Separate conflict-specific cognitive control mechanisms in the human brain

Tobias Egner,* Margaret Delano, and Joy Hirsch

Functional MRI Research Center, Neurological Institute Box 108, Columbia University, 710 W 168th St, New York, NY 10032, USA

To ensure optimal task performance, the human brain detects and resolves conflict in information processing via a cognitive control system. However, it is not known whether conflict resolution relies on a single central resource of cognitive control, or on a collection of independent control mechanisms that deal with different types of conflict. In order to address this question, we assessed behavioral and blood–oxygen-level-dependent (BOLD) responses during the simultaneous detection and resolution of two sources of conflict in a modified color-naming Stroop task: conflict stemming from incompatibility between the task-relevant and an irrelevant stimulus feature (stimulus-based or Stroop conflict), and conflict stemming from incompatibility between an irrelevant stimulus feature and response features (response-based or Simon conflict). Results show that control mechanisms recruited by stimulus-based conflict resolve stimulus-based conflict, but do not affect the resolution of response-based conflict, and vice versa. The resolution of response-based conflict was distinguished by modulation of activity in premotor cortex, whereas resolution of stimulus-based conflict was distinguished by the modulation of activity in parietal cortex. These results suggest that the human brain flexibly adopts, and independently controls, conflict-specific resolution strategies, biasing motor programming to resolve response-based conflict, and biasing stimulus representations to resolve stimulus-based conflict. We propose a non-centralized, modular architecture of cognitive control, where separate control resources operate in parallel, and are recruited in a context-sensitive manner.
© 2006 Elsevier Inc. All rights reserved.

Introduction

Human performance regulation involves mechanisms that detect and resolve conflict in information processing (Botvinick et al., 2001). A classic example of conflict is provided by the color-naming Stroop task: subjects are required to name the ink color (e.g., red) of a printed color–word, the meaning of which can be either compatible (RED) or

incompatible (e.g., GREEN) with that color (Stroop, 1935; MacLeod, 1991). When ink color and word meaning are semantically incompatible, color and word processing streams lead to conflicting representations, resulting in slowed performance (Cohen et al., 1990). For optimal performance, such conflict must be detected and resolved by cognitive control mechanisms (Botvinick et al., 2001).

One neural strategy for conflict resolution is to bias stimulus processing in sensory pathways, where cortical representations of task-relevant stimulus features (e.g., ink color) may be amplified relative to task-irrelevant ones (e.g., word meaning) (Cohen et al., 1990; Desimone and Duncan, 1995; Kastner and Ungerleider, 2000). In tasks such as the Stroop protocol, where conflict stems from incompatibility between task-relevant and task-irrelevant stimulus features (stimulus-based conflict), such a "stimulus bias" conflict resolution mechanism has indeed been documented; specifically, conflict resolution has been found to be associated with enhanced processing of task-relevant stimulus information in sensory cortices (Egner and Hirsch, 2005a).

A second strategy for overcoming conflict is to bias the response selection process (Nieuwenhuis and Yeung, 2005), for instance by inhibiting the influence of task-irrelevant information on motor output (Sturmer et al., 2002; Sturmer and Leuthold, 2003). It is thought that such a "response bias" conflict resolution strategy is employed to resolve conflict in the Simon task (Simon, 1969), where conflict occurs due to incompatibility between a task-irrelevant stimulus feature and response features (response-based conflict) (Stoffels, 1996; Praamstra et al., 1999; Ridderinkhof, 2002; Sturmer et al., 2002; Sturmer and Leuthold, 2003). Here, subjects categorize the ink color of a stimulus presented to either the left or right of a central fixation, by pushing response buttons with their left (e.g., for green) or right hand (e.g., for red). Conflict occurs when the position of the stimulus is spatially incompatible with the position of the correct response effecter (e.g., a red stimulus presented on the left side) resulting in slowed performance (Simon, 1969; Lu and Proctor, 1995).

Two questions regarding the nature of cognitive control mechanisms arise from these findings: first, it is not known whether control mechanisms involved in resolving stimulus- versus response-based conflict are engaged independently of each other,

* Corresponding author. Cognitive Neurology and Alzheimer's Disease Center, Feinberg School of Medicine, Northwestern University, 320 East Superior, Searle 11, Chicago, IL 60611, USA. Fax: +1 312 908 8789.
E-mail address: t-egner@northwestern.edu (T. Egner).
Available online on ScienceDirect (www.sciencedirect.com).

or whether they rely on shared central resources. We addressed this question by independently manipulating sources of conflict, between stimulus-based (Stroop) and response-based (Simon) conflict, and assessing whether control mechanisms recruited by one type of conflict would affect the resolution of the other type of conflict. Secondly, if there were independent conflict resolution mechanisms, it is not known whether these would conform to the stimulus-biasing versus response-biasing strategies implied by the literature. We tested this proposal by acquiring functional magnetic resonance imaging (fMRI) data during task performance, which allowed us to contrast neural activity related to resolving stimulus-based conflict to that associated with resolving response-based conflict.

Manipulating sources of conflict

In order to directly contrast stimulus-based and response-based conflict processes, we factorially combined the classic color-naming Stroop and Simon tasks into a single experimental protocol (cf. Simon and Berbaum, 1990; Kornblum, 1994; Hommel, 1997). Note that in the current paper we employ the terms 'stimulus-based' and 'response-based' to refer to the origin of conflict in the Stroop and Simon tasks, respectively. Specifically, 'response-based' conflict should not be confounded with 'response conflict': we use the former to describe conflict that originates with an overlap between an irrelevant stimulus dimension and the response dimension, as is the case in the Simon task (Kornblum et al., 1990; Kornblum and Lee, 1995; Zhang et al., 1999), while the latter is used to refer to a co-activation of mutually incompatible response pathways. Therefore, both the Stroop and the Simon task entail 'response conflict' in the sense that incompatible trials are associated with incompatible response tendencies; however, the genesis of response conflict differs between the two tasks, in that it is response-based in the Simon task, and stimulus-based in the Stroop task. Below, these conflicts are described in more detail.

In the color-naming Stroop task, conflict arises from a dimensional overlap between the relevant stimulus dimension (ink color) and an irrelevant stimulus dimension[1] (word meaning) (Kornblum et al., 1990; Kornblum and Lee, 1995; Zhang et al., 1999). As attentional selection of the task-relevant stimulus dimension (ink color) is not perfect, involuntary processing of the word meaning on incompatible trials leads to 'conceptual conflict' (often referred to as 'stimulus conflict') between color (e.g., red) and word (e.g., 'GREEN') processing streams. The processing of word meaning is thought to interfere particularly strongly with ink color naming because it constitutes a more highly practiced process (MacLeod and Dunbar, 1988). If the two processing streams are furthermore associated with two eligible but incompatible responses, the conceptual (stimulus) conflict will additionally result in simultaneous activation of mutually incompatible response pathways, thus also producing response conflict (Kornblum et al., 1990; Kornblum and Lee, 1995; Zhang et al.,

1999; Milham et al., 2001; De Houwer, 2003; van Veen and Carter, 2005). While conflict in a typical Stroop protocol can thus be argued to reflect an additive effect of stimulus (conceptual) and response conflict (Milham et al., 2001; De Houwer, 2003; van Veen and Carter, 2005), we are here not concerned with this distinction. Instead, our concern is the *origin* of both these conflicts, which lies with the semantic incompatibility between relevant and irrelevant stimulus dimensions; therefore, Stroop conflict represents *stimulus-based conflict* (Kornblum et al., 1990; Kornblum and Lee, 1995; Zhang et al., 1999).

In the Simon task (Simon, 1969), on the other hand, conflict is due to an overlap between an irrelevant stimulus dimension (stimulus location) and the response dimension (left/right button press) (Kornblum et al., 1990; Kornblum and Lee, 1995; Zhang et al., 1999). This effect is thought to be due to an unintentional or 'direct' route of activation of the spatially corresponding response effecter by the (irrelevant) stimulus location (Kornblum et al., 1990; Hommel, 1993; De Jong et al., 1994). In other words, there appears to be an inherent propensity of the motor system to react towards the source of stimulation (Simon, 1969). This fast, direct route of response activation (or response priming) competes with a slower, 'indirect' route, represented by the intentional processing of the task-relevant color information in relation to the instructed stimulus–response mappings (Kornblum et al., 1990; Hommel, 1993; De Jong et al., 1994). On incompatible trials, direct route response activation conflicts with the response selection derived from processing the relevant color stimulus feature, resulting in response conflict (Kornblum et al., 1990; De Jong et al., 1994; Zhang et al., 1999). Therefore, like Stroop conflict, Simon conflict is associated with conflicting response tendencies; however, unlike Stroop conflict, it does not originate with incompatibility between stimulus dimensions, but with a direct interference of an irrelevant stimulus dimension with the response selection process (Acosta and Simon, 1976; Simon, 1982). Simon conflict therefore is held to represent *response-based conflict* (Kornblum et al., 1990; Kornblum and Lee, 1995; Zhang et al., 1999).

We combined the classic Stroop and Simon tasks by presenting color–word stimuli (RED and GREEN), printed in either red or green ink, either to the left or right of a central fixation cross, and requiring subjects to identify the ink color of a given stimulus by pressing a response button with their left index finger for stimuli of green ink color and with their right index finger for stimuli of red ink color (Fig. 1). Each stimulus could thus be compatible or incompatible with respect to the color–word, and with respect to the spatial location, resulting in a 2 (Stroop compatibility: compatible versus incompatible) × 2 (Simon compatibility: compatible versus incompatible) factorial design, while the task-relevant stimulus feature (ink color) was held constant. Behavioral studies employing similar designs have supported the notion that Stroop and Simon compatibility effects involve different, independent processing resources, as Stroop and Simon compatibilities both produce main effects, but do not interact (Simon and Berbaum, 1990; Kornblum, 1994, Hommel, 1997).

Dissociating control-related from conflict-related processes

In order to dissociate control- from conflict-related processes associated with Stroop and Simon stimulus dimensions, we assessed the "conflict adaptation effect", a sequential trial effect that has been argued to reflect the workings of the conflict-monitoring/cognitive control loop (Botvinick et al., 1999, 2001; Kerns et al.,

---

[1] Note that in a Stroop protocol that requires an oral response (verbally naming the ink color), there are additional compatibility effects due to both relevant and irrelevant stimulus dimensions overlapping with the response dimension (Zhang et al., 1999). However, like most neuroimaging studies of the Stroop protocol, the current investigation employs arbitrarily mapped manual button press responses, thus restricting the source of conflict to a stimulus–stimulus overlap only.
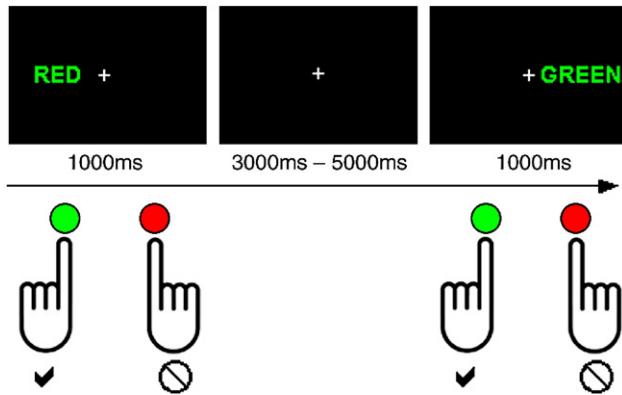
Fig. 1. Behavioral protocol. Subjects were presented with the color words "RED" and "GREEN", colored in either red or green ink, to the left or right of a central fixation cross. Subjects were required to identify the ink color of the stimulus by pushing a left hand button for green ink, and a right hand button for red ink. The example trials displayed here consists of one stimulus (to the left) that is incongruent with respect to the Stroop stimulus dimension, but congruent with respect to the Simon stimulus dimension, followed by another stimulus (to the right) that is congruent with respect to the Stroop stimulus dimension, but incongruent with respect to the Simon stimulus dimension. The correct response to either stimulus is a left button push (for green ink).

2004; Egner and Hirsch, 2005a,b), and which characterizes performance patterns both on the Stroop task (Kerns et al., 2004; Egner and Hirsch, 2005b; Notebaert et al., 2006) as well as on the Simon task (Stoffels, 1996; Praamstra et al., 1999; Ridderinkhof, 2002; Sturmer et al., 2002; Sturmer and Leuthold, 2003; Wuhr, 2005; Wuhr and Ansorge, 2005). The conflict adaptation effect is reflected in the finding that the degree to which task-irrelevant information interferes with the processing of task-relevant information varies as a function of trial sequence: conflict is reduced following incompatible trials compared to compatible trials (Gratton et al., 1992). According to the conflict-monitoring model, this previous by current trial compatibility interaction effect arises because high conflict on an incompatible trial leads to an up-regulation in cognitive control, resulting in improved selection of target information on the next trial, which is reflected in faster responses to incompatible trials (reduced interference) and slower responses to compatible ones (reduced facilitation) (Botvinick et al., 2001). Alternative accounts of this effect (Mayr et al., 2003; Hommel et al., 2004) are addressed in the Discussion section.

Here, we analyzed trial-to-trial conflict adaptation effects with respect to Stroop and Simon compatibility factors, in order to assess whether the cognitive control processes that resolve conflict are specific to the original source of the conflict (see also Wendt et al., 2006). For this purpose, the aforementioned 2×2 factorial design was expanded to incorporate previous stimulus type into the analysis, resulting in a 4-way $2 \times 2 \times 2 \times 2$ factorial design, with the factors of previous and current trial compatibility (compatible versus incompatible), current trial stimulus dimension (Stroop versus Simon) and previous trial stimulus dimension (same versus different) (a trial exemplar is displayed in Fig. 1). Based on our *a priori* hypotheses, adaptation effects were assessed with respect to the Stroop compatibility factor, to reveal whether stimulus-based conflict on the previous trial results in superior conflict resolution of stimulus-based conflict on the current trial, as documented in previous research

(Kerns et al., 2004; Egner and Hirsch, 2005b; Notebaert et al., 2006). Adaptation effects were also assessed with respect to the Simon compatibility factor, to reveal whether response-based conflict on the previous trial results in superior conflict resolution of response-based conflict on the current trial, as documented in previous research (Stoffels, 1996; Praamstra et al., 1999; Ridderinkhof, 2002; Sturmer et al., 2002; Sturmer and Leuthold, 2003; Wuhr, 2005; Wuhr and Ansorge, 2005). Most importantly, however, the current design allowed us to test whether control processes triggered by stimulus-based conflict on the previous trial would affect the resolution of response-based conflict on the current trial, and vice versa, by assessing conflict adaptation across the Stroop and Simon compatibility factors.

Hypotheses

If a single central cognitive control resource were responsible for resolving both stimulus-based and response-based conflict, one would expect the recruitment of one type of resolution mechanism to impair the resolution of the other type of conflict, that is, control processes triggered by stimulus-based conflict on the previous trial would impair the resolution of response-based conflict on the current trial, and vice versa. On the other hand, if there were independent resources for dealing with stimulus-based and response-based conflicts, two alternative predictions could be made. Either, any type of conflict may trigger both stimulus- and response-related control processes, in which case control processes triggered by stimulus-based conflict on the previous trial would enhance the resolution of response-based conflict on the current trial, and vice versa. Or, alternatively, the two conflict resolution strategies may be recruited in a conflict-specific manner, such that control processes triggered by stimulus-based conflict on the previous trial would have no effect on the resolution of response-based conflict on the current trial, and vice versa.

As noted above, both the theoretical and the empirical literature suggest that Stroop conflict is resolved via a stimulus-biasing strategy (Cohen et al., 1990; Botvinick et al., 2001; Egner and Hirsch, 2005a), whereas Simon conflict is resolved via a response-biasing strategy (Stoffels, 1996; Praamstra et al., 1999; Sturmer et al., 2002; Sturmer and Leuthold, 2003). If these assumptions were true, we would expect our fMRI data to show different brain regions to be implicated in the two resolution processes. Specifically, we would expect Simon conflict resolution to be associated with differential activation in premotor and/or motor cortices, while Stroop conflict resolution would be expected to be associated with differential activity in areas implicated in top-down stimulus biasing, such lateral frontal and superior parietal cortices.

Materials and methods

Subjects

Participants were 15 native English-speaking, healthy volunteers (mean age = 27 years, 7 females) with normal or corrected-to-normal vision, who provided informed consent conforming to institutional guidelines. Participants were screened via self-report for neurological or psychological conditions, use of psychiatric medication, color blindness, and dyslexia. Due to excessive movement artifacts in the MRI data, 2 subjects were excluded from all analyses.

Experimental protocol

Procedure

The task programming, stimulus delivery, and recording of behavioral responses were carried out with Presentation software (Neurobehavioral Systems, http://nbs.neuro-bs.com/nbs_online). Stimuli were presented to the subjects on a back-projection screen, which could be viewed via a mirror attached to the MRI headcoil. The visual angle of the word stimuli subtended approximately 1.5°. Stimuli were presented in a pseudo-random manner, so as to produce a counter-balanced sequence of equal numbers of the 16 possible 1st order trial transitions (see Table 1). No direct repetitions of identical stimuli were included in the task in order to avoid potential repetition priming effects (Mayr et al., 2003), and trial types were counter-balanced across responses. Note that, on some trials, a distracter feature of the previous stimulus becomes the target feature of the current stimulus, and vice versa. These transitions may incur priming effects (such as "negative priming"), but these are typically very small compared to the compatibility effects of interest (Fox, 1995; May et al., 1995), and are often not detectable when presenting stimuli with varying inter-stimulus intervals (ISIs) longer than 2000 ms (Neill and Valdes, 1992; Egner and Hirsch, 2005c), as was the case in the current study.

Stimuli were displayed for 1000 ms with a jittered inter-stimulus interval (ISI), evenly distributed from 3000 to 5000 ms in 500-ms steps (mean ISI=4000 ms). A central fixation cross was present throughout the experiment, and subjects were asked to maintain fixation during the ISI, but were allowed to overtly orient their eyes towards the color–word stimuli once they appeared on screen. Stimuli were delivered in blocks of 17, which were separated by the words "New Block". Note that different 'blocks' do not connote different conditions, and that all analyses were carried out by trial types (across 'blocks'), in an event-related fashion. The experiment consisted of 3 runs of 10 blocks each, producing 540 trials, with each run lasting approximately 12 min. Prior to the scanning session, the task was explained to the subjects, and a brief practice run was administered outside the scanner. At the beginning of each run, subjects were reminded of the task instructions.

Image acquisition

Images were acquired with a GE 1.5-T scanner. Functional data were acquired along the AC–PC line with a T2*-weighted EPI sequence of 24 contiguous axial slices (TR=2000 ms, TE=40 ms, flip angle=90°, FoV=190*190 mm) of 4.5-mm thickness and 3-mm in-plane resolution. The functional data were recorded in three runs of 365 acquisitions each. Structural data were acquired with a high-resolution T1-weighted SPGR scan (TR=19 ms, TE=5 ms, flip angle=20°, FoV=220*220 mm), recording 124 slices at a slice thickness of 1.5 mm and an in-plane resolution of 0.86×0.86 mm.

Image analysis

Spatial pre-processing and statistical analyses were performed using SPM2 software (Functional Imaging Laboratory, University College London, http://www.fil.ion.ucl.ac.uk/spm/). Functional images were slice timing corrected and spatially realigned to the first volume of the first run. For each subject, the structural scan was co-registered to a mean image of the realigned functional scans. The co-registered structural image was then used to calculate transformation parameters for normalizing the functional images to the MNI template brain. The normalized functional images were spatially smoothed with a Gaussian kernel of 10 mm³. The first five scans of each run were discarded prior to further analysis. Vectors of stimulus onsets were created for each trial type, along with error trials, post-error trials, and a miscellaneous condition (modeling the "New Block" stimuli and the first stimulus of each block). These vectors were then convolved with SPM2's canonical hemodynamic response function (hrf) and employed as event-related regressors to model the BOLD responses associated with the task. A 128-s temporal high pass filter was applied to the data to remove low-frequency artifacts. Temporal autocorrelation in the time series data was estimated using restricted maximum like-lihood estimates of variance components using a first-order autoregressive model (AR-1), and the resulting non-sphericity was used to form maximum likelihood estimates of the activations.

For each subject, voxelwise statistical parametric maps (SPM) were calculated for linear contrasts between regressors of interest. SPMs from each subject for a given contrast were then entered into group analyses, where participants were treated as random effects. The anatomical search space of the analyses was restricted to cortical gray matter voxels in *a priori* regions of interest (ROIs) (employing the WFU Pickatlas, http://www.fmri.wfubmc.edu/download.htm (Maldjian et al., 2003)), namely the frontal and parietal lobes, which represented ROIs due to their well-documented involvement in top-down conflict resolution.

The analyses focused on identifying regions sub-serving conflict resolution processes that were specific to either the Stroop or Simon task, in order to determine how conflict resolution strategies may differ between stimulus- and response-based conflicts. Our analysis strategy utilized an important feature of the conflict adaptation effect that has been exploited in functional neuroimaging studies: it allows a distinction between otherwise identical incompatible trials on the basis of whether they have been preceded by a compatible trial (a compatible–incompatible or "CI" trial), or whether they have been preceded by an incompatible trial (an incompatible–incompatible or "II" trial) (Botvinick et al., 1999; Kerns et al., 2004; Egner and Hirsch, 2005a). CI trials are associated with low cognitive control, and therefore high conflict, whereas II trials are associated with high cognitive control, and therefore low conflict. A direct contrast of the neural activity associated with these types of incompatible trials can reveal neural correlates of control-related processing (II>CI). Note that areas identified by this contrast may encompass regions that are sources of control signals and/or regions that are targets of such control processes (as well as non-specific attendant processes).

The goal of the imaging analyses was to identify brain regions that display task-specific effects of control in either the Stroop or

Table 1
Descriptive statistics of behavioral data

	Current trial			
	Stroop		Simon	
	Compatible	Incompatible	Compatible	Incompatible
Previous trial				
Stroop comp	610 (67)	650 (89)	622 (80)	637 (75)
Stroop incomp	621 (83)	638 (91)	622 (86)	636 (87)
Simon comp	612 (73)	638 (93)	603 (84)	647 (81)
Simon incomp	619 (78)	650 (87)	642 (82)	627 (81)

Reaction time (standard deviation) in milliseconds; comp=compatible, incomp=incompatible.

the Simon task. Therefore, our analysis strategy was designed to detect regions that showed an effect of control in one task, while showing null effects (i.e., neither an effect of control nor conflict) in the other task. Contrasts identifying control-related processing were carried out for the Stroop stimulus dimension in order to detect potential neural correlates of stimulus-based conflict resolution, and for the Simon stimulus dimension in order to detect potential neural correlates of response-based conflict resolution. Statistical maps for Stroop and Simon control-related activations within the anatomical ROIs were thresholded at $p < 0.005$ (uncorrected), with a minimum spatial extent of > 10 voxels. Additionally, we used an exclusive masking procedure to constrain the search for control-related regions in each task to areas that showed no effects (F-test, $p > 0.05$) in the other task. Crucially, our factorial design allowed us to then assess possible interaction effects between task and control factors, thus determining whether control-related activity in any of these regions was really specific to either Stroop or Simon conflict resolution, i.e., whether a given region was activated to a significantly greater degree during Stroop conflict resolution than during Simon conflict resolution, or vice versa. To this end, mean activity in regions displaying significant Stroop or Simon control effects was interrogated for possible interaction effects (i.e., [(Stroop II–Stroop CI)–(Simon II–Simon CI)] and [(Simon II–Simon CI)–(Stroop II–Stroop CI)]).

Results

Behavioral results

Mean reaction times (RT) were calculated for each of the trial transitions of interest in each subject, excluding error trials, post-error trials, and condition-specific outlier values (> 2 SDs from the mean); group means are presented in Table 1. Analysis of variance (ANOVA) showed that there were significant main effects of both Stroop compatibility (compatible trial mean= 615 ms, incompatible trial mean=644 ms; $F_{(1,12)} = 14.5$, $p < 0.005$) and Simon compatibility (compatible trial mean=622 ms, incompatible trial mean=637 ms; $F_{(1,12)} = 13.1$, $p < 0.005$). Stroop and Simon compatibility effects did not interact ($F_{(1,12)} = 0.1$, $p > 0.5$), replicating previous research (Simon and Berbaum, 1990; Kornblum, 1994; Hommel, 1997). However, a priori, the main goal of the analyses was to assess the degree of conflict adaptation (previous × current trial compatibility interaction) within and across Stroop and Simon stimulus dimensions. Within the Stroop dimension (Fig. 2a), a main effect of current trial compatibility ($F_{(1,12)} = 14.5$, $p < 0.005$), was qualified by a previous × current trial Stroop compatibility interaction effect ($F_{(1,12)} = 5.5$, $p < 0.05$), reflecting a reduction in conflict following incompatible trials (conflict=17 ms; $T_{(12)} = 2.1$, $p = 0.058$) compared to that following compatible trials (conflict=40 ms; $T_{(12)} = 4.0$, $p < 0.005$). This interaction was mediated by a combination of faster responses to incompatible trials (speed-up=12 ms; $T_{(12)} = 1.6$, $p = 0.14$), and slowed responses to compatible ones (slow-down=12 ms; $T_{(12)} = 1.9$, $p = 0.078$). Similarly, within the Simon dimension (Fig. 2b), a main effect of current trial compatibility ($F_{(1,12)} = 13.1$, $p < 0.005$) was qualified by a previous × current trial Simon compatibility interaction effect ($F_{(1,12)} = 106.4$, $p < 0.001$); the conflict effect seen after compatible trials (conflict=44 ms; $T_{(12)} = 7.4$, $p < 0.001$) was in fact reversed after incompatible trials (conflict=−15 ms; $T_{(12)} = 4.2$, $p < 0.005$). Again, this interaction was mediated by faster responses to incompatible trials (speed-up=20 ms; $T_{(12)} = 5.0$, $p < 0.001$) and
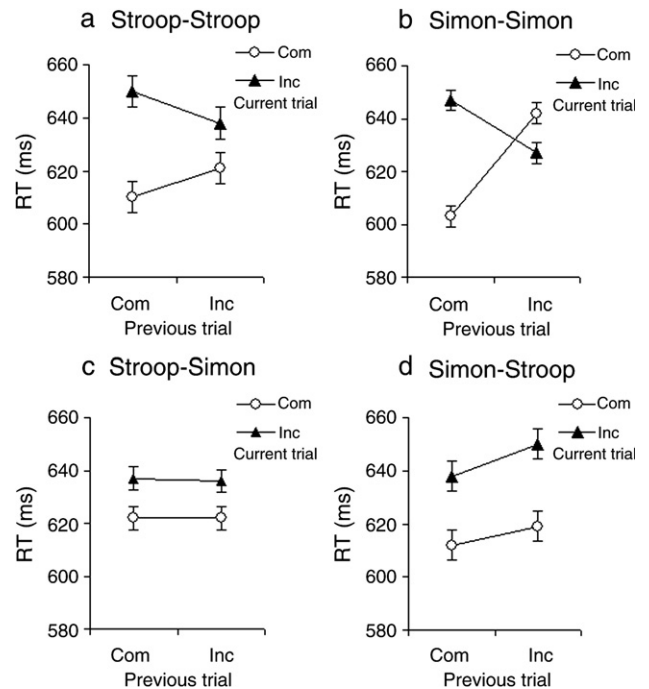
Fig. 2. Behavioral results. Group mean RT data (±within-subjects SEM) for current trial compatibility are displayed depending on previous trial compatibility (com=compatible, inc=incompatible). Data are plotted for (a) effects of previous trial Stroop compatibility on current trial Stroop compatibility (Stroop–Stroop), (b) effects of previous trial Simon compatibility on current trial Simon compatibility (Simon–Simon), (c) effects of previous trial Stroop compatibility on current trial Simon compatibility (Stroop–Simon), and (d) effects of previous trial Simon compatibility on current trial Stroop compatibility (Simon–Stroop).

slower responses to compatible ones (slow-down=40 ms; $T_{(12)} = 5.8$, $p < 0.001$).

While these results replicated previous findings of conflict adaptation effects in Stroop and Simon tasks, there was no evidence for conflict resolution generalizing across sources of conflict: when assessing current trial Simon compatibility effects as a function of previous trial Stroop compatibility (Fig. 2c), we found a main effect of current trial compatibility ($F_{(1,12)} = 13.1$, $p < 0.005$) but no previous × current trial interaction effect ($F_{(1,12)} = 0.1$, $p > 0.5$). Similarly, when analyzing current trial Stroop compatibility effects as a function of previous trial Simon compatibility (Fig. 2d), we obtained a main effect of current trial compatibility ($F_{(1,12)} = 14.5$, $p < 0.005$), but no interaction between previous trial Simon compatibility and current trial Stroop compatibility ($F_{(1,12)} = 0.4$, $p > 0.5$).

As accuracy on this task was rather high (mean=97%, SD=2%), and did not constitute our primary measure of interest, these data are not exhaustively reported here. However, in order to ascertain that the RT conflict adaptation effects within Stroop and Simon distracter dimensions reported above were not mediated by speed–accuracy trade-offs, the corresponding analyses were carried out on the accuracy data. Both the Stroop accuracy data ($F_{(1,12)} = 23.6$, $p < 0.001$) and the Simon accuracy data ($F_{(1,12)} = 25.4$, $p < 0.001$) displayed conflict adaptation effects akin to the RT data, hence ruling out the possibility of speed–accuracy trade-offs underlying the RT results. Finally, we also re-analyzed the behavioral data with a more lenient outlier exclusion criterion

(>3SDs from the mean). This did not qualitatively alter any of the results.

In line with the hypotheses of modular cognitive control resources and conflict-specific conflict resolution strategies, stimulus-based conflict on the previous trial was associated with stimulus-based conflict resolution on the current trial, but did not affect response-based conflict resolution, and vice versa. Thus, stimulus- and response-based conflict resolution processes appeared to be recruited in a conflict-specific manner, and operate independently of each other. In an effort to further corroborate the independence of stimulus- and response-based conflict resolution processes, we correlated individuals' Stroop and Simon interference scores, as well as the degree of Stroop and Simon conflict resolution (II<CI RTs). None of these scores were significantly correlated (all $ps > 0.25$), further suggesting that Stroop and Simon conflict- and control-related processes do not rely on shared resources.

Imaging results

Having established that stimulus-based and response-based conflicts appear to recruit independent conflict resolution mechanisms, we interrogated the neuroimaging data for regions that were differentially activated by Stroop and Simon conflict resolution. First, we assessed stimulus-based and response-based control-related activations via Stroop II>CI and Simon II>CI contrasts, respectively, in order to determine candidate regions of task-specific control effects. The search space for control regions in each task was restricted to regions that showed null effects (*F*-test $p > 0.05$) with respect to conflict and control variables on the other task. Activity in these regions was subsequently subjected to a task (Stroop versus Simon) × control (low versus high control) factorial analysis, in order to pinpoint the areas where control processes were specific to either Stroop or Simon conflict resolution.

As displayed in Fig. 3 and listed in Table 2, conflict resolution processes specific to stimulus-based Stroop conflict (shown in red)

Table 2
Brain regions displaying distinct effects of cognitive control during stimulus- versus response-based conflict resolution

Conflict	Region	BA	MNI x, y, z	Cluster	z-score
Stimulus-based	Precuneus/SPL	7	−20, −56, 46	33	3.54
Response-based	Precentral Gyrus	4, 43	58, −14, 28	114	3.97
	Precentral Gyrus	6	−62, 2, 18	17	3.14

BA = Brodmann area, MNI x, y, z = Montreal Neurological Institute coordinates for peak activation, cluster = number of voxels in cluster, z-score = z statistic for peak voxel in cluster, SPL = superior parietal lobule.

were found in a dorsal region of the left SPL (BA 7), stretching medially into the precuneus (interaction $p = 0.01$). Conflict resolution processes specific to response-based Simon conflict (shown in green), on the other hand, were evident in bilateral ventral premotor cortex, with a larger cluster in the caudal aspect of the right lateral precentral gyrus (BAs 4, 43) (right PCG, interaction $p = 0.001$), and a smaller cluster in the rostral aspect (BA 6) of the left lateral precentral gyrus (left PCG, interaction $p = 0.005$) (see Fig. 3 and Table 2). To summarize, processes associated with the resolution of stimulus-based Stroop conflict were characterized by the recruitment of superior parietal cortex, whereas processes associated with the resolution of response-based Simon conflict were characterized by recruitment of ventral premotor cortex.

However, one concern with these analyses is that the differential brain activities between the two conflict types could in theory reflect different degrees of conflict resolution between the Stroop and Simon conflicts, rather than different types of processes. In order to control for this possibility, we compared behavioral effects corresponding to the contrasts we employed for the imaging analyses, contrasting performance on II and CI trials (i.e., the degree of 'speed-up' due to cognitive control) between stimulus dimensions (Stroop versus Simon). The mean Stroop
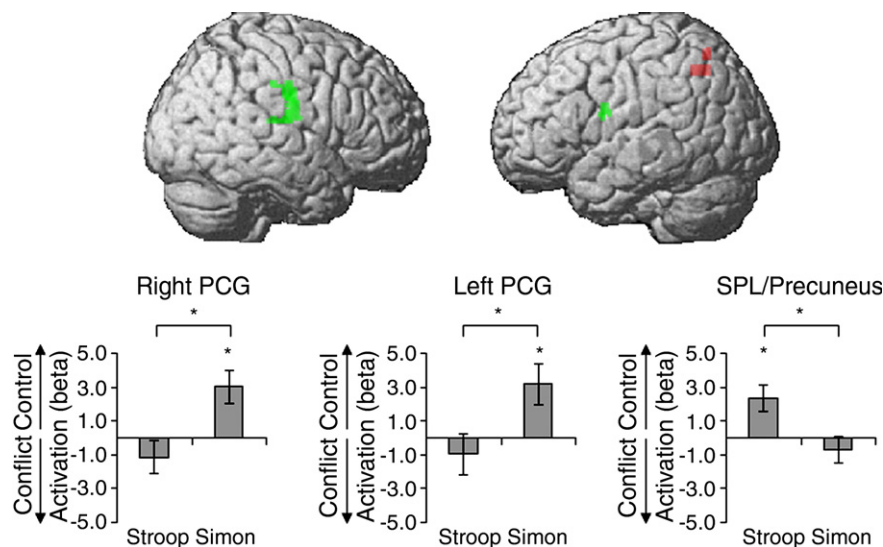

Fig. 3. Regions involved in resolving stimulus-based versus response-based conflict. Top panels: regions displaying activation specific to Stroop control processes are displayed in red (SPL = superior parietal lobule), and regions displaying activation specific to Simon control processes are displayed in green (PCG = precentral gyrus). Statistical maps (thresholded at voxelwise $p < 0.005$ [uncorrected], and a cluster extent of >10 voxels) are shown rendered onto lateral surfaces of a normalized single-subject brain. Bottom panels: the bar graphs display mean cluster activation estimates (beta values ± SEM) of Stroop control (Stroop control > Stroop conflict) and Simon control (Simon control > Simon conflict). Asterisks (*) indicate significant effects ($p < 0.05$).

speed-up was 12.3 ms (SD=28), while the mean Simon speed-up was 19.5 ms (SD=15). Importantly, there were no significant differences in the degree of speed-up between the dimensions ($T_{(12)}$=0.7, p>0.45), thus discounting an explanation of the imaging data in terms of differences in conflict resolution.

Finally, we also tested in an unconstrained search whether there were regions of overlapping control (or conflict) effects between the two tasks, by conducting conjunction analyses (at uncorrected p<0.005, extent>10 voxels). There were no shared regions detected at this threshold.

Discussion

Cognitive control mechanisms are thought to resolve conflict in information processing in two principal ways, by biasing the processing of stimulus features, and by biasing response processes (Nieuwenhuis and Yeung, 2005). Our behavioral results document that these conflict resolution mechanisms appear to be recruited and implemented in a conflict-specific manner, and do not rely on a single central resource: stimulus-based (Stroop) conflict on the previous trial resulted in superior resolution of stimulus-based conflict on the current trial, but did not affect the resolution of response-based (Simon) conflict. Conversely, response-based conflict on the previous trial resulted in superior resolution of response-based conflict on the current trial, but did not affect the resolution of stimulus-based conflict (see also Wendt et al., 2006). These findings suggest that cognitive control mechanisms flexibly adapt to different types of conflict by modulating information processing in ways that specifically address the source of conflict, and that the resources underlying these control processes are independent of each other.

The factorial nature of our design furthermore allowed us to directly assess differential neural activation involved in resolving stimulus- versus response-related conflict, which had not been possible in previous studies (Peterson et al., 2002; Fan et al., 2003; Liu et al., 2004). The results from this analysis supported the assumption that the independence of control mechanisms observed in the behavioral data may stem from the fact that they reflect distinct stimulus-biasing and response-biasing strategies: control-related activations specific to the resolution of stimulus-based Stroop conflict were found in superior parietal cortex, while control-related activations specific to the resolution of response-based Simon conflict were found in ventral premotor cortex.

Stimulus biasing

The prevalent theoretical account of Stroop task performance suggests that the resolution of such stimulus-based conflict is achieved through excitatory biasing of task-relevant stimulus feature processing (Cohen et al., 1990; Botvinick et al., 2001). In other words, Stroop conflict is thought to be resolved by a stimulus-biasing strategy, where processing of the task-relevant stimulus information is amplified relative to the processing of task-irrelevant features, and this proposal has recently received empirical support from neuroimaging data (Egner and Hirsch, 2005a). The current finding that task-specific control processes in the resolution of Stroop conflict were associated with activity in superior parietal cortex corresponds well with how top-down selective attention mechanisms are thought to bias visual stimulus processing to favor task-relevant stimulus information: the top-down signals initiating selective stimulus feature biasing are

thought to originate in parietal cortex (Desimone and Duncan, 1995; Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Yantis and Serences, 2003), which in turn takes its input from prefrontal regions. The superior parietal cortex in particular has been shown to mediate the attentional top-down influence of prefrontal regions on the processing of task-relevant stimulus features in extrastriate cortex, as shown in fMRI studies of effective connectivity (Buchel and Friston, 1997; Friston and Buchel, 2000). Finally, in extrastriate neurons, the biasing of responses to specific stimulus features has been shown to be mediated by a selective gain mechanism, which enhances firing rates in neurons that preferentially respond to the attended feature (Treue and Martinez Trujillo, 1999; Maunsell and Treue, 2006).

Response biasing

Resolution of response-based conflict in the Simon task is thought to be mediated through top-down inhibition or 'suppression' of the output of direct route processing on response activation, thus reducing the influence of the task-irrelevant stimulus location on response selection (Stoffels, 1996; Praamstra et al., 1999; Sturmer et al., 2002; Sturmer and Leuthold, 2003). At the neural level, the contention that spatial stimulus location 'automatically' activates the ipsilateral motor cortex has been supported by electroencephalographic (EEG) data in humans (Eimer, 1995; De Jong et al., 1994), as well as by single neuron recordings in monkeys (Zhang et al., 1997; Riehle et al., 1997). Furthermore, measuring lateralized readiness potentials (LRPs) of the EEG in the Simon task, Sturmer and colleagues (2002) found that motor preparation of the (incorrect) response that corresponded to the spatial stimulus position was present following compatible trials, but suppressed following incompatible trials. This strategic suppression of direct route activation is not observable in the stimulus processing stream prior to motor regions (Sturmer and Leuthold, 2003), and appears to be mediated by premotor cortex: Praamstra and associates (1999) have shown that this effect can be removed through repetitive transcranial magnetic stimulation (rTMS) of the dorsal premotor cortex before stimulus presentation.

The modulation of activity in premotor cortex in the resolution of Simon conflict in the current study directly corroborates the proposal that adaptation to response-based conflict is implemented by response biasing. While previously the dorsal premotor cortex has been implicated in the inhibition of direct route activation (Praamstra et al., 1999), the loci activated in the current study are situated in a region of the lateral precentral gyrus corresponding to the ventral premotor cortex (Picard and Strick, 2001). Interestingly, the function of this ventral premotor area in monkeys has been described to consist of the generating movements *towards* visual object locations (Rizzolatti et al., 1998). It is therefore tempting to speculate that 'direct response activation' from external stimuli may be suppressed by modulating activity in these regions, thus possibly inhibiting a natural propensity to react towards the source of visual stimulation (Simon, 1969).

It is important to emphasize that the type of inhibitory process suggested to affect response selection in the Simon task is different from a more common notion of 'response inhibition': the latter deals with directly suppressing an already initiated erroneous motor output, for instance in the stop-signal paradigm (for an in-depth discussion, see Burle et al., 2004), while the former relates to inhibiting the influence of a particular source of stimulation on

response activation (e.g., Sturmer et al., 2002). In fact, in the current context, where superior conflict resolution is characterized by faster accurate responses to incompatible trials, it is difficult to envisage how such a control process *could* be mediated by 'response inhibition'. This is because by the time it is possible to intentionally inhibit the incorrect response, the correct response has to already be known to the system. While a lateral (or feed-forward) inhibition of the incorrect response in parallel with the execution of the correct response may aid to reduce the likelihood of making an accidental error, it should not result in speeding up the execution of the correct response. Therefore, conflict adaptation effects in the Simon task must be mediated by a response-biasing process that suppresses the direct route of response activation, rather than inhibiting an initially selected but erroneous response.

Compatibility sequence effects

The above interpretation of the behavioral and neuroimaging results depends on the assumption that compatibility sequence effects in the Stroop and Simon tasks reflect the workings of a conflict-monitoring cognitive control loop. However, alternative accounts for this effect have been advanced (Mayr et al., 2003; Hommel et al., 2004). One potential confound concerns repetition priming effects (Mayr et al., 2003), but we precluded this confound by not including any direct stimulus repetitions in our task. Another interpretation of compatibility sequence effects, which can be applied to our data, is that it may stem not from conflict-triggered control processes but rather from episodic memory effects of stimulus–response associations, which could facilitate processing of successive stimuli of equal compatibility (e.g., two successive incompatible trials) (Hommel et al., 2004; Nieuwenhuis et al., 2006; Wendt et al., 2006). However, for both stimulus-based and response-based conflict paradigms, it has been demonstrated that sequential effects persist even when controlling for these confounds (Gratton et al., 1992; Egner and Hirsch, 2005a; Ullsperger et al., 2005; Wuhr, 2005; Wuhr and Ansorge, 2005; Notebaert et al., 2006; see also Kerns, 2006). Furthermore, with respect to the current data, it is difficult to envisage how a single mechanism (the episodic encoding of each stimulus–response association) could explain the fact that Simon and Stroop sequence effects did not correlate with each other within subjects. The assumption that two independent sources of conflict are resolved by separate, conflict-specific control systems can easily account for these data.

In conclusion, our data suggest that cognitive control mechanisms address the occurrence of conflict in information processing in a conflict-specific fashion. If conflict is caused by incompatibility between task-relevant and task-irrelevant stimulus features, it is resolved through biasing stimulus feature representations towards preferential processing of the task-relevant stimulus characteristics. If conflict is caused by incompatibility between an irrelevant stimulus feature and a response feature, it is resolved through biasing response processes, presumably by inhibiting the influence of the task-irrelevant stimulus feature on motor-planning and execution. Importantly, these processes are carried out in parallel and independently, without affecting each other. Our data therefore suggest that the neural architecture of these cognitive control mechanisms is modular, that is, stimulus-bias and response-bias conflict resolution strategies do not appear to rely on a unitary central resource. In line with this, a recent study suggests that even the nature of incompatible stimulus information (in this case,

emotional distracter information) can lead to the recruitment of an alternative regulatory circuitry for conflict resolution (Etkin et al., 2006). The current study further supports the proposal that there exist various independent pools of high-level cognitive control resources, which are employed in a context-sensitive manner (see also Navon and Gopher, 1979; Kim et al., 2005).

Acknowledgments

References

Acosta, E., Simon, J.R., 1976. The effect of irrelevant information on the stages of processing. J. Mot. Behav. 8, 181–187.

Botvinick, M., Nystrom, L.E., Fissell, K., Carter, C.S., Cohen, J.D., 1999. Conflict monitoring versus selection-for-action in anterior cingulate cortex. Nature 402, 179–181.

Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. Psychol. Rev. 108, 624–652.

Buchel, C., Friston, K.J., 1997. Modulation of connectivity in visual pathways by attention: cortical interactions evaluated with structural equation modelling and fMRI. Cereb. Cortex 7, 768–778.

Burle, B., Vidal, F., Tandonnet, C., Hasbroucq, T., 2004. Physiological evidence for response inhibition in choice reaction time tasks. Brain Cogn. 56, 153–164.

Cohen, J.D., Dunbar, K., McClelland, J.L., 1990. On the control of automatic processes: a parallel distributed processing account of the Stroop effect. Psychol. Rev. 97, 332–361.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3, 201–215.

De Houwer, J., 2003. On the role of stimulus–response and stimulus–stimulus compatibility in the Stroop effect. Mem. Cognit. 31, 353–359.

De Jong, R., Liang, C.C., Lauber, E., 1994. Conditional and unconditional automaticity: a dual-process model of effects of spatial stimulus–response correspondence. J. Exp. Psychol. Hum. Percept. Perform. 20, 731–750.

Desimone, R., Duncan, J., 1995. Neural mechanisms of selective visual attention. Annu. Rev. Neurosci. 18, 193–222.

Egner, T., Hirsch, J., 2005a. Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. Nat. Neurosci. 8, 1784–1790.

Egner, T., Hirsch, J., 2005b. The neural correlates and functional integration of cognitive control in a Stroop task. Neuroimage 24, 539–547.

Egner, T., Hirsch, J., 2005c. Where memory meets attention: neural substrates of negative priming. J. Cogn. Neurosci. 17, 1774–1784.

Eimer, M., 1995. Stimulus–response compatibility and automatic response activation: evidence from psychophysiological studies. J. Exp. Psychol. Hum. Percept. Perform. 21, 837–854.

Etkin, A., Egner, T., Peraza, D.M., Kandel, E.R., Hirsch, J., 2006. Resolving emotional conflict: a role for the rostral cingulated cortex in modulating activity in the amygdala. Neuron 51, 871–882.

Fan, J., Flombaum, J.I., McCandliss, B.D., Thomas, K.M., Posner, M.I., 2003. Cognitive and brain consequences of conflict. NeuroImage 18, 42–57.

Fox, E., 1995. Negative priming from ignored distractors in visual selection: a review. Psychon. Bull. Rev. 2, 145–173.

Friston, K.J., Buchel, C., 2000. Attentional modulation of effective connectivity from V2 to V5/MT in humans. Proc. Natl. Acad. Sci. U. S. A. 97, 7591–7596.

Gratton, G., Coles, M.G., Donchin, E., 1992. Optimizing the use of information: strategic control of activation of responses. J. Exp. Psychol. Gen. 121, 480–506.

Hommel, B., 1993. The relationship between stimulus processing and response selection in the Simon task: evidence for a temporal overlap. Psychol. Res. 55, 280–290.

Hommel, B., 1997. Interactions between stimulus–stimulus congruence and stimulus–response compatibility. Psychol. Res. 59, 248–260.

Hommel, B., Proctor, R.W., Vu, K.P., 2004. A feature-integration account of sequential effects in the Simon task. Psychol. Res. 68, 1–17.

Kastner, S., Ungerleider, L.G., 2000. Mechanisms of visual attention in the human cortex. Annu. Rev. Neurosci. 23, 315–341.

Kerns, J.G., 2006. Anterior cingulate and prefrontal cortex activity in an fMRI study of trial-to-trial adjustments on the Simon task. NeuroImage, doi:10.1016/j.neuroimage.2006.06.012.

Kerns, J.G., Cohen, J.D., MacDonald III, A.W., Cho, R.Y., Stenger, V.A., Carter, C.S., 2004. Anterior cingulate conflict monitoring and adjustments in control. Science 303, 1023–1026.

Kim, S.Y., Kim, M.S., Chun, M.M., 2005. Concurrent working memory load can reduce distraction. Proc. Natl. Acad. Sci. U. S. A. 102, 16524–16529.

Kornblum, S., 1994. The way irrelevant dimensions are processed depends on what they overlap with: the case of Stroop- and Simon-like stimuli. Psychol. Res. 56, 130–135.

Kornblum, S., Lee, J.W., 1995. Stimulus–response compatibility with relevant and irrelevant stimulus dimensions that do and do not overlap with the response. J. Exp. Psychol. Hum. Percept. Perform. 21, 855–875.

Kornblum, S., Hasbroucq, T., Osman, A., 1990. Dimensional overlap: cognitive basis for stimulus–response compatibility—A model and taxonomy. Psychol. Rev. 97, 253–270.

Liu, X., Banich, M.T., Jacobson, B.L., Tanabe, J.L., 2004. Common and distinct neural substrates of attentional control in an integrated Simon and spatial Stroop task as assessed by event-related fMRI. NeuroImage 22, 1097–1106.

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, 174–207.

MacLeod, C.M., 1991. Half a century of research on the Stroop effect: an integrative review. Psychol. Bull. 109, 163–203.

MacLeod, C.M., Dunbar, K., 1988. Training and Stroop-like interference: evidence for a continuum of automaticity. J. Exp. Psychol. Learn. Mem. Cogn. 14, 126–135.

Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H., 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. NeuroImage 19, 1233–1239.

Maunsell, J.H., Treue, S., 2006. Feature-based attention in visual cortex. Trends Neurosci. 29, 317–322.

May, C.P., Kane, M.J., Hasher, L., 1995. Determinants of negative priming. Psychol. Bull. 118, 35–54.

Mayr, U., Awh, E., Laurey, P., 2003. Conflict adaptation effects in the absence of executive control. Nat. Neurosci. 6, 450–452.

Milham, M.P., Banich, M.T., Webb, A., Barad, V., Cohen, N.J., Wszalek, T., Kramer, A.F., 2001. The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. Brain Res. Cogn. Brain Res. 12, 467–473.

Navon, D., Gopher, D., 1979. On the economy of the human information processing system. Psychol. Rev. 86, 214–255.

Neill, W.T., Valdes, L.A., 1992. Persistence of negative priming: steady state or decay? J. Exp. Psychol. Learn. Mem. Cogn. 18, 565–576.

Nieuwenhuis, S., Yeung, N., 2005. Neural mechanisms of attention and control: losing our inhibitions? Nat. Neurosci. 8, 1631–1633.

Nieuwenhuis, S., Stins, J.F., Posthuma, D., Polderman, T.J.C., Boomsma, D. M., de Geus, E.J., 2006. Conflict adaptation or associative priming? Mem. Cognit. 34, 1260–1272.

Notebaert, W., Gevers, W., Verbruggen, F., Liefooghe, B., 2006. Top-down and bottom-up sequential modulations of congruency effects. Psychon. Bull. Rev. 13, 112–117.

Peterson, B.S., Kane, M.J., Alexander, G.M., Lacadie, C., Skudlarski, P., Leung, H.C., May, J., Gore, J.C., 2002. An event-related functional MRI study comparing interference effects in the Simon and Stroop tasks. Brain Res. Cogn. Brain Res. 13, 427–440.

Picard, N., Strick, P.L., 2001. Imaging the premotor areas. Curr. Opin. Neurobiol. 11, 663–672.

Praamstra, P., Kleine, B.U., Schnitzler, A., 1999. Magnetic stimulation of the dorsal premotor cortex modulates the Simon effect. NeuroReport 10, 3671–3674.

Ridderinkhof, K.R., 2002. Activation and suppression in conflict tasks: empirical classification through distributional analyses. In: Prinz, W., Hommel, B. (Eds.), Common Mechanisms in Perception and Action. Oxford University Press, Oxford, pp. 494–519.

Riehle, A., Kornblum, S., Requin, J., 1997. Neuronal correlates of sensorimotor association in stimulus–response compatibility. J. Exp. Psychol. Hum. Percept. Perform. 23, 1708–1726.

Rizzolatti, G., Luppino, G., Matelli, M., 1998. The organization of the cortical motor system: new concepts. Electroencephalogr. Clin. Neurophysiol. 106, 283–296.

Simon, J.R., 1969. Reactions toward the source of stimulation. J. Exp. Psychol. 81, 174–176.

Simon, J.R., 1982. Effect of any auditory stimulus on the processing of a visual stimulus single- and dual-tasks conditions. Acta Psychol. 51, 61–73.

Simon, J.R., Berbaum, K., 1990. Effect of conflicting cues on information processing: the 'Stroop effect' vs. the 'Simon effect'. Acta Psychol. 73, 159–170.

Stoffels, E.J., 1996. On stage robustness and response selection: further evidence. Acta Psychol. 91, 67–88.

Stroop, J.R., 1935. Studies of interference in serial verbal reactions. J. Exp. Psychol. 18, 643–662.

Sturmer, B., Leuthold, H., 2003. Control over response priming in visuomotor processing: a lateralized event-related potential study. Exp. Brain Res. 153, 35–44.

Sturmer, B., Leuthold, H., Soetens, E., Schroter, H., Sommer, W., 2002. Control over location-based response activation in the Simon task: behavioral and electrophysiological evidence. J. Exp. Psychol. Hum. Percept. Perform. 28, 1345–1363.

Treue, S., Martinez Trujillo, J.C., 1999. Feature-based attention influences motion processing gain in macaque visual cortex. Nature 399, 575–579.

Ullsperger, M., Bylsma, L.M., Botvinick, M.M., 2005. The conflict adaptation effect: it's not just priming. Cogn. Affect. Behav. Neurosci. 5, 467–472.

van Veen, V., Carter, C.S., 2005. Separating semantic conflict and response conflict in the Stroop task: a functional MRI study. NeuroImage 27, 497–504.

Wendt, M., Kluwe, R.H., Peters, A., 2006. Sequential modulation of interference evoked by processing task-irrelevant stimulus features. J. Exp. Psychol. Hum. Percept. Perform. 32, 644–667.

Wuhr, P., 2005. Evidence for gating of direct response activation in the Simon task. Psychon. Bull. Rev. 12, 282–288.

Wuhr, P., Ansorge, U., 2005. Exploring trial-by-trial modulations of the Simon effect. Q. J. Exp. Psychol. A 58, 705–731.

Yantis, S., Serences, J.T., 2003. Cortical mechanisms of space-based and object-based attentional control. Curr. Opin. Neurobiol. 13, 187–193.

Zhang, J., Riehle, A., Requin, J., Kornblum, S., 1997. Dynamics of single neuron activity in monkey primary motor cortex related to sensorimotor transformation. J. Neurosci. 17, 2227–2246.

Zhang, H.H., Zhang, J., Kornblum, S., 1999. A parallel distributed processing model of stimulus–stimulus and stimulus–response compatibility. Cogn. Psychol. 38, 386–432.