] and between the congruent and neutral conditions [t(17) = 2.07, p = .05], but no significant difference between the incongruent and the neutral conditions [t(17) = -1.55, p = n.s.].

Functional Imaging Findings

Comparisons of the three experimental conditions with each other revealed relatively small, discrete activation foci



Fig. 1. Median reaction time (RT; upper panel) and accuracy (percent correct; lower panel) for the congruent (C), neutral (N), and incongruent (I) conditions. Error bars = SEM.

(Table 1, Figure 2). Subtraction of the incongruent and congruent conditions resulted in significant activation of the left inferior precentral sulcus (IpreCS) during the interference task (Figure 2, upper panel), at the junction of the pars opercularis of the inferior frontal gyrus (BA 44) and the left ventral premotor area (BA 6). Foci in both the posterior cingulate and rostral portion of the anterior cingulate regions showed significantly greater activation during the congruent condition relative to the incongruent condition. When the neutral condition was compared to the incongruent condition (Figure 2, lower panel), an identical region of activation was seen in the left IpreCS region during the incongruent condition. In addition, a focus in the left posterior cingulate showed greater activity during the neutral than the incongruent conditions, similar to that seen in the incongruent-congruent subtraction. A comparison of the neutral and congruent conditions resulted in no significant activation foci.

Each of the three experimental conditions was also compared to the baseline rest periods. As expected, numerous areas of activation were identified, including the left primary motor cortex, left IpreCS, left and right lateral cerebellum, ACC, visual cortex, left thalamus, and right inferior parietal cortex. A large volume of activation was observed within the ACC region for each of the three conditions (I: $5,563 \ \mu$ l; C: $5,566 \ \mu$ l; N: $5,703 \ \mu$ l) and spanned the cingulate sulcus involving both areas 24 and 32. Table 1. Center of mass, volume, and intensity of significant activation foci

Activated region	L–R (<i>x</i>)	A–P (y)	S–I (z)	Volume (µl)	Intensity (max. t)
Incongruent > Congruent					
L inferior precentral sulcus (BA 44, 6)	-44	3	30	885	0.78
Congruent > Incongruent					
M posterior cingulate gyrus (BA 31)	3	-43	33	858	0.63
L inferior anterior cingulate gyrus (BA 24)	-16	30	-3	331	0.64
Incongruent > Neutral					
L inferior precentral sulcus (BA 44, 6)	-44	4	29	478	0.61
Neutral > Incongruent					
L posterior cingulate gyrus (BA 31)	-4	-45	32	399	0.64

Coordinates are in mm (x, y, z) from the 0,0,0 point situated at the midline of the brain (x), at the anterior commissure (y), and at the level of the anterior and posterior commissures (z). L, left; R, right; M, midline; A, anterior; P, posterior; S, superior; I, inferior; BA, Brodmann area.

DISCUSSION

The primary finding from this study is the consistent activation of the left IpreCS during performance of the Stroop interference task. Left IpreCS activation located adjacent to the pars opercularis of the inferior frontal gyrus (IFG) was observed relative to two different lexical control conditions, suggesting that this region plays a critical role in processing incongruent Stroop stimuli. Given the proximity of the identified region to Broca's area, these results may suggest that Stroop interference is mediated by competing subvocal articulatory responses. The use of a manual response suggests that activation of this region is not specifically related to overt speech articulation. Isolated activation of the left IFG related to Stroop interference has also been described by Taylor et al. (1997). Other studies have reported activation of the IFG in conjunction with other brain regions (Brown et al., 1999; Carter et al., 2000; George et al., 1994). In examining the time course of activation in an event-related fMRI study, Carter et al. (2000) reported that IFG activation preceded activation of the ACC by about 2.5 s, suggesting that the IFG is involved in the early response selection demands of the task.

The left IpreCS findings are compatible with previous studies designed to examine the neural basis of the Stroop effect. Perret (1974) reported that patients with left prefrontal lesions performed more poorly on the Stroop task than normals and patient groups with other lesion locations. Studies using divided visual fields (Guiard, 1981; Schmit & Davis, 1974; Tsao et al., 1979) and auditory Stroop analogs (Cohen & Martin, 1975) have shown that incongruent stimuli produce a greater interference effect when presented to the left hemisphere. Greater effects on evoked potentials (Aine & Harter, 1984) occur in the left hemisphere during the interference effect. Although there have also been scattered reports suggesting right hemisphere contribution to the Stroop effect (Long & Lyman, 1987; Vendrell et al., 1995), the bulk of the evidence clearly points to the left hemisphere as the site for resolution of the interference effect.

In addition to the left IpreCS activation during the incongruent condition, we found increased activation in the posterior cingulate during both control conditions as compared to the incongruent condition. The posterior cingulate is frequently activated during rest or during the performance of low-level sensorimotor control tasks in PET and fMRI studies, regardless of the specific experimental task requirements (Binder et al., 1999; Shulman et al., 1997). This finding has been attributed to non-task-related activities that subjects might be performing during rest or during relatively undemanding control tasks, including unconstrained verbal thought processes and monitoring of the external environment, their body and its position in space, and current emotional state. Given that the control conditions in the present study are less demanding than the incongruent condition, the same factors which result in increased posterior cingulate activation during rest periods may have been operating during these control conditions.

Finally, significant activation of the left rostral ACC was obtained in the congruent condition relative to the incongruent condition. This region is considerably more anterior and inferior than the ACC activations reported in previous Stroop studies. Furthermore, the focus demonstrates deactivation during the interference condition. Our ACC focus is located within the so-called "affect" rather than "cognitive" division of the anterior cingulate (Devinsky et al., 1995; Vogt et al., 1992). Decreased activation in this region was also reported by Whalen et al. (1998) during counting and "emotional" counting Stroop tasks relative to a fixation condition. Whalen et al. (1998) hypothesized that decreased activation in this region "reflects active inhibition of this limbic region in the service of allocating resources toward effective cognitive performance" (p. 1225). Considering the relatively automatic nature of the congruent condition in the present study, it is possible that similar mechanisms may be active here.

One of the more intriguing aspects of this study was the absence of increased activation within the cognitive division of the ACC during the interference condition. An analysis



Fig. 2. Subtraction of incongruent minus congruent (upper panel) and incongruent minus neutral (lower panel) conditions. The red activation foci (positive *t* values) in the left inferior precentral sulcus (IpreCS) indicated greater activation in the incongruent condition relative to both the congruent and neutral conditions (see Table 1 for stereotaxic coordinates). The blue activation foci (negative *t* values) indicate greater activation in the control tasks. Midline activation of the posterior cingulate gyrus (PCG) was observed during the congruent and neutral conditions relative to the incongruent condition. Significantly greater activation is seen in the left inferior anterior cingulate gyrus (ACG) during the congruent condition relative to the incongruent condition. Activation is overlayed on a single rendered brain.

exploring the null hypothesis was conducted by comparing the differences of each of the three experimental conditions relative to the baseline rest periods. Results revealed that the ACC was significantly activated at approximately the same intensity in each of the three conditions. Two explanations may be offered for these negative results. First, the majority of studies that have found ACC activation during the interference condition (Bench et al., 1993; Brown et al., 1999; George et al., 1994, 1997) have used nonverbal control conditions, such as colored crosses or colored blocks, stimuli that have grossly different stimulus characteristics and processing requirements than a verbal interference condition. In comparison, lexical control conditions often do not produce increased ACC activation (Bench et al., 1993; Taylor et al., 1997). In fact, comparison of a *neutral* word condition to a non-lexical condition has been shown to result in activation of the right cingulate (Bench et al., 1993), confirming the role of the ACC in language processing (Crosson et al., 1999).

The second explanation involves the putative role of the ACC in anticipating response conflict or brokering strategy shifts. In their event-related fMRI study, Carter et al. (2000) examined response conflict expectancies elicited by the Stroop task by comparing high expectancy congruent blocks (80% congruent, 20% incongruent) and high expectancy incongruent blocks (80% incongruent, 20% congruent). Selective activation of the ACC occurred only on the incongruent trials during the high expectancy congruent blocks. This result was attributed to an evaluative role of the ACC, in which it provided an "on-line conflict signal" serving to engage other brain regions in the appropriate strategic processes. Another possibility is that the ACC activation was contingent upon the strategy shift required when responding to an incongruent stimulus during a high expectancy congruent block. In either case, the negative findings of the present study may be attributable in part to our block design format, in which trials are grouped based on condition type, thereby minimizing the effects of expectancies and precluding major shifts in response strategy within blocks.

Further elucidation of the role of the ACC will require studies explicitly designed to compare these competing hypotheses. For example, the importance of the lexical aspect of control conditions can be examined through inclusion of both lexical and nonlexical controls, where stimulus parameters are matched as closely as possible to each other and to the experimental condition. The role of expectancies and response conflict monitoring may be evaluated through designs pitting different expectancy conditions against each other, such as including some blocks consisting of 100% incongruent or congruent trials and some blocks consisting of mixed trial types in the fashion of Carter et al. (2000). Differentiating whether ACC effects are associated with response conflict monitoring or with strategy shifts may be accomplished through the use of cues in some blocks that alert subjects that a strategy shift may be necessary. For example, in the midst of a set of congruent stimuli, participants may receive a cue that the next stimulus will be incongruent, presumably leading to a strategy shift to respond to the ink color rather than the word, and resulting in reduced response conflict. Noncued trials would be expected to produce a heightened response conflict, and comparisons could be made between the cued and noncued trials. Use of event-related fMRI designs would facilitate this avenue of research.

The present study represents the first neuroimaging study to use button-press responses rather than a spoken or covert verbal response. A large experimental literature, reviewed by MacLeod (1991), has shown that the Stroop effect is consistently obtained using a manual response, although the magnitude of the interference effect is smaller than that observed with a vocal response. The issue of stimulusresponse compatibility has been shown to be important, with a heightened interference effect when the prepotent response mode for the irrelevant dimension (i.e., the word) coincides with the designated response mode for the relevant dimension (i.e., the color). Nonetheless, we have demonstrated that activation within the left IpreCS during the Stroop interference condition is not contingent upon subjects generating an overt vocal response. Given its proximity to Broca's area and the premotor mouth area, this activation may reflect the conflict in subvocal articulatory processes generated by the interference condition, and is presumed to precede translation to the button-press response. The manual response itself was expected to result in significant activation in the left motor cortex, equivalent in all three conditions, and this was found to be the case. We believe that the manual Stroop has the advantage of minimizing head movement and susceptibility artifacts that are common in fMRI scans during speech, and is a viable method for further study in this area. It is also possible using event-related fMRI designs to directly compare vocal and manual responses to the Stroop effect.

In summary, our primary finding strongly implicates the left IpreCS as a key brain structure mediating the interference effect associated with the Stroop paradigm. This conclusion is based on several methodological improvements present in this investigation, including the use of wellmatched verbal control conditions, a blocked trial design that minimizes the role of expectancies, and a manual response that minimizes the role of overt speech output. The proximity of the IpreCS to the left IFG and its role in speech production would suggest that the Stroop effect is mediated by increased response competition associated with subvocal articulatory processes.

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