

# Common and distinct neural substrates of attentional control in an integrated Simon and spatial Stroop task as assessed by event-related fMRI

Xun Liu,<sup>a,\*</sup> Marie T. Banich,<sup>a,\*</sup> Benjamin L. Jacobson,<sup>a</sup> and Jody L. Tanabe<sup>b</sup>

<sup>a</sup>Department of Psychology, University of Colorado, Boulder, CO 80309-0345, USA

<sup>b</sup>Department of Radiology, University of Colorado Health Sciences Center, Denver, CO 80262, USA

Received 8 October 2003; revised 29 January 2004; accepted 21 February 2004

Available online 7 May 2004

The purpose of this experiment was to directly examine the neural mechanisms of attentional control involved in the Simon task as compared to a spatial Stroop task using event-related fMRI. The Simon effect typically refers to the interference people experience when there is a stimulus–response conflict. The Stroop effect refers to the interference people experience when two attributes of the same stimulus conflict with each other. Although previous imaging studies have compared the brain activation for each of these tasks performed separately, none had done so in an integrated task that incorporates both types of interference, as was done in the current experiment. Both tasks activated brain regions that serve as a source of attentional control (dorsolateral prefrontal cortex) and posterior regions that are sites of attentional control (the visual processing stream—middle occipital and inferior temporal cortices). In addition, there were also specific brain regions activated to a significantly greater degree by one task and/or only by a single task. The brain regions significantly more activated by the Simon task were those sensitive to detection of response conflict, response selection, and planning (anterior cingulate cortex, supplementary motor areas, and precuneus), and visuospatial–motor association areas. In contrast, the regions significantly more activated by the Stroop task were those involved in biasing the processing toward the task-relevant attribute (inferior parietal cortex). These findings suggest that the interference effects of these two tasks are caused by different types of conflict (stimulus–response conflict for the Simon effect and stimulus–stimulus conflict for the Stroop effect) but both invoke similar sources of top-down modulation.

© 2004 Elsevier Inc. All rights reserved.

**Keywords:** Simon task; Spatial Stroop task; Event-related fMRI

## Introduction

Regardless of one's theoretical outlook, attentional control involves selection. This selection process can occur at multiple stages of processing—at the perceptual stage with regards to a specific attribute (e.g., the red item) or a particular location (e.g., the right hand item), at a more central stage concerning an abstract attribute (e.g., fruits but not vegetables), or at the response stage (e.g., pressing a right-hand key not a left-hand one). There are several paradigms that have been used extensively to examine attentional control, the Stroop task being one and the Simon task being another.

In the standard color–word Stroop task (Stroop, 1935), which was described by MacLeod (1992) as the “gold standard” of attentional measures, individuals see a colored word. The task is to identify a task-relevant dimension, such as the item's ink color, while ignoring a task-irrelevant dimension, such as the word's meaning or the response to which it leads. Typically, performance on incongruent trials in which the word and its ink color conflict (e.g., the word “red” in blue ink) is compared to that on neutral trials in which the word's meaning is not color-related (e.g., the word “lot” in blue ink). The former requires more attentional control than the latter as the color word has the ability to interfere with selection of a response based on ink color. Numerous neuroimaging studies have indicated that incongruent Stroop trials activate a series of brain regions involved in selection at the central and response stages. These regions include the dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC), and posterior parietal cortex (PPC) (Banich et al., 2000a,b, 2001; Barch et al., 2001; Bench et al., 1993; Brown et al., 1999; Bush et al., 1998; Carter et al., 1995; Leung et al., 2000; MacDonald et al., 2000; Milham et al., 2001, 2002, 2003; Pardo et al., 1990; Peterson et al., 1999). Similar regions are activated by spatial variants of the Stroop task. In a typical spatial Stroop task, individuals are told to respond to the location of a word and responses are generally slower on the incongruent trials in which the word is incompatible with its location (e.g., the word “above” positioned below a box) than on the neutral trials in which the word (e.g., “hope”) does not denote any spatial location (Banich et al., 2000b).

---

\* Corresponding authors. X. Liu is to be contacted at the Department of Anatomy and Neurobiology, University of Kentucky, Lexington, KY 40536-0298. Fax: +1-859-257-3625. M.T. Banich, Department of Psychology, University of Colorado, Campus Box 345, Boulder, CO 80309-0345. Fax: +1-303-492-2967.

E-mail addresses: xun.liu@uky.edu (X. Liu),  
mbanich@psych.colorado.edu (M.T. Banich).

Available online on ScienceDirect (www.sciencedirect.com.)

Another well-studied behavioral paradigm of attentional selection, the Simon task (Simon and Small, 1969), examines competition at the stimulus–response level (for a review, see Proctor and Reeve, 1990). In this task, performance of the incompatible trials on which one must give a response that is spatially incompatible with the stimulus (e.g., respond with the right hand to a left-hand stimulus) is compared to that of the compatible trials (e.g., respond with the right hand to a right-hand stimulus). Generally, responses are longer for the incompatible as compared to compatible stimuli. The neural basis of this phenomenon has not been well studied (Bush et al., 2003; Dassonville et al., 2001; Fan et al., 2003; Iacoboni et al., 1998; Peterson et al., 2002).

Although both the Simon and spatial Stroop tasks share many similar properties (e.g., the location of the stimulus being the task-irrelevant dimension), they have been studied in distinct manners to examine different theoretical issues (Lu and Proctor, 1995). Behavioral research on these two paradigms has focused on diverse theoretical issues, in spite of the similarity among the task characteristics. For the Simon effect, researchers have focused on elucidating how the spatial stimulus–response conflict arises (Hasbroucq and Guiard, 1991; Hommel, 1995; Proctor and Reeve, 1990). For the spatial Stroop effect, researchers have focused on how the stimulus–stimulus conflict between the task-relevant (e.g., location) and task-irrelevant (e.g., word meaning or response mapping) attributes is resolved by attentional selection (MacLeod, 1991).

Despite the similarities between the Simon and spatial Stroop effects as reviewed in Lu and Proctor (1995), Kornblum (1992) classified them into different categories of stimulus–response ensembles. In Kornblum's terms, ensembles are characterized according to the dimensional overlaps between (1) the relevant and irrelevant stimulus dimensions, (2) the relevant stimulus dimension and the response dimension, and (3) the irrelevant stimulus dimension and the response dimension. According to Kornblum, the classic Simon task is a Type 3 stimulus–response ensemble, in which the relevant stimulus dimension does not overlap with the response dimension while the irrelevant stimulus dimension does. In contrast, he considers the classic color–word Stroop task as a Type 8 ensemble, in which there is overlap not only between the relevant stimulus and response dimensions and between the irrelevant stimulus and response dimensions, but also between the relevant and irrelevant stimulus dimensions. Thus, the Stroop effect is distinct from the Simon effect in that it has the addition of overlap between the relevant and irrelevant stimulus dimensions. Moreover, we conceptualize these two effects as representing somewhat different types of response conflict. The Simon effect results from the direct *stimulus–response* conflict, due to the need to overcome the potent association between the stimulus and response of the same side (e.g., left hand response to left-side stimulus). In contrast, the Stroop effect results from the *stimulus–stimulus* conflict between the two attributes, which also lead to the conflicting responses (e.g., word “red” and blue ink lead to conflicting responses when both red and blue are potential responses).

Given the superficial and taxonomical similarities and differences between the Simon and Stroop effects, Lu and Proctor (1995) suggested, based on the analysis of behavioral performance that they share a common theoretical foundation: attentional and response selection. Several theoretical and computational models have been proposed that provide an integrated account for both

the Simon and Stroop effects (Hasbroucq and Guiard, 1991; Kornblum et al., 1999; Zhang et al., 1999). However, there is still a debate over whether there is a common source for both effects, especially with regards to their neural substrates. Lu and Proctor (1995) noted that “None of the accounts developed for the Simon effect or the spatial Stroop effect seems capable of handling the majority of findings from both task domains without significant modification. However, many of the central features of these accounts are supported by the existing evidence, and a model that combines several of these features in a principled manner would seem to be most promising.”

An examination of the findings of recent neuroimaging studies on each task in isolation suggests that these two measures of attentional control activate similar neural structures (Bush et al., 2003; Peterson et al., 2002), although each appears to activate unique brain regions as well (Banich et al., 2000b; Brown et al., 1999; Carter et al., 1995; Fan et al., 2003; Iacoboni et al., 1996, 1998; Leung et al., 2000; MacDonald et al., 2000; Pardo et al., 1990; Praamstra et al., 1999). Typically, the Stroop effect activates broadly distributed brain areas, including DLPFC, ACC, inferior frontal, inferior parietal, and inferior temporal cortices, while the Simon effect usually activates dorsal premotor, posterior, and superior parietal areas. Across studies, regions activated by both tasks appear to be the DLPFC and dorsal ACC.

We are aware of only two studies to date in which the standard color–word Stroop and Simon effects have been directly compared (Fan et al., 2003; Peterson et al., 2002). In one study, Peterson et al. (2002) conducted two event-related fMRI experiments on the same group of participants. In one experiment, participants were given a color–word Stroop task and in the other a Simon task. For the Stroop task, they were presented either a congruent (e.g., the word “red” in red color) or incongruent (e.g., the word “red” in blue color) color–word stimulus and asked to *silently* respond to the ink color of the word. For the Simon task, they were presented a white arrow pointing either to the *left* or *right* against a black background, either to the *left* or *right* of a central fixation cross. Participants were instructed to press a key to either the *left*-pointing or *right*-pointing arrow with the index (relative *leftward*) or middle (relative *rightward*) finger of their right hand, respectively. On congruent trials, the direction of the arrow was the same as the location of the arrow relative to the fixation (e.g., a *rightward* pointing arrow to the *right* of fixation), whereas on incongruent trials, the direction of the arrow was opposite to the location of the arrow relative to the fixation (e.g., a *rightward* pointing arrow to the *left* of fixation). In both the Stroop and Simon tasks, the incongruent trials were more infrequent than the congruent trials.

These researchers found remarkably similar results for both the Simon and Stroop tasks. The brain regions activated by the incongruent stimuli as compared to the congruent stimuli in both tasks included DLPFC, ACC, supplementary motor areas (SMA), visual association cortex, inferior temporal, inferior parietal, and inferior frontal cortices, as well as the caudate nuclei. In addition, the time courses of the brain activity were also very similar across the tasks. They concluded that the neural systems that subserved successful performance in both tasks are likely to be similar.

However, the Simon task employed in the Peterson et al. (2002) study is not a “pure” one. A typical Simon effect refers to the interference people experience when the response required by a task is spatially opposite to the location of the stimulus (e.g., right finger press to a stimulus left to the fixation), which creates a stimulus–response conflict. There is usually no conflict between the relevant

and irrelevant stimulus dimensions, which is the critical distinction between the Simon and Stroop effects (Kornblum, 1992). By presenting the left-pointing or right-pointing arrow on either the left or right of the fixation, the investigators obscured this distinction. Hence, their so-called Simon effect was in fact a combination of both the Simon and Stroop effects, since there was not only conflict on the incongruent trials between the irrelevant stimulus attribute (e.g., the *left* of the fixation) and response (e.g., *right* key press), but also conflict between the relevant (e.g., *right*-pointing arrow) and irrelevant (e.g., the *left* of fixation) dimensions as well. Therefore, their findings showing the common activation patterns by both the Simon and Stroop effects cannot be unambiguously interpreted that these two effects indeed share a common neural basis.

The other study that compared the color–word Stroop task and the Simon spatial conflict task also employed the Eriksen flanker task (Fan et al., 2003) so that the neural substrates of conflict monitoring and resolution could be compared across the three tasks. They found that although three tasks shared a common attentional control and conflict resolution network involving the brain areas such as dorsal ACC and prefrontal cortex, these tasks activated other distinct brain regions within the posterior parietal cortex and visual processing areas. The interpretation of this study has the converse problem to that of the Petersen study as the Stroop task employed utilized different stimulus dimension (i.e., colors and words) than the Simon task (spatial dimensions). Hence, it is difficult to determine whether differences in the neural substrates activated by each task are due to the difference in stimulus attributes (color and word information vs. spatial information) or the nature of the selection of each task.

To resolve the issue of the extent to which the neural substrates of attentional control in the Simon and Stroop tasks are common or distinct, we utilized an event-related fMRI experiment that incorporated both types of interference within an integrated task (see Fig. 1). Participants were presented with an *upward* or *downward* arrow at the fixation and trained to respond to one arrow with the index finger and to the other with the middle finger of their right hand. The mapping of the *upward* and *downward* arrows to fingers was counterbalanced across participants. During the fMRI testing session, the arrows were presented in one of the four locations surrounding the central fixation cross. This display created two types of conflict within a single paradigm. The Simon effect was elicited when an arrow was presented in a location incompatible with the relative spatial position of the finger used to respond (e.g., an *upward* arrow placed to the *right* of the fixation, which required response of the index finger—the more *leftward* of the two fingers). The spatial Stroop effect was elicited when the direction of the arrow (i.e., the task-relevant dimension) was incompatible with its spatial location (i.e., the task-irrelevant dimension) (e.g., an *upward* arrow *below* the fixation), as compared to the compatible condition (e.g., an *upward* arrow *above* the fixation).

Given the distinction made by Kornblum (1992), we hypothesize that both tasks will yield highly similar patterns of activation in prefrontal regions as both tasks require the top-down control of attention (Posner and Petersen, 1990). We also hypothesize, however, that each task will uniquely activate specific brain regions because the two tasks differ in the nature of the conflict that is engendered by each task. More specifically, we predict that the brain regions previously theorized as the source of attentional selection such as DLPFC will be commonly activated more in the incongruent trials than in the congruent trials for both tasks, since

both require people to selectively respond to the task-relevant information (i.e., the direction of the arrow) while ignoring the conflicting task-irrelevant information (i.e., the location of the arrow). We further predict similar brain areas of visual processing will be modulated by the top-down attentional control so that the conflict between the task-relevant and task-irrelevant attributes is resolved by biasing the processing toward the task-relevant attribute (i.e., the direction of the arrow). In contrast, according to the taxonomy of Kornblum (1992), the core and unique component of the Stroop effect is the *stimulus–stimulus* conflict while the nature of the conflict of the Simon effect is more *stimulus–response*. Therefore, we predict that the resolution of the conflict in these two effects will involve different neural substrates. In particular, we predict that parietal areas involved in multi-attribute processing and visual attention will be more activated in the Stroop task. In contrast, we predict that regions involved in stimulus–response processing, such as portions of the anterior cingulate and premotor regions, will be more activated in the Simon task.

## Methods

### Participants

Eleven right-handed, native English speakers (age range 24–40 years; 8 women) were recruited from the local community. All participants had normal or corrected to normal vision. A signed informed consent form approved by Colorado Multiple Institutional Review Board was obtained from each participant before the experiment.

### Stimuli

The stimulus was an upward or downward arrow. During the training session (40 trials), an arrow was presented in the center of the screen. Participants were taught to press a *left* side button for one arrow and a *right* side button for another arrow, with the index and middle fingers of their right hand, respectively (see Fig. 1). The mapping between the arrows and the response buttons (fingers) was counterbalanced across participants. During the fMRI testing session, an arrow was presented in one of the four positions surrounding the central fixation cross (i.e., left, right, above, and below). The visual angle of the arrow from the center was estimated to be less than 5°. Participants were asked to respond to the direction of the arrow while ignoring the location of the arrow.

### Design and procedures

Individuals performed the integrated Simon Stroop task during one fMRI testing session. There were eight different stimulus–location configurations during the test (see Fig. 1). Since people were trained to map a certain stimulus (e.g., an upward arrow) to a response (e.g., left button press with leftward finger), those eight different trials were classified into four different conditions: Simon Congruent (SmC)—the location of the arrow and the response button were compatible (e.g., left finger press to the upward arrow on the left of the fixation), Simon Incongruent (SmI)—the location of the arrow and the response button were opposite (e.g., left finger press to the upward arrow on the right of the fixation), Stroop Congruent (StC)—the location of the arrow and the direction of the arrow were congruent (e.g., an upward arrow above the fixation),

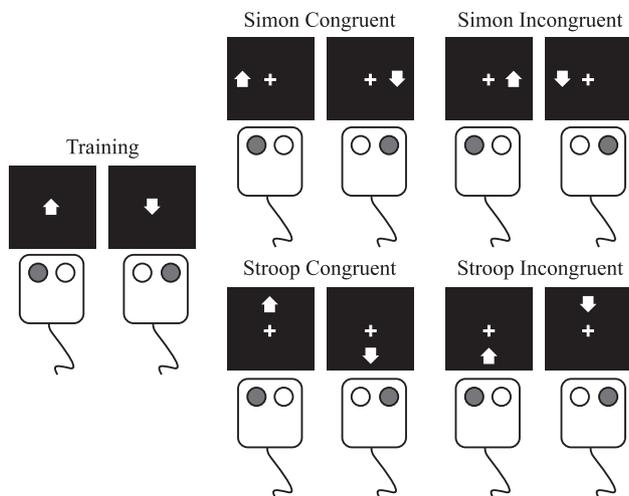


Fig. 1. Stimuli used in the current experiment during training and testing. Participants were trained to press a button to respond to an upward or downward arrow before the fMRI testing session. The arrows were presented at one of the four positions surrounding the central fixation during the test, which created four different experimental conditions: Simon Congruent (SmC), Simon Incongruent (SmI), Stroop Congruent (StC), and Stroop Incongruent (StI).

and Stroop Incongruent (StI)—the location of the arrow and the direction of the arrow were incongruent (e.g., an upward arrow below the fixation). The interference effects of the Simon and Stroop tasks were measured by comparing behavioral performance (reaction time and accuracy) and brain activation patterns between the respective incongruent and congruent trials. From the perspective of the participants, there was no difference between the Simon and Stroop tasks. Therefore, there was no effect of switching between different tasks.

This experiment consisted of a single session of fMRI scanning during which participants responded to the arrows by pressing the buttons they learned during training. Half way through the scan, there were 18 fixation trials during which participants were told to rest. They were warned before the second half resumed after the rest block. The whole session consisted of 218 trials. After discarding the first eight trials to allow the magnet to reach steady state, there were 48 trials for

each of the four conditions. The trials were synchronized with the fMRI scans. Each trial lasted for 2500 ms, starting with a central fixation cross for 500 ms, followed by a target display for 700 ms and a blank screen for another 1300 ms. The target display was relatively short to minimize the effect of eye movement and gaze shift. However, participants were allowed 1500 ms to respond from the onset of the target display.

*Image acquisition*

A 1.5-T Siemens Vision magnetic resonance imaging system located at the University of Colorado Health Sciences Center equipped for echo-planar imaging (EPI) was used for data acquisition. A total of 220 EPI images were acquired using the BOLD technique (TR = 2500 ms, TE = 40 ms, flip angle = 90°), each consisting of 20 contiguous axial slices (matrix = 64 × 64, in-plane resolution = 3.75 × 3.75 mm<sup>2</sup>, thickness = 6 mm, gap = 0.9 mm), parallel to the AC–PC line. Before the EPI images, a high-resolution T1-weighted MP-RAGE anatomical set (full head-168 coronal slices, matrix = 256 × 256, field-of-view = 250 × 250 mm<sup>2</sup>, slice thickness = 1.5 mm, no gap) was collected for each participant. At the end of the experiment, a T1-weighted spin echo data set (part head-20 axial slices, matrix = 512 × 512, field-of-view = 230 × 230 mm<sup>2</sup>, slice thickness = 6 mm, gap = 0.9 mm) was acquired using the same slice angle as the EPI images.

Stimuli were presented using a high-resolution rear projection system with responses recorded via a fiber-optics response pad with two buttons. A laptop computer running E-Prime controlled stimulus presentation and the recording of responses. In addition, the timing of the stimulus presentation was synchronized with the magnet trigger pulses.

*Image preprocessing*

Before data analysis, images in each participant’s time series were motion-corrected using FMRIB’s MCFLIRT module of FSL package (<http://www.fmrib.ox.ac.uk/fsl>). The first eight volumes of the session were discarded to allow the MR signal to reach steady state. Images in the data series were spatially smoothed with a 3D Gaussian kernel (FWHM = 8 × 8 × 8 mm<sup>3</sup>), and temporally smoothed using a high-pass filter (120 s). The FEAT module of FSL package was used for image processing and statistical analyses.

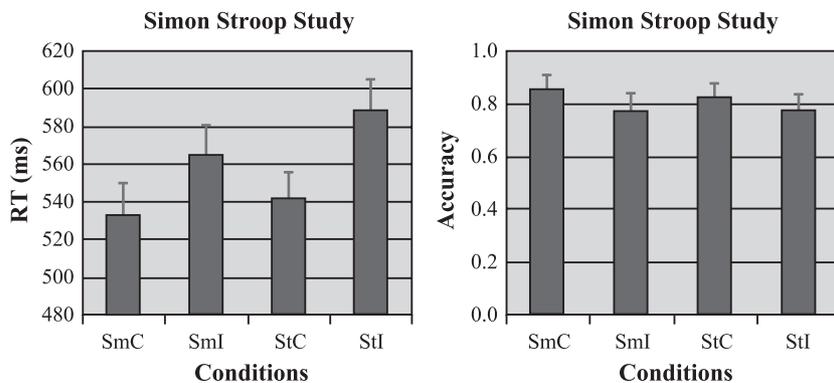


Fig. 2. Behavioral results of the Simon Stroop study. Reaction time is shown on the left and accuracy is shown on the right. The bars represent the means and the lines represent the standard errors.

Table 1  
Brain areas activated by the Simon effect (Simon Incongruent > Simon Congruent)

Lobe	Label	BA	x	y	z	Cluster size	Max <i>t</i>
Frontal	Anterior cingulate cortex	24/32	-12	44	0	1458	5.56
	Inferior frontal cortex	45	-34	36	10	39	3.22
	Middle frontal cortex	46	32	60	26	97	5.30
	SMA/preSMA	9	30	42	44	137	4.50
	Superior frontal cortex	6/8	12	32	62	412	4.31
Parietal	Precuneus	8	26	18	36	67	3.50
	Superior parietal cortex	7	-12	-66	74	482	4.45
	Supramarginal gyrus	7	-36	-44	70	62	4.34
		7	22	-62	74	269	3.79
Occipital	Inferior occipital cortex	48	-46	-36	28	383	5.02
	Lingual gyrus	19	30	-80	-12	732	6.71
	Middle occipital cortex	19	-16	-52	-6	31	3.71
	Superior occipital cortex	19	-46	-78	34	811	5.78
		20	48	-78	34	39	3.59
Temporal	Fusiform gyrus	18	-14	-96	20	51	4.18
		20	42	-10	-32	95	5.16
	Hippocampus	20	-36	-20	-20	33	3.41
	Inferior temporal cortex	37	32	-38	-2	87	5.58
		37	-48	-54	-10	1355	7.07
	Middle temporal cortex	20	-64	-14	-26	233	4.36
		37	58	-68	-2	190	4.30
		21	-56	-26	-4	61	4.53
		37	-44	-56	8	43	4.03
		37	42	-60	8	65	3.89
Other	Superior temporal cortex	48	44	-26	18	3687	4.70
	Superior temporal pole	38	-38	22	-30	619	6.22
	Temporal pole		-32	0	-26	2341	6.57
	Insula	48	-36	-20	16	275	4.61
		48	36	-10	-2	42	3.26
	48	34	-12	16	58	3.20	
	Paracentral cortex	4	-4	-30	72	35	3.22
	Postcentral cortex	3	-44	-32	68	860	5.46
	Precentral cortex	4	40	-20	64	250	8.15
		4	36	-18	50	94	5.09

#### Analysis on individual participant

Customized square waveforms (on-off) were generated for each participant according to the order of experimental conditions in which he or she participated. These customized waveforms were generated for each condition (e.g., Simon incongruent) representing the trials in which the participant experienced that condition (i.e., on) as compared to the trials in which he or she did not (i.e., off). These waveforms were then convolved with a double-gamma hemodynamic response function (HRF). For each participant, we used FILM (FMRIB's Improved Linear Model) to estimate the hemodynamic parameters for different explanatory variables (EVs) (e.g., one for incongruent Simon condition and another for congruent Simon condition) and to generate statistical contrast maps of interest (e.g., a contrast between EVs for incongruent and congruent Simon conditions).

After statistical analysis for each participant's time series, contrast maps were normalized into common stereotaxic space before random-effects group analyses were performed. This involved registering average EPI image to part head, part head to full head, and full head to ICBM152 T1 template, using FLIRT (FMRIB's Linear Image Registration Tool) module of FSL package.

#### Random-effects group analysis

Spatially normalized contrast maps from individual participants were entered into random-effects group analysis. To identify the regions of brain activation, we defined the ROIs first by clusters of 30 or more contiguous voxels (Xiong et al., 1995) in which PE values differ significantly from zero ( $P < 0.05$ , two-tailed). Using the Mintun peak algorithm (Mintun et al., 1989), we further located the local peaks (maximal activation) within each ROI. We then obtained a significant activation map for each effect alone.

We also conducted a conjunction analysis to obtain the common activation between the Simon and Stroop effects. Two masks were generated by applying the significant *t* value threshold on the activation map for each effect. Then, a conjunction mask was created by intersecting these two masks. The common activation map was obtained by applying the conjunction mask on the brain activation map of both the Simon and Stroop effects pooled together. In the disjunction analysis, we identified those regions that were uniquely activated for each effect. The conjunction mask was used as an exclusive mask and applied back on the activation map of each effect alone. The resulting statistical maps showed the distinct activation patterns for each effect.

Finally, we directly compared the activation patterns between the Simon and Stroop effects by examining the contrast map

Table 2  
Brain areas activated by the Stroop effect (Stroop Incongruent > Stroop Congruent)

Lobe	Label	BA	x	y	z	Cluster size	Max <i>t</i>
Frontal	Inferior frontal cortex	47	-32	42	10	35	4.18
	Middle frontal cortex	9	-32	12	52	36	3.32
	Middle orbitofrontal cortex	47	-30	42	-4	42	4.67
	Postcentral cortex	2	-44	-32	50	66	3.54
	SMA	6	-6	-4	72	55	4.87
Parietal	Inferior parietal cortex	40	-28	-38	54	48	4.61
Occipital	Middle occipital cortex	19	-42	-88	30	85	3.41
Temporal	Fusiform gyrus	37	46	-58	-30	122	4.54
		20	-24	-2	-44	43	4.44
		37	26	-38	-18	72	3.73
		37	-44	-50	-20	35	3.29
	Middle temporal cortex	37	-40	-60	-2	116	3.76
		37	40	-56	2	35	3.65
	Middle temporal pole	38	-54	16	-28	46	3.78
Other	Insula	48	30	-32	22	281	5.57

Table 3

Brain areas commonly activated by both the Simon and Stroop effect (Simon Incongruent > Simon Congruent and Stroop Incongruent > Stroop Congruent)

Lobe	Label	BA	x	y	z	Cluster size	Max <i>t</i>
Frontal	Middle cingulate cortex	23	-6	-34	40	40	4.58
	Middle frontal cortex	9	-36	10	52	44	4.57
Occipital	Middle occipital cortex	19	-42	-84	36	76	5.42
Temporal	Inferior temporal cortex	37	46	-56	-28	37	5.19
Other	Insula	48	32	-32	22	100	5.50

between the two effects. The resulting statistical map showed brain regions activated significantly more (activation) or less (deactivation) in the Simon effect than in the Stroop effect.

## Results

### Behavioral data

We observed significant effects on both the Simon and Stroop tasks (see Fig. 2). People responded more slowly to the incongruent Simon stimuli ( $M = 565$  ms,  $SD = 50$  ms) than to the congruent Simon stimuli ( $M = 533$  ms,  $SD = 54$  ms),  $t(10) = 3.92$ ,  $P < 0.01$ . They also responded less accurately to the incongruent Simon stimuli ( $M = 78\%$ ,  $SD = 20\%$ ) than to the congruent Simon stimuli ( $M = 86\%$ ,  $SD = 16\%$ ),  $t(10) = 2.48$ ,  $P < 0.05$ . Similarly, they responded more slowly to the incongruent Stroop stimuli ( $M = 589$  ms,  $SD = 51$  ms) than to the congruent Stroop stimuli ( $M = 542$  ms,  $SD = 43$  ms),  $t(10) = 6.77$ ,  $P < 0.01$ . The accuracy of incongruent ( $M = 83\%$ ,  $SD = 15\%$ ) and congruent ( $M = 77\%$ ,  $SD = 22\%$ ) Stroop stimuli did not differ significantly,  $t(10) = 1.58$ ,  $P = 0.15$ . Finally, a comparison of the interference effects in the two tasks revealed that they did not differ significantly from one another, indicating that two tasks were of similar difficulty [for interference effect of reaction

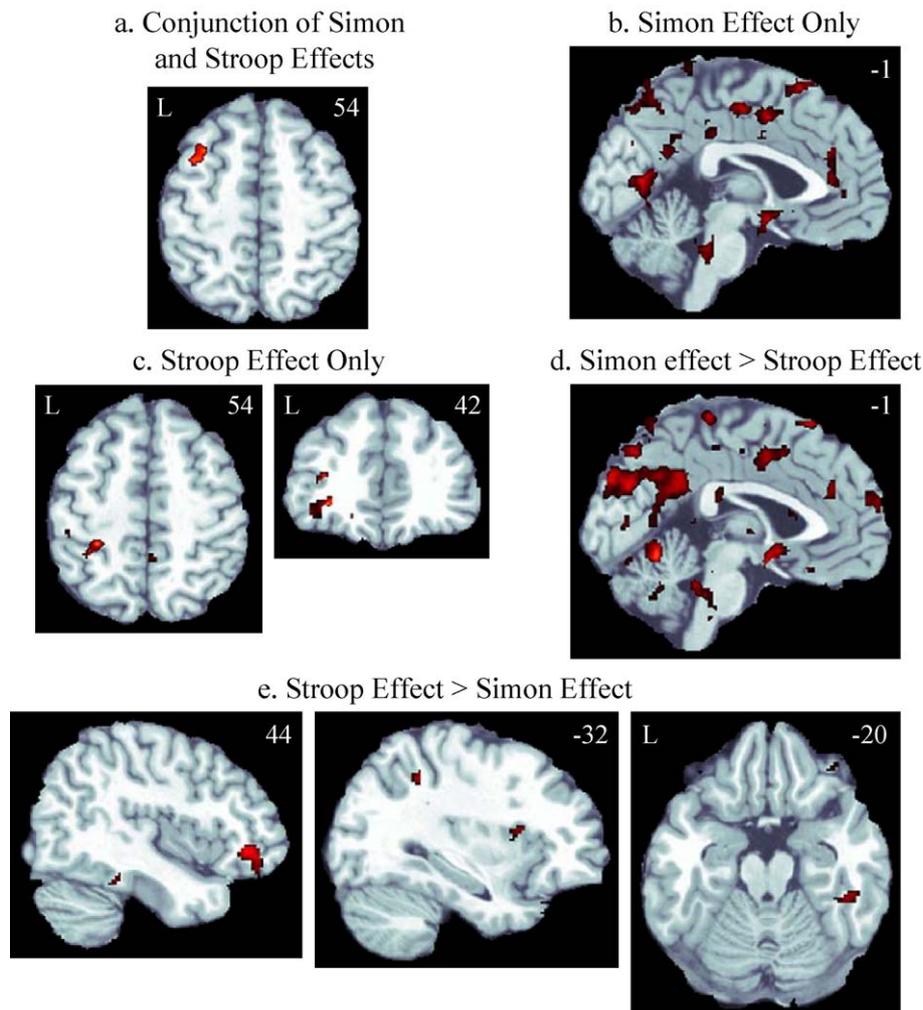


Fig. 3. Imaging results of the Simon Stroop study. (a) Left DLPFC activation of both the Simon and Stroop effects ( $S_{ml} > S_{mC}$  and  $StI > StC$ ) from the conjunction analysis. (b) Midsagittal activation pattern of the Simon effect alone from the disjunction analysis ( $S_{ml} > S_{mC}$ ), including ACC, SMA/preSMA, and precuneus cortex. (c) The activation of the Stroop effect alone from the disjunction analysis ( $StI > StC$ ), including right inferior frontal and left inferior parietal cortices. (d) The brain activation greater in the Simon effect than the Stroop effect ( $S_{ml} - S_{mC} > StI - StC$ ). (e) The brain activation greater in the Stroop effect than the Simon effect ( $StI - StC > S_{ml} - S_{mC}$ ). Letter "L" represents the left side of the brain and the numbers represent the coordinates in the corresponding view of the MNI space.

time between two tasks,  $t(10) = 1.77, P = 0.11$ ; for interference effect of accuracy between two tasks,  $t(10) = 0.62, P = 0.55$ ].

### Imaging data

#### Whole-brain analysis

We found that the brain areas activated by the incongruent Simon stimuli as compared to the congruent Simon stimuli were the middle frontal cortex, ACC, midcingulate cortex, superior medial frontal areas (SMA and pre-SMA), and precuneus (see Table 1), as well as the posterior visual processing areas (e.g., lingual gyrus, inferior temporal cortex, and middle temporal cortex, etc.) The areas activated by the incongruent Stroop stimuli as compared to the congruent Stroop stimuli were the middle frontal cortex, orbito-frontal cortex, inferior parietal cortex, and visual association areas (see Table 2).

#### Conjunction analysis

The brain areas that emerged from this analysis included left DLPFC, the posterior boundary of insula and posterior visual processing areas (see Table 3 and Fig. 3a).

#### Disjunction analysis

The areas uniquely activated by the Simon effect were ACC (BA 24/32), midcingulate cortex, pre-SMA, and precuneus cortex (see Fig. 3b), while areas uniquely activated by the Stroop effect were inferior frontal cortex and inferior parietal cortex (see Fig. 3c).

#### Contrast analysis between both effects

We also compared the Simon and Stroop effects by making a direct contrast between them (similar to an interaction analysis). The results are comparable to those identified in the disjunction analysis above. The areas more active in the Simon effect than the Stroop effect were again ACC (BA 32), pre-SMA, and precuneus (see Fig. 3d). The areas more active in the Stroop effect than the Simon effect were inferior frontal, inferior parietal, and inferior temporal cortices (see Fig. 3e).

## Discussion

These results are quite consistent with the previous findings obtained with the Simon and Stroop tasks performed separately. The Simon effect activated many midline structures including dorsal ACC, dorsal premotor, posterior and superior parietal areas (Bush et al., 2003; Dassonville et al., 2001; Fan et al., 2003; Iacoboni et al., 1998; Peterson et al., 2002), while the Stroop effect activated DLPFC, ACC, inferior frontal and inferior parietal cortices (Banich et al., 2000a,b, 2001; Barch et al., 2001; Bench et al., 1993; Brown et al., 1999; Bush et al., 1998; Carter et al., 1995; Leung et al., 2000; MacDonald et al., 2000; Milham et al., 2001, 2002, 2003; Pardo et al., 1990).

Unlike Peterson et al. (2002), though these two effects similarly activated DLPFC and posterior visual processing regions, they showed distinct activation patterns in many other brain areas. For example, these two effects activated considerably different posterior parietal areas. Moreover, ACC was only activated in the Simon effect but not in the Stroop effect. These distinct patterns will be discussed in detail later.

The conjunction and disjunction of patterns of neural activation that we obtained on the Simon and spatial Stroop tasks help to shed

some light on the nature of attentional control in the human brain. Many accounts of attentional control suggest that prefrontal regions are important in exerting top-down modulation on the posterior processing areas to guide the response selection toward the task-relevant information (Botvinick et al., 2001; Cohen et al., 2000; Posner and DiGirolamo, 1998). In many studies, ACC is coactivated along with DLPFC (Corbetta et al., 1991; George et al., 1994; Peterson et al., 2002), which has caused a great deal of debate about whether DLPFC and/or ACC are responsible for cognitive control (Cohen et al., 2000). However, the exact roles played by these prefrontal regions, how they interact with each other, and how they modulate processing of posterior regions are still an area of intense investigation. The current study helps to address some of these issues.

One major theory (Botvinick et al., 2001) suggests that ACC functions as an *evaluative* device, which monitors for conflict and response errors and sends a request for increased top-down control to DLPFC. In contrast, DLPFC serves as a *regulative* device and modulates the processing in the posterior regions by biasing toward the task-relevant stream. Other theories suggest that ACC is the source of attentional control (Posner and DiGirolamo, 1998). However, these views of the roles of DLPFC and ACC are challenged by the recent neuroimaging (Milham et al., 2001; Van Veen et al., 2001) and neuropsychological (Swick and Jovanovic, 2002; Swick and Turken, 2002) findings. These studies have found that activation of DLPFC is relatively independent of ACC's activity and the ACC's role in attentional control may be limited to more response-related processes. Such a conclusion is consistent with observations of individuals who have undergone cingulotomy (Cohen et al., 1999; Ochsner et al., 2001). These individuals tend to not show severe deficits in Stroop performance, either showing a diminution of Stroop interference with time, or increased errors but not increased interference. Given that their performance on sensory selection tasks did not suffer, the results are consistent with the cingulate playing more of a role in response selection and control.

One such fMRI study suggesting distinct roles for DLPFC and ACC was conducted in our laboratory (Milham et al., 2001). We used a modified Stroop task, in which the irrelevant stimulus set (e.g., color words—"red", "orange", and "brown") did not overlap with the response set (e.g., ink colors—blue, green, and yellow) although they shared the same semantic property (i.e., color related). Therefore, the conflict between the task-relevant and task-irrelevant attributes was restricted to nonresponse levels because the incongruent words did not name a competing response. Although such words still activated DLPFC (relative to neutral words), they did not activate ACC. This suggests that the predominant role of DLPFC in top-down attentional selection is independent of ACC, which seems more involved in response-related processes. Support for these distinct roles of DLPFC and ACC also came from another study by Van Veen et al. (2001), who used a modified Eriksen flanker task. In their study, they presented three different target-flanker ensembles such that in the congruent condition (CO) the target and the distractors were the same; in the stimulus incongruent condition (SI) the target and the distractors were different but led to the same response; and in the response incongruent condition (RI) the distractors not only differed from the target perceptually but also led to a conflicting response. They obtained significant ACC activation only in the RI condition, which engendered conflict at the response level, but not in the SI condition in which there was no response conflict. This result also suggests that the conflict at the response level is critical to the activation of ACC.

The results of the current study also support the idea that the DLPFC and ACC have distinct roles in attentional control. We observed common activation of DLPFC for both the Simon and Stroop effects, consistent with the idea that both tasks require attentional selection to help resolve the conflict caused by the task-irrelevant dimension. In contrast, we obtained ACC activation only for the Simon task but not for the Stroop task. The incongruent condition of the Simon task engendered strong response conflict between the preprogrammed response tendency (e.g., *left* key press to the *left* location) and the desired response (e.g., *right* key press to the *left* location). In contrast, in the incongruent condition of the Stroop task, there was no direct response conflict between the locations (i.e., *above* and *below*) and the desired response (i.e., *left* and *right*), although semantically the task-irrelevant attribute (e.g., *above* the fixation) conflicted with the task-relevant attribute (e.g., *downward* arrow). Therefore, ACC, which is presumed to be involved in selection between competing responses, was activated only in the Simon task but not in the Stroop task.

A variety of evidence from neuroimaging (Braver et al., 2001; Menon et al., 2001; Milham et al., 2003) and lesion studies (Swick and Jovanovic, 2002; Swick and Turken, 2002) suggests that distinct regions of the ACC may be involved in error detection as compared to response selection. In particular, more rostral regions have been implicated as being critical for error detection whereas more caudal regions are suggested to be involved in response selection.

We observed that both these subregions of ACC were more significantly activated in the Simon task as compared to the Stroop task. Greater activation of the more rostral region, which is associated with error detection, in the Simon task than the Stroop task is consistent with our behavioral findings. Significantly more errors were made to incongruent than congruent trials in the Simon task. This was not the case, however, for the Stroop task. It should be noted, however, that the Stroop task may produce some sub-threshold activation in this region since the disjunction analysis for the Simon task activated a slightly larger cluster than did the direct contrast analysis between the Simon and Stroop tasks. Activation of caudal ACC was only observed for the Simon task. This finding supports the view that this subregion of ACC is sensitive to conflict and making selection at the response level, as a strong prepotent stimulus–response mapping must be overcome to perform correctly on the Simon task.

We also found some differences in patterns of activation for the Simon and Stroop tasks in the posterior cortex. With regards to the parietal cortex, activation was mainly observed in the inferior parietal region (BA 40) in the spatial Stroop task. In our prior studies (Banich et al., 2000a,b; Milham et al., 2001), we often find that the inferior parietal cortex is usually coactivated with DLPFC in the attention-demanding incongruent Stroop condition as compared to the neutral condition. The exact role of the inferior parietal cortex is not clear, but we speculate that it serves as the “middle man” to pass the modulatory signal to the posterior processing areas. Its function may involve allocation of attentional resources to different posterior processing streams as to bias processing toward the task-relevant stream so that the processing of such information is up-regulated. Patients with unilateral parietal damage suffer from spatial neglect to the contralateral space, which may also result from the failure to properly distribute attentional resources (Marshall and Fink, 2001; Mesulam, 1999; Posner et al., 1982). Toth and Assad (2002) found that an analogous area in the monkey (i.e., lateral intraparietal area, LIP) also responded to behaviorally relevant

stimuli in a dynamic fashion. These results from patient and animal studies further support our speculation.

In contrast to the inferior parietal activation observed in the spatial Stroop task, we observed a more medial and superior activation of the parietal cortex for the Simon task. These regions include superior parietal and precuneus cortices (BA 7). Other accompanying midline activation was also obtained, including SMA/pre-SMA, midcingulate, precentral, postcentral, and paracentral cortices. This is consistent with the findings obtained from the previous brain imaging studies of the Simon effect. Activation of these midline regions (with the exception of the precuneus) is usually not observed in the Stroop effect. We speculate that this activation pattern may reflect the nature of the direct stimulus–response conflict. Unlike the response conflict contained in the Stroop task, which is caused by the task-relevant and task-irrelevant attributes leading to conflicting responses, the conflict in the Simon task is caused by an almost preprogrammed or hard-wired visuo-spatial-motor circuitry, since the association between the same side visuospatial perception and motor response is so strong.

Despite the distinction between patterns of activation of ACC and parietal regions in the Simon and Stroop tasks, some other regions besides DLPFC were similarly activated in both tasks. One of the most prominent was the precuneus cortex, whose functional role, at present, is not well understood. Many tasks requiring response selection activate this area (Banich et al., 2001; Dassonville et al., 2001; Dove et al., 2000), as do tasks requiring other types of central control such as working memory (LaBar et al., 1999) and problem solving and reasoning (Acuna et al., 2002; Elliott and Dolan, 1998; Van den Heuvel et al., 2003). Most studies consisting of a visual-spatial or visual-motor component activate the precuneus (Berman et al., 1999; Luna et al., 1998; Petit and Haxby, 1999; Sakai et al., 1998), as do tasks involving verbal and semantic processing (Pinel et al., 2001). Difficulty level of attention-demanding tasks cannot completely explain activation of this region since precuneus activation is not always correlated with the behavioral performance. Mazoyer et al. (2002) even found that along with ACC and medial superior frontal cortex, activation of precuneus was negatively correlated with reaction time.

Another region activated by both tasks was the inferior frontal region, although the exact areas differed (Simon effect—BA 45 and Stroop effect—BA 47). Other previous Stroop studies also report activation of these areas (Banich et al., 2001; Peterson et al., 2002). We speculate that these areas are in charge of storing the information extracted from both the task-relevant and task-irrelevant processing streams before DLPFC further selects the relevant information for response. In both tasks, selection between the task-relevant and task-irrelevant information becomes harder on incongruent trials since these two sources of information conflict with each other. Therefore, stronger activation of inferior frontal region is required to hold the information online before the correct response is made.

Though the posterior processing regions that were activated did not overlap entirely between the Simon and Stroop tasks, both tasks activated the visual processing stream including middle occipital (BA 19) and inferior temporal (BA 37) cortices (see Table 3). This may reflect the effect of top-down modulation of attentional selection on posterior processing regions. Since the direction of the arrow (its shape) is the task-relevant attribute, activity of the ventral visual system is increased to favor the processing of “what” over the processing of “where” (Mishkin et al., 1983).

In conclusion, although both the Simon and Stroop effects share a common neural mechanism of attentional control (DLPFC) as well as its top-down modulation on the posterior processing streams (BA 19 and 37), the exact brain activation patterns are not the same across these two tasks. The Simon task activated more brain areas sensitive to detection of response conflict (ACC), response planning and selection (SMA/pre-SMA), and visuospatial-motor association (superior parietal), while the Stroop task activated more brain regions involved in biasing the processing toward the task-relevant attribute (inferior parietal cortex). Thus, the present findings indicate that the Simon interference effect arises more from the *stimulus–response* conflict and is overcome by the top-down modulation on the brain regions of visuospatial-motor association, whereas the Stroop interference effect arises more from the *stimulus–stimulus* conflict between the task-relevant and task-irrelevant dimensions and is overcome by the up-regulation of the task-relevant stream.

## References

- Acuna, B.D., Eliassen, J.C., Donoghue, J.P., Sanes, J.N., 2002. Frontal and parietal lobe activation during transitive inference in humans. *Cereb. Cortex* 12 (12), 1312–1321.
- Banich, M.T., Milham, M.P., Atchley, R.A., Cohen, N.J., Webb, A., Wszalek, T., et al., 2000a. Prefrontal regions play a predominant role in imposing an attentional ‘set’: evidence from fMRI. *Brain Res. Cogn. Brain Res.* 10 (1–2), 1–9.
- Banich, M.T., Milham, M.P., Atchley, R.A., Cohen, N.J., Webb, A., Wszalek, T., et al., 2000b. fMRI studies of Stroop tasks reveal unique roles of anterior and posterior brain systems in attentional selection. *J. Cogn. Neurosci.* 12 (6), 988–1000.
- Banich, M.T., Milham, M.P., Jacobson, B.L., Webb, A., Wszalek, T., Cohen, N.J., et al., 2001. Attentional selection and the processing of task-irrelevant information: insights from fMRI examinations of the Stroop task. *Prog. Brain Res.* 134, 459–470.
- Barch, D.M., Braver, T.S., Akbudak, E., Conturo, T., Ollinger, J., Snyder, A., 2001. Anterior cingulate cortex and response conflict: effects of response modality and processing domain. *Cereb. Cortex* 11 (9), 837–848.
- Bench, C.J., Frith, C.D., Grasby, P.M., Friston, K.J., Paulesu, E., Frackowiak, R.S., et al., 1993. Investigations of the functional anatomy of attention using the Stroop test. *Neuropsychologia* 31 (9), 907–922.
- Berman, R.A., Colby, C.L., Genovese, C.R., Voyvodic, J.T., Luna, B., Thulborn, K.R., et al., 1999. Cortical networks subserving pursuit and saccadic eye movements in humans: an FMRI study. *Hum. Brain Mapp.* 8 (4), 209–225.
- Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. *Psychol. Rev.* 108 (3), 624–652.
- Braver, T.S., Barch, D.M., Gray, J.R., Molfese, D.L., Snyder, A., 2001. Anterior cingulate cortex and response conflict: effects of frequency, inhibition and errors. *Cereb. Cortex* 11 (9), 825–836.
- Brown, G.G., Kindermann, S.S., Siegle, G.J., Granholm, E., Wong, E.C., Buxton, R.B., 1999. Brain activation and pupil response during covert performance of the Stroop Color Word task. *J. Int. Neuropsychol. Soc.* 5 (4), 308–319.
- Bush, G., Whalen, P.J., Rosen, B.R., Jenike, M.A., McInerney, S.C., Rauch, S.L., 1998. The counting Stroop: an interference task specialized for functional neuroimaging—validation study with functional MRI. *Hum. Brain Mapp.* 6 (4), 270–282.
- Bush, G., Shin, L.M., Holmes, J., Rosen, B.R., Vogt, B.A., 2003. The Multi-Source Interference Task: validation study with fMRI in individual subjects. *Mol. Psychiatry* 8 (1), 60–70.
- Carter, C.S., Mintun, M., Cohen, J.D., 1995. Interference and facilitation effects during selective attention: an H215O PET study of Stroop task performance. *NeuroImage* 2 (4), 264–272.
- Cohen, R.A., Kaplan, R.F., Moser, D.J., Jenkins, M.A., Wilkinson, H., 1999. Impairments of attention after cingulotomy. *Neurology* 53 (4), 819–824.
- Cohen, J.D., Botvinick, M., Carter, C.S., 2000. Anterior cingulate and prefrontal cortex: who’s in control? *Nat. Neurosci.* 3 (5), 421–423.
- Corbetta, M., Miezin, F.M., Dobmeyer, S., Shulman, G.L., Petersen, S.E., 1991. Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. *J. Neurosci.* 11 (8), 2383–2402.
- Dassonville, P., Lewis, S.M., Zhu, X.H., Ugurbil, K., Kim, S.G., Ashe, J., 2001. The effect of stimulus–response compatibility on cortical motor activation. *NeuroImage* 13 (1), 1–14.
- Dove, A., Pollmann, S., Schubert, T., Wiggins, C.J., von Cramon, D.Y., 2000. Prefrontal cortex activation in task switching: an event-related fMRI study. *Brain Res. Cogn. Brain Res.* 9 (1), 103–109.
- Elliott, R., Dolan, R.J., 1998. Activation of different anterior cingulate foci in association with hypothesis testing and response selection. *NeuroImage* 8 (1), 17–29.
- Fan, J., Flombaum, J.I., McCandliss, B.D., Thomas, K.M., Posner, M.I., 2003. Cognitive and brain consequences of conflict. *NeuroImage* 18 (1), 42–57.
- George, M.S., Ketter, T.A., Parekh, P.I., Rosinsky, N., Ring, H.A., Casey, B.J., et al., 1994. Regional brain activity when selecting a response despite interference: an O-15 PET study of the Stroop and an emotional Stroop. *Hum. Brain Mapp.* 1, 194–209.
- Hasbroucq, T., Guiard, Y., 1991. Stimulus–response compatibility and the Simon effect: toward a conceptual clarification. *J. Exp. Psychol., Hum. Percept. Perform.* 17 (1), 246–266.
- Hommel, B., 1995. Stimulus–response compatibility and the Simon effect: Toward an empirical clarification. *J. Exp. Psychol., Hum. Percept. Perform.* 21 (4), 764–775.
- Iacoboni, M., Woods, R.P., Mazziotta, J.C., 1996. Brain–behavior relationships: evidence from practice effects in spatial stimulus–response compatibility. *J. Neurophysiol.* 76 (1), 321–331.
- Iacoboni, M., Woods, R.P., Mazziotta, J.C., 1998. Bimodal (auditory and visual) left frontoparietal circuitry for sensorimotor integration and sensorimotor learning. *Brain* 121 (Pt 11), 2135–2143.
- Kornblum, S., 1992. Dimensional overlap and dimensional relevance in stimulus–response and stimulus–stimulus compatibility. In: Stelmach, G., Requin, J. (Eds.), *Tutorials in Motor Behavior II*. North-Holland, Amsterdam, pp. 743–777.
- Kornblum, S., Stevens, G.T., Whipple, A., Requin, J., 1999. The effects of irrelevant stimuli: 1. The time course of stimulus–stimulus and stimulus–response consistency effects with Stroop-like stimuli, Simon-like tasks, and their factorial combinations. *J. Exp. Psychol., Hum. Percept. Perform.* 25 (3), 688–714.
- LaBar, K.S., Gitelman, D.R., Parrish, T.B., Mesulam, M., 1999. Neuroanatomic overlap of working memory and spatial attention networks: a functional MRI comparison within subjects. *NeuroImage* 10 (6), 695–704.
- Leung, H.C., Skudlarski, P., Gatenby, J.C., Peterson, B.S., Gore, J.C., 2000. An event-related functional MRI study of the Stroop color word interference task. *Cereb. Cortex* 10 (6), 552–560.
- Lu, C.H., Proctor, R.W., 1995. The influence of irrelevant location information on performance: a review of the Simon and spatial Stroop effects. *Psychon. Bull. Rev.* 2 (2), 174–207.
- Luna, B., Thulborn, K.R., Strojwas, M.H., McCurtain, B.J., Berman, R.A., Genovese, C.R., et al., 1998. Dorsal cortical regions subserving visually guided saccades in humans: an fMRI study. *Cereb. Cortex* 8 (1), 40–47.
- MacDonald 3rd, A.W., Cohen, J.D., Stenger, V.A., Carter, C.S., 2000. Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science* 288 (5472), 1835–1838.
- MacLeod, C.M., 1991. Half a century of research on the Stroop effect: an integrative review. *Psychol. Bull.* 109 (2), 163–203.
- MacLeod, C.M., 1992. The Stroop task: the “gold standard” of attentional measures. *J. Exp. Psychol. Gen.* 121 (1), 12–14.

- Marshall, J.C., Fink, G.R., 2001. Spatial cognition: where we were and where we are. *Neuroimage* 14 (1 Pt. 2), S2–S7.
- Mazoyer, P., Wicker, B., Fonlupt, P., 2002. A neural network elicited by parametric manipulation of the attention load. *NeuroReport* 13 (17), 2331–2334.
- Menon, V., Adelman, N.E., White, C.D., Glover, G.H., Reiss, A.L., 2001. Error-related brain activation during a Go/NoGo response inhibition task. *Hum. Brain Mapp.* 12 (3), 131–143.
- Mesulam, M.M., 1999. Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philos. Trans. R. Soc. London, Ser. B* 354 (1387), 1325–1346.
- Milham, M.P., Banich, M.T., Webb, A., Barad, V., Cohen, N.J., Wszalek, T., et al., 2001. The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Brain Res. Cogn. Brain Res.* 12 (3), 467–473.
- Milham, M.P., Erickson, K.I., Banich, M.T., Kramer, A.F., Webb, A., Wszalek, T., et al., 2002. Attentional control in the aging brain: insights from an fMRI study of the Stroop task. *Brain Cogn.* 49 (3), 277–296.
- Milham, M.P., Banich, M.T., Claus, E.D., Cohen, N.J., 2003. Practice-related effects demonstrate complementary roles of anterior cingulate and prefrontal cortices in attentional control. *NeuroImage* 18 (2), 483–493.
- Mintun, M.A., Fox, P.T., Raichle, M.E., 1989. A highly accurate method of localizing regions of neuronal activation in the human brain with positron emission tomography. *J. Cereb. Blood Flow Metab.* 9 (1), 96–103.
- Mishkin, M., Ungerleider, L.G., Macko, K., 1983. Object vision and spatial vision: two cortical pathways. *Trends Neurosci.* 6, 414–417.
- Ochsner, K.N., Kosslyn, S.M., Cosgrove, G.R., Cassem, E.H., Price, B.H., Nierenberg, A.A., et al., 2001. Deficits in visual cognition and attention following bilateral anterior cingulotomy. *Neuropsychologia* 39 (3), 219–230.
- Pardo, J.V., Pardo, P.J., Janer, K.W., Raichle, M.E., 1990. The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. *Proc. Natl. Acad. Sci. U. S. A.* 87 (1), 256–259.
- Peterson, B.S., Skudlarski, P., Gatenby, J.C., Zhang, H., Anderson, A.W., Gore, J.C., 1999. An fMRI study of Stroop word–color interference: evidence for cingulate subregions subserving multiple distributed attentional systems. *Biol. Psychiatry* 45 (10), 1237–1258.
- Peterson, B.S., Kane, M.J., Alexander, G.M., Lacadie, C., Skudlarski, P., Leung, H.C., et al., 2002. An event-related functional MRI study comparing interference effects in the Simon and Stroop tasks. *Brain Res. Cogn. Brain Res.* 13 (3), 427–440.
- Petit, L., Haxby, J.V., 1999. Functional anatomy of pursuit eye movements in humans as revealed by fMRI. *J. Neurophysiol.* 82 (1), 463–471.
- Pinel, P., Dehaene, S., Riviere, D., LeBihan, D., 2001. Modulation of parietal activation by semantic distance in a number comparison task. *NeuroImage* 14 (5), 1013–1026.
- Posner, M.I., DiGirolamo, G.J., 1998. Executive attention: Conflict, target detection and cognitive control. In: Parasuraman, R. (Ed.), *The Attentive Brain*. MIT Press, Cambridge, MA.
- Posner, M.I., Petersen, S.E., 1990. The attention system of the human brain. *Annu. Rev. Neurosci.* 13, 25–42.
- Posner, M.I., Cohen, Y., Rafal, R.D., 1982. Neural systems control of spatial orienting. *Philos. Trans. R. Soc. London, Ser. B* 298 (1089), 187–198.
- Praamstra, P., Kleine, B.U., Schnitzler, A., 1999. Magnetic stimulation of the dorsal premotor cortex modulates the Simon effect. *NeuroReport* 10 (17), 3671–3674.
- Proctor, R.W., Reeve, T.G. (Eds.), 1990. *Stimulus–Response Compatibility: An Integrated Perspective*. North-Holland, Amsterdam.
- Sakai, K., Hikosaka, O., Miyachi, S., Takino, R., Sasaki, Y., Putz, B., 1998. Transition of brain activation from frontal to parietal areas in visuomotor sequence learning. *J. Neurosci.* 18 (5), 1827–1840.
- Simon, J.R., Small Jr., A.M., 1969. Processing auditory information: interference from an irrelevant cue. *J. Appl. Psychol.* 53 (5), 433–435.
- Stroop, J.R., 1935. Studies of interference in serial verbal reactions. *J. Exp. Psychol.* 18, 643–662.
- Swick, D., Jovanovic, J., 2002. Anterior cingulate cortex and the Stroop task: neuropsychological evidence for topographic specificity. *Neuropsychologia* 40 (8), 1240–1253.
- Swick, D., Turken, A.U., 2002. Dissociation between conflict detection and error monitoring in the human anterior cingulate cortex. *Proc. Natl. Acad. Sci. U. S. A.* 99 (25), 16354–16359.
- Toth, L.J., Assad, J.A., 2002. Dynamic coding of behaviourally relevant stimuli in parietal cortex. *Nature* 415 (6868), 165–168.
- van den Heuvel, O.A., Groenewegen, H.J., Barkhof, F., Lazeron, R.H., van Dyck, R., Veltman, D.J., 2003. Frontostriatal system in planning complexity: a parametric functional magnetic resonance version of Tower of London task. *NeuroImage* 18 (2), 367–374.
- van Veen, V., Cohen, J.D., Botvinick, M.M., Stenger, V.A., Carter, C.S., 2001. Anterior cingulate cortex, conflict monitoring, and levels of processing. *NeuroImage* 14 (6), 1302–1308.
- Xiong, J., Gao, J.H., Lancaster, J.L., Fox, P.T., 1995. Clustered pixels analysis for functional MRI activation studies of the human brain. *Hum. Brain Mapp.* 3, 287–301.
- Zhang, H.H., Zhang, J., Kornblum, S., 1999. A parallel distributed processing model of stimulus–stimulus and stimulus–response compatibility. *Cogn. Psychol.* 38 (3), 386–432.