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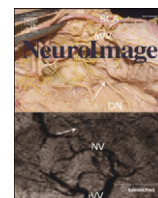
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The neural mechanisms of semantic and response conflicts: An fMRI study of practice-related effects in the Stroop task

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ABSTRACT

Previous studies have demonstrated that there are separate neural mechanisms underlying semantic and response conflicts in the Stroop task. However, the practice effects of these conflicts need to be elucidated and the possible involvements of common neural mechanisms are yet to be established. We employed functional magnetic resonance imaging (fMRI) in a 4–2 mapping practice-related Stroop task to determine the neural substrates under these conflicts. Results showed that different patterns of brain activations are associated with practice in the attentional networks (e.g., dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC), and posterior parietal cortex (PPC)) for both conflicts, response control regions (e.g., inferior frontal junction (IFJ), inferior frontal gyrus (IFG)/insula, and pre-supplementary motor areas (pre-SMA)) for semantic conflict, and posterior cortex for response conflict. We also found areas of common activation in the left hemisphere within the attentional networks, for the early practice stage in semantic conflict and the late stage in “pure” response conflict using conjunction analysis. The different practice effects indicate that there are distinct mechanisms underlying these two conflict types: semantic conflict practice effects are attributable to the automation of stimulus processing, conflict and response control; response conflict practice effects are attributable to the proportional increase of conflict-related cognitive resources. In addition, the areas of common activation suggest that the semantic conflict effect may contain a partial response conflict effect, particularly at the beginning of the task. These findings indicate that there are two kinds of response conflicts contained in the key-pressing Stroop task: the vocal-level (mainly in the early stage) and key-pressing (mainly in the late stage) response conflicts; thus, the use of the subtraction method for the exploration of semantic and response conflicts may need to be further examined.

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Introduction

Conflict control tasks such as the Stroop, Flanker and Simon tasks have long been used to research human cognitive control functions (Eriksen and Eriksen, 1974; Simon and Small, 1969; Stroop, 1935). Cognitive control is a key process of flexible behavior. It helps us move toward our goals, especially in conflict situations, through the setting and maintaining of goals, the inhibition of inappropriate responses, and/or the amplification of target-relevant responses during behavioral execution (Aron, 2007; Egner and Hirsch, 2005; Miller, 2000; Ridderinkhof et al., 2004b).

The brain regions most frequently associated with cognitive control are the top-down frontal cortex networks, including the dorsolateral prefrontal cortex (DLPFC), and anterior cingulate cortex (ACC), and the response organization regions, including the posterior parietal cortex

(PPC), supplementary motor areas (SMA), and pre-supplementary motor areas (pre-SMA) (Aron, 2011; Banich et al., 2000; Wang et al., 2010). The DLPFC is an integrative system; it receives and represents information from other cortical structures and initiates top-down biases based on task demands (Brass et al., 2005a,b; Mansouri et al., 2009; Miller and Cohen, 2001). The ACC is responsible for conflict monitoring, and emotion- or motivation-related cognitive control operations (Botvinick et al., 2001, 2004; Carter and van Veen, 2007; Ridderinkhof et al., 2004a). The PPC modulates attentional orientation to task-relevant information and prepares the stimulus–response (S–R) mapping (Coulthard et al., 2008; Scherberger and Andersen, 2007). The SMA and pre-SMA are considered to play a role in the selection and execution of responses (Lau et al., 2006; Nachev et al., 2008; Rushworth et al., 2007).

Experiments that focus on the practice-related effects of the Stroop task are important for elucidating the mechanisms of the Stroop task and cognitive control (MacLeod, 1991). In the Stroop task, inked color words are presented to subjects, who are instructed to respond to the color of word while ignore its meaning. Regardless of whether the word and color are congruent (e.g. “red” in red) or

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incongruent (e.g., “red” in green), the word reading tends to be automatically processed with higher priority over the color naming, which is also the task-relevant task. The transferring from the early stage of practice to the late stage of practice in the Stroop task is associated with the reduction of this discrepancy through the reinforcement of color naming pathways and changes in brain activity (Cohen et al., 1990; Davidson et al., 2003; Polk et al., 2008), which may involve quantitative functional change, qualitative reorganization, or even the reorganization of cognitive control brain networks (Jonides, 2004; Kelly and Garavan, 2005; Schumacher et al., 2005). Thus, examining the practice effects can help us to understand the role of specific brain areas in a dynamic way.

Erickson and colleagues studied the practice effects associated with cognitive control using the Stroop task. They found a dramatic decrease in ACC activity and an increase in DLPFC activation when the first half of the trials were compared with the second half of trials (Erickson et al., 2004; Milham et al., 2002). However, employment of traditional Stroop paradigm prevented them from separating semantic and response conflicts during the practice of the task. Thus, they were unable to determine whether the changes in brain activity were caused by the practice effects for semantic or response conflict, or both. In addition, their experiment was comprised of only 162 trials, markedly fewer trials than those used in other studies, which often consist of hundreds or thousands of practice trials (Dulany and Rogers, 1994; Macleod, 1998). Erickson and colleagues did not observe practice effects at the behavioral level, which further suggests that the amount of practice was limited. As a result, the respective practice effects of semantic and response conflicts remain unclear.

In this study, we attempted to clarify this issue using different types of conflict and practice design. De Houwer (2003) was the first to identify the distinctions between semantic and response conflicts using the Stroop task. This was discovered via the logic of subtraction. The Stroop task comprises congruent (CO) stimuli (e.g., the word “red” in red), semantic incongruent (SI) stimuli, and response incongruent (RI) stimuli. Therefore, if red and yellow are mapped to the left hand, and blue and green are mapped to the right hand, the word “red” in yellow color (SI) is likely to provoke semantic conflict (of word reading and color naming), but responses are congruent; and the word “red” in blue color (RI) has both a semantic conflict and a conflict in response selection. Hence, SI-CO can produce a semantic conflict and RI-SI can prompt a response conflict (van Veen and Carter, 2005).

Previous research has successfully distinguished response conflict from semantic conflict. For instance, Kim et al. (2010) and van Veen and Carter (2005) revealed the parallel attentional control mechanisms underlying semantic and response conflicts using the Stroop task (Kim et al., 2010; van Veen and Carter, 2005). Likewise, Banich and colleagues were able to separate the response conflict by subtracting the effects of response-ineligible incongruent trials (e.g., the word “brown” in blue color, when red, blue are the set of potential responses) from the response-eligible incongruent trials (e.g., the word “red” in blue color, when red, blue are the set of potential responses). The semantic conflict was distinguished by contrasting the response-ineligible incongruent trials with the neutral trials (Liu et al., 2006; Milham et al., 2001, 2003a).

However, the study by van Veen and Carter (2005) revealed no overlap in activation between semantic and response conflicts using conjunction analysis. This appears to go against evidence from electrophysiological studies, which showed common activation in terms of N2 and N450 event-related potential (ERP) components (they are associated with the ACC activation in conflict detection) for both response and non-response conflict conditions (Wendt et al., 2007; West et al., 2004). Furthermore, Liu et al. (2004) found that the stimulus–stimulus conflict Stroop effects and stimulus–response conflict Simon effects had some common brain sources; both of them

implicated the DLPFC top-down modulation of the posterior cortex (Liu et al., 2004). This indicates that semantic and response conflict types may both correlate with the common mechanisms underlying conflict monitoring and top-down conflict resolution processes.

In order to explore the common neural basis of semantic and response conflicts, we employed a novel strategy for the conjunction analysis. Since the stimulus–response mapping in the manual Stroop task (color to key-pressing) is usually weaker than that in the oral Stroop task (color to vocal response), the semantic conflict in our manual Stroop task may also include some components of the vocal-level response conflict (Gordon and Deborah, 1977; Repovš, 2004). We speculated that the effect of the early practice stage SI-CO would be eliminated after practice. Because the practice would reduce the vocal-level response conflict in SI stimuli due to the increased connection between key-pressing and color naming (S–R mapping) during the practice, which would also make the effects of RI-SI be “purer” in the late practice stage. Therefore, instead of directly testing the overlap in activation between these conflicts within the same practice stage, we examined the overlap between the early stage SI-CO condition and the late stage “pure” RI-SI condition to see whether the semantic conflict effect contained response conflict components or not.

Based on previous research investigating practice effects and attentional control, we anticipated that brain activity associated with semantic and response interference may appear as distinct distributions, and that many of the active areas will primarily belong to the attentional networks (e.g., the DLPFC, ACC and PCC) (Adleman et al., 2002; Kim et al., 2010; van Veen and Carter, 2005). The findings of Erickson et al. (2004) expressed a rapid decline in ACC activity and increased DLPFC activity in the incongruent condition after practice. According to the subtraction logic, the RI stimuli will prompt both semantic and response conflicts at the same time; the practice-related changes of RI stimuli might be caused by both the semantic and response conflict effects. Thus, in the current study, we anticipated that the SI-CO and/or RI-SI would be associated with a decrease in ACC activity and an increase in DLPFC activity after practice. In addition, based on our previous behavioral study (Chen et al., 2010), we expected that the practice effects of semantic conflict might be responsible for the decrease of activity in these areas, while the practice effects of response conflict might be responsible for the increase.

In summary, the present study was an attempt to address above unresolved issues related to cognitive control and examine the subtraction logic of the separateness for semantic and response conflicts, through the exploration of the respective practice effects and the common neural mechanisms of these two conflicts.

Materials and methods

Subjects

Twenty five right-handed college students, were recruited for the study with a compensation (15 females; $M = 21$, $SD = 1.67$). All participations had normal or corrected-to-normal vision, without achromatopsia or color weakness. The fMRI data of two subjects was excluded due to excessive head movement artifacts. This study was approved by the University Human Ethics Committee for the Brain Mapping Research, and written consent was obtained from each subject before scanning.

Stimuli

A 4–2 Stroop paradigm was employed using four Chinese characters “Hong” (red), “Huang” (yellow), “Lan” (blue) and “Lv” (green). Each character was presented in one of the four colors (i.e., red, yellow, blue and green; 16 stimuli altogether). Subjects were asked to respond according to the color of the characters; the red and yellow

colors were mapped onto the thumb of the left hand, while the blue and green colors were mapped onto the thumb of the right hand. There were three types of stimuli: the congruent stimuli (CO, e.g., “Hong” printed in red), the semantically incongruent stimuli (SI, e.g., “Hong” in yellow) and the response incongruent stimuli (RI, e.g., “Hong” in blue).

Design

Our experiment comprised 12 blocks; the first two and the last two blocks were performed inside the scanner. The first two blocks represented the early stage and the last two represented the late stage. The other eight blocks were completed outside the scanner and represented the practice stage. Each block consisted of 24 CO trials, 18 SI trials and 18 RI trials, (720 trials in total), which were presented in a pseudo-random order. Besides, there were only eight practice trials before the experiment in order to make our practice effects more pure.

Procedure

Stimuli were presented on a black background. Each trial started with a white fixation for 500 ms. After the characters had been displayed for 300 ms, there was a grey fixation for 1200 ms, which was the response period, followed by an additional 12,000 ms grey fixation, which acted as the inter-trial interval (ITI). The extended time period between the Stroop stimuli allowed us to rule out the possibility of any carryover effects from previous trials to current trials (e.g., the Gratton effect, Gratton et al., 1992), and allowed time for the BOLD signal to return to baseline, to achieve purer conflict effects and practice effects. According to Bandettini and Cox (2000), the slow event-related design can promote the detection ability of the BOLD signal, and reduce the signal interference between trials (Bandettini and Cox, 2000).

Image acquisition and analysis

Images were acquired with a Siemens 3 T scanner (Siemens Magnetom Trio TIM, Erlangen, Germany). An echo-planar imaging (EPI) sequence was used for data collection, and 432 T2*-weighted images were recorded per run (TR=2000 ms; TE=30 ms; flip angle = 90°; FoV = 220 × 220 mm²; matrix size = 64 × 64; 32 interleaved 3 mm-thick slices; in-plane resolution = 3.4 × 3.4 mm²; interslice skip = 0.99 mm). T1-weighted images were recorded with a total of 176 slices at a thickness of 1 mm and in-plane resolution of 0.98 × 0.98 mm² (TR=1900 ms; TE=2.52 ms; flip angle = 9°; FoV = 250 × 250 mm²).

We used SPM8 (Wellcome Department of Cognitive Neurology, London, UK, <http://www.fil.ion.ucl.ac.uk/spm/spm8>) to pre-process the functional images (Friston et al., 1994). Slice timing was used to correct slice order, the data was realigned to estimate and modify the six parameters of head movement, and first six images were discarded to achieve magnet-steady images. These images were then normalized to MNI space in 3 × 3 × 3 mm³ voxel sizes. The normalized data were spatially smoothed with a Gaussian kernel; the full width at half maximum (FWHM) was specified as 8 × 8 × 8 mm³.

After pre-processing, the four regressors from each run (i.e., congruent, stimulus incongruent, response incongruent and error) were modeled to create the design matrix, and for each subject all the four runs were modeled in one general linear model (GLM). They were convolved with the canonical hemodynamic response function, and the six realignment parameters for each subject were also included as confounding factors. The contrasts of interest were RI vs. CO, reflecting the traditional Stroop effects; SI vs. CO, reflecting the semantic conflict; and RI vs. SI, reflecting the response conflict. These contrasts were generated for both the early and late stages for group level analysis. In the second-level model specification, we defined 2 × 2 conditions in the

practice stage (early and late) and conflict type (SI-CO and RI-SI) factors; thus, there were four cells in our design (i.e., (SI-CO)_{early}, (SI-CO)_{late}, (RI-SI)_{early} and (RI-SI)_{late}). The practice effects were defined as the two sample paired *t*-test between (SI-CO)_{late} and (SI-CO)_{early} for the semantic conflict and the two sample paired *t*-test between (RI-SI)_{late} and (RI-SI)_{early} for the response conflict. Additionally, the contrasts of each conflict type were combined across the early and late stages in order to define regions of interest (ROIs). The practice stage × conflict type interaction was used to represent differential changes in activity between the early and late stages for each conflict type. The MNI coordinates of activation were transformed into Talairach space (Talairach and Tournoux, 1988) using the Brett transform (Brett et al., 2001).

The conjunction analysis for the (SI-CO)_{early} condition and the (RI-SI)_{late} condition was performed based on the conjunction null hypothesis (Friston et al., 2005; Nichols et al., 2005). The contrast images of each subject for the (SI-CO)_{early} and (RI-SI)_{late} were modeled together in the full factorial design matrix and obtained with the conjunction null option.

The significance level of the image threshold for fMRI data was first set to $p < 0.005$, uncorrected at the individual voxel level. Then we performed AFNI's AlphaSim program (<http://afni.nimh.nih.gov/pub/dist/doc/manual/AlphaSim.pdf>) for multiple comparison. We ran 1000 Monte Carlo simulations with the correct value $p < 0.005$, Gaussian filter width in 8 mm and Cluster connection radius in 5 mm. The correction at $p < 0.05$ for multiple comparison revealed a clusters size of 70 contiguous voxels. We used this corrected AlphaSim threshold as the significance level for our fMRI data below.

In order to avoid the circular argument, the ROIs were determined according to the overall positive activations of early and late stages under RI-CO, SI-CO, and RI-SI conditions, using MarsBaR software (Brett et al., 2002). These ROIs were masked using automatic anatomical labeling (AAL; Tzourio-Mazoyer et al., 2002) within the DLPFC, dorsomedial frontal cortex (dmFC; including the ACC, SMA and pre-SMA), and PPC to extract the percent signal change of the ROIs for further analysis. Specifically, the ROIs of RI-CO were used to extract the signal of raw stimuli, and the ROIs of SI-CO and of RI-SI were used to extract the signal of SI-CO and RI-SI, respectively.

Results

Behavioral data

Error trials were excluded from all analyses, which left at least 37 trials for congruent (CO) condition and 27 trials for stimulus incongruent (SI) and response incongruent (RI) conditions in each stage. Table 1 shows the mean accuracy rate and response times (RTs) for raw stimuli under CO, SI and RI conditions. There was no significant difference in accuracy rate between the practice stages for each stimulus type, but there were significant differences in RTs between the early and late stages under each stimulus type. Moreover, there were significant differences in RTs and accuracy rate between CO and SI, and SI and RI in the early stage as well as SI and RI in the late stage.

The RTs for the traditional Stroop effect (RI-CO), the semantic conflict (SI-CO) and the response conflict (RI-SI) during each practice stage were summarized in Fig. 1. The main effect of practice stage was significant, ($F[1, 22] = 4.09, p < 0.05$); the main effect of conflict type was marginally significant ($F[1, 22] = 3.06, p < 0.09$) and the interaction between practice stage and conflict type was not significant ($F[1, 22] = 0.67, p > 0.41$). The two-sample paired *t*-test revealed a significant difference between the early and late stages for SI-CO, ($t[22] = 1.99, p < 0.05$), whereas the practice stage effect was not significant for RI-SI, ($t[22] = 1.14, p > 0.25$). These suggested that the RT for SI-CO declined significantly after practice, whereas the degree of interference for RI-SI was relatively stable.

Table 1

The statistics for the response times and the accuracy rates from behavioral performance data by stimulus types and stages.

RT,SD _{RT} (ms) (ACC,SD _{ACC})	CO	SI	RI	SI vs. CO	RI vs. SI
Early	593,119 (95.20%, 4.68%)	621,156 (96.50%, 3.67%)	657,161 (93.00%, 5.97%)	0.02 (0.02)	<0.001 (<0.001)
Late	558,113 (95.47%, 6.43%)	562,122 (96.01%, 5.48%)	588,136 (93.84%, 6.70%)	0.21 (0.23)	<0.001 (<0.001)
Early vs. Late	0.04 (0.40)	0.01 (0.33)	0.004 (0.28)		

Note. The numbers in the parenthesis are the accuracy rates (ACC) and their corresponding SDs and *p*-values.

Functional MRI data

In order to compare our results with the results of Kim et al. (2010) and Van Veen and Carter (2005), we reanalyzed our data to achieve two stages aggregate effects of semantic and response conflict (Fig. S1 in the Supplementary Materials). Results showed that the activations of these two conflicts were mostly separate in the DLPFC and completely separate in the PPC, which were consistent to the results of Kim et al. (2010) and Van Veen and Carter (2005). However, the activation in the ACC was only found under the RI-SI condition but not existed under the SI-CO condition.

The comparison between the late and early stages under SI-CO condition showed that for the late stage, there were significantly decreased activations in the response control areas that included the inferior frontal junction (IFJ), inferior frontal gyrus (IFG)/insula, pre-SMA, subthalamic nucleus (STN), striatum, and cerebellum as well as the posterior cortex areas (parietal, temporal and occipital lobes) (Aron, 2011; Aron et al., 2007) (see Fig. 2a and Table 2). The comparison of the late and early stages under RI-SI condition showed significantly increased activations in the parietal, temporal and occipital lobes, striatum, and cerebellum in the late stage (see Fig. 2b and Table 2). The activation changes in traditional Stroop effects (RI-CO) from the early to the late stages showed that the activations of RI-CO were significantly decreased in the DLPFC after practice (Fig. S2 in the Supplementary Materials).

Fig. 3 shows the percent signal change of the conflict process-related activity in the DLPFC, dMFC and PPC areas from the early to the late stage for each raw stimulus (CO, SI, RI), and conflict condition (SI-CO and RI-SI). There were significant practice effects for each raw stimulus in these areas ($p < 0.05$ – 0.001). In the early stage, there were significant differences in raw stimulus under SI vs. CO condition in these areas ($p < 0.005$ – 0.001), but then these differences were disappeared after practice (p -values > 0.25); however, under the RI vs. SI condition, there was a significant difference only in the DLPFC in the early stage ($p < 0.05$), but in the late stage the differences existed in all of these areas ($p < 0.01$ – 0.005) (see Fig. 3a).

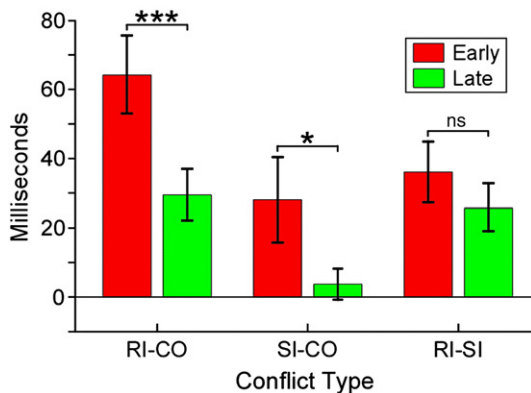


Fig. 1. Mean response times for the early and late practice stages in the RI-CO, SI-CO and RI-SI conditions. NB. Error bars show the mean of standard error (SEM); * represents $p < 0.05$; *** represents $p < 0.001$.

For SI-CO, activity in these regions significantly decreased after practice (paired *t*-test: $t_{\text{DLPFC}}[22] = 2.05$, $p < 0.05$; $t_{\text{dMFC}}[22] = 2.57$, $p < 0.01$; $t_{\text{PPC}}[22] = 2.94$, $p < 0.005$). However, there were significant or marginal significant increases in activity for RI-SI in these areas from the early to the late stage (paired *t*-test: $t_{\text{DLPFC}}[22] = 1.67$, $p < 0.06$; $t_{\text{dMFC}}[22] = 1.79$, $p < 0.05$; $t_{\text{PPC}}[22] = 1.92$, $p < 0.05$). In addition, there was a significant interaction between practice stage and conflict type in these areas ($F_{\text{DLPFC}}[1, 22] = 7.20$, $p < 0.01$; $F_{\text{dMFC}}[1, 22] = 7.68$, $p < 0.01$; $F_{\text{PPC}}[1, 22] = 11.46$, $p < 0.001$) (see Fig. 3b).

For each single stage, the activations of the early and late stages for the SI-CO condition showed that the brain areas activated in the early stage did not stay activated into the late stage of practice (Fig. S3(a) and Table S1 in the Supplementary Materials). For the RI-SI conflict type, the activations in the conflict control networks (e.g., left DLPFC, dMFC, and PPC) increased in the late stage. In addition, more posterior areas were activated in the late stage compared with the early stage (e.g., visual cortex, inferior template gyrus, and cerebellum) (Fig. S3(b) and Table S2 in the Supplementary Materials).

The specific areas of activity associated with the Stage \times Conflict type interaction are displayed in Fig. 4, involving the DLPFC, pre-SMA, ACC, PPC, temporoparietal junction (TPJ), parietal, temporal and occipital lobes, basal ganglia and cerebellum.

The conjunction analysis revealed no overlapping activity between semantic and response conflict within each practice stage, which is in line with the results of van Veen and Carter (2005). However, for (SI-CO)_{early} and (RI-SI)_{late}, a significant conjunction was found in the left hemisphere within the DLPFC, ACC and PPC (see Fig. 5).

Discussion

The behavioral and percent signal change data of raw stimuli showed that in the early stage the RI invoked more response errors than did SI, and the SI invoked more response errors than CO, indicating that in the early stage RI and SI invoked more conflicts than CO. However, after practice the accuracy became similar between CO and SI but lower for RI in comparison to SI and CO. The changes of RTs and of percent signal changes in the attentional networks of these stimuli also showed the similar trend to the changes of accuracy, which indicated that there were more response conflicts in RI than SI and CO in the late stage (van Veen and Carter, 2005). Moreover, the reduced RTs and signal changes of these stimuli in late stage suggested the practice effects, which was further discussed below.

Consistent with the findings of Kim et al. (2010) and Van Veen and Carter (2005), the separate activations in the DLPFC and PPC suggested that there may be two parallel neural substrates under the semantic and response conflicts at the conflict resolution and response levels (Kim et al., 2010; van Veen and Carter, 2005). The disappearance of activation in the ACC under semantic conflict indicated that the ACC is more sensitive to the response conflict than the semantic conflict (Liu et al., 2006; Milham et al., 2001, 2003a,b).

One of the main aims of the present study was to investigate the respective practice effects of semantic conflict and response conflict. The comparison of the late and early stages SI-CO showed that there

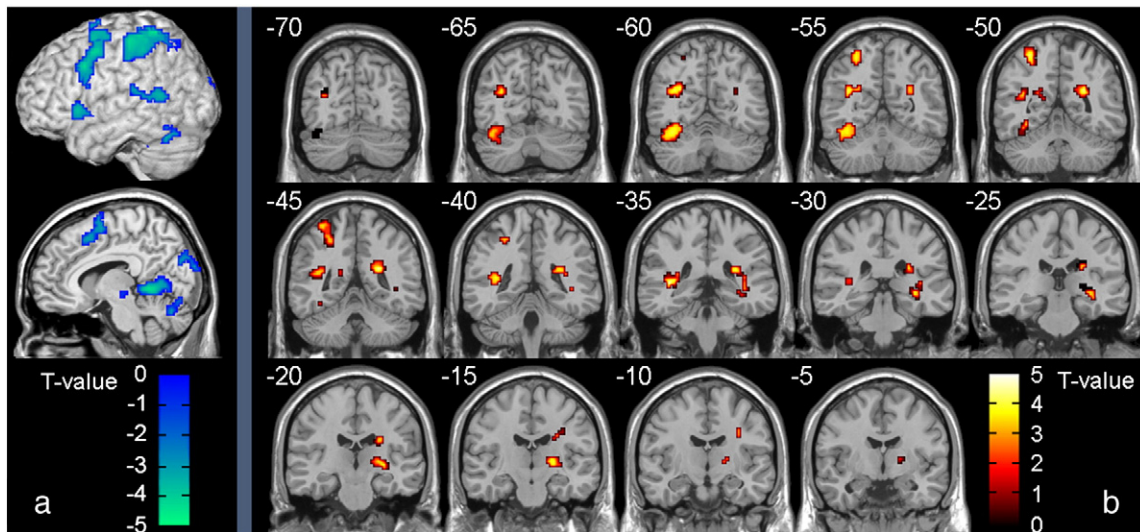


Fig. 2. The comparisons of brain area activations between late and early stages for the SI-CO (a) and RI-SI (b) conditions, $p < 0.05$, corrected.

were more activations in the response control areas in the early stage than the late stage (Aron, 2011; Aron et al., 2007). This finding indicated that the practice effects of semantic conflict might contain the automation of response control, and some response conflict components were included in the early stage semantic conflict. In addition, the comparing of the late and early stages RI-SI showed that there was more activation in the posterior cortex, indicating that the increasing cognitive resources were allocated to the stimulus processing and response output for the response conflict stimuli. These changes might be influenced by the top-down modulation from the frontal lobes (Miller and Cohen, 2001; Wang et al., 2010).

Moreover, the findings of ROI analysis and stage-wise random group effects for SI-CO and RI-SI at the early and late stages revealed differential activation changes of these two conflicts. Specifically, there was a reduced activity within the DLPFC, ACC, PPC and other regions for semantic conflict and an increased activity within these areas for response conflict. Two possible reasons for these practice-related changes are quantitative automation of conflict control and qualitative processing reorganization (Schumacher et al., 2005). In the current experiment, we suggested that practice-related changes took place as a result of automatic processing for SI-CO and proportional reallocation of conflict-related cognitive resources for RI-SI.

For the semantic conflict, along with the disappearance of activity in the ACC, DLPFC and posterior cortex associated with practice, we found a concomitant reduction in behavioral RT. This practice-induced reduction in activation indicates that the processing of semantic conflict had become more effective. According to the functions of the attentional networks in cognitive control (Fan et al., 2002, 2005; Posner and Petersen, 1990; Raz and Buhle, 2006), the automation of semantic conflict is reflected by fewer resources needed for alerting, detecting and the executive control of semantic incongruent stimuli at the late stage of practice. The disappearance of the activation in the posterior cortex might stem from a reduction in cognitive resources, which included the enhancement of automatic stimulus processing at the stimulus input level and color naming pathway (task-relevant dimension) (Cohen et al., 1990; MacLeod, 1998; MacLeod and Dunbar, 1988). However, although brain regions previously activated during semantic conflict were not activated at the late stage of practice, we cannot arbitrarily deduce that these areas were no longer involved (Kelly and Garavan, 2005).

Besides, it might be that a part of response conflicts were contained within the semantic conflict, because the relatively innate connection between color naming and vocal response is much more automatic and of higher priority than its learned mapping to the

Table 2

Contrasts of brain activations between the late and early stages for SI-CO and RI-SI (Talairach Atlas).

Region	BA	No. voxels	Peak t -value	x	y	z
<i>(SI-CO) late stage-(SI-CO) early stage</i>						
L. Superior/Medial Frontal/Cingulate Gyrus	6/32	80	-3.46	-9	14	49
L. Middle/ Inferior Frontal/Precentral Gyrus	6/9	208	-4.54	-57	11	34
L. Inferior Frontal/Superior Temporal Gyrus	47/38	80	-3.76	-45	17	-5
R. Inferior Frontal Gyrus/Insula	47/13	132	-4.04	27	23	-2
L. Superior Temporal Gyrus/Insula/Thalamus	41/22	367	-5.30	-33	-37	10
R. Lingual Gyrus/Cerebellum	18	78	-3.61	3	-82	-11
L. Superior/Inferior Parietal Lobule/Postcentral Gyrus/Precuneus	40/7/2	538	-4.47	-33	-52	64
L. Cuneus	18/19	71	-3.68	-3	-94	22
R. Thalamus/Striatum		126	-3.84	30	-22	-5
L. Cerebellum/Lingual/Posterior Cingulate Gyrus	30/18/19	219	-5.14	-3	-49	-5
L. Cerebellum/Fusiform Gyrus	37	139	-4.20	-33	-61	-23
R. Cerebellum		175	-5.13	30	-55	-29
<i>(RI-SI) late stage-(RI-SI) early stage</i>						
L. Superior/Middle Temporal Gyrus	39	138	4.87	-39	-37	4
L. Superior/Inferior Parietal Lobule/Precuneus	7	82	4.27	-27	-55	58
R. Striatum/Thalamus		181	4.90	24	-49	19
L. Cerebellum/Fusiform Gyrus	37	117	4.04	-36	-61	-23

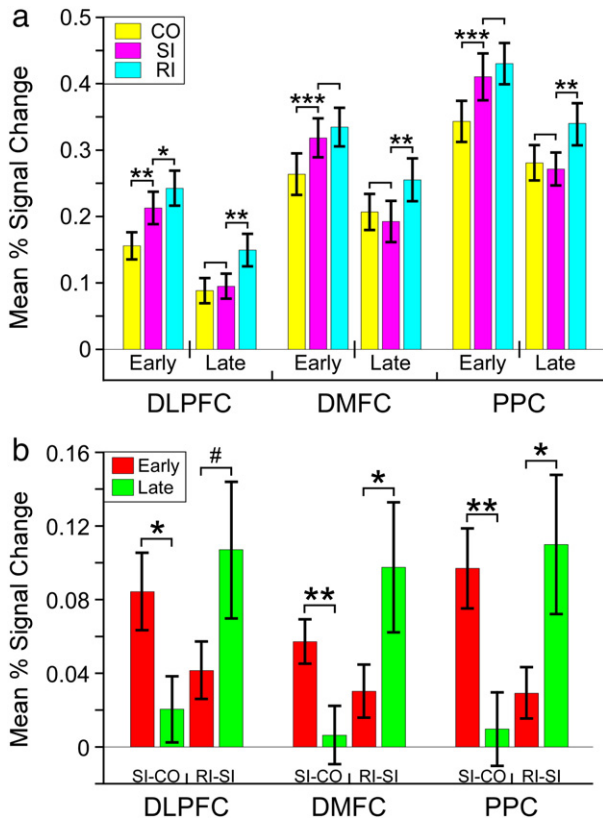


Fig. 3. The changes in neural activity in the DLPFC, dMFC and PPC during the early and late practice stages for each raw stimulus (a) and conflict type (b). NB. Error bars show the SEM; # = marginally significant ($p < 0.1$); * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

key-pressing (Gordon and Deborah, 1977; Repovš, 2004). Although the color naming and word reading were mapped to the same key in the semantic conflict condition, they were different at the verbal level; and so the semantic conflict would comprise an element of vocal-level response conflict, especially in the early stage of practice when the subjects had not yet mastered the rule of response to an appropriate level, and the connection between key pressing and color

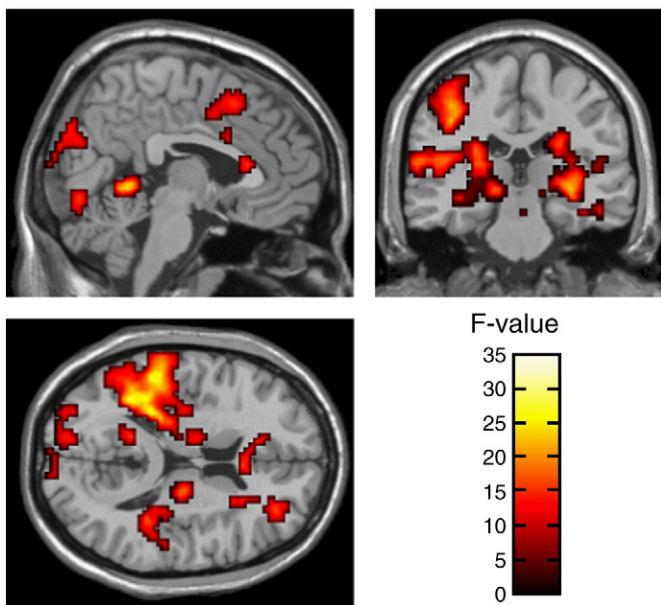


Fig. 4. Areas of neural activation associated with the practice Stage × Conflict type interaction. Sagittal, coronal, and axial views of the spatial map are presented with a threshold of $p < 0.05$, corrected.

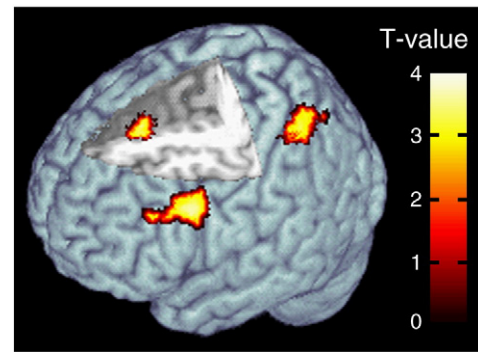


Fig. 5. The conjunction areas of neural activation for SI-CO in the early practice stage and RI-SI in the late practice stage, $p < 0.005$, cluster ≥ 10 voxels, uncorrected (as the activation cluster size is 57 voxels in the dMFC).

naming was not yet strong enough. After practice, however, the familiarity of the S–R mapping of the key-pressing would cause the disappearance of semantic conflict effects through the transferring of the vocal-level response conflict components from the semantic conflict effects to the key-pressing response conflict. This process may make the activations of semantic conflict to decline and the activations of response conflict to increase as the semantic and response conflicts became purer.

For the response conflict, our results suggest that changes in resource allocation are reflected in variations in brain activity related to RI-SI. Unlike brain activations associated with semantic conflict, we found that the activations in the DLPFC, ACC and posterior cortex increased after practice for RI-SI. One reason may be that the subjects were more familiar with the CO and SI stimuli in the late stage and needed minimal cognitive resources to process these two conditions. However, the response conflict was more difficult to be settled. Hence, more resources were needed to be allocated to the RI conflict (Schumacher et al., 2005).

In order to allocate more resources to the RI stimuli, the subject would first need to improve their detection of the RI stimuli, which is reflected in the increased activity within the ACC, an area responsible for conflict monitoring (Botvinick et al., 2001). The DLPFC also became more active, which may reflect the subjects' increased attention and their attempts to amplify task-relevant information and/or inhibit task irrelevant information for RI stimuli (Aron, 2007; Egner and Hirsch, 2005). In addition, because of the increased top-down modulation from the PFC to the posterior cortex (e.g., the fronto-parietal network) (Brass et al., 2005b; Liu et al., 2004; Miller and Cohen, 2001; Wang et al., 2010), there was more activity in the visual cortex, PPC, inferior and superior template gyri, and so on. These changes suggest that the subjects used a resource reallocation strategy that emphasized the processing of the RI stimuli both at the stimulus input level and response conflict control level. Maybe because of this emphasis, there was a decreasing trend in the response time for RI-SI from 36 ms to 26 ms, although the decreasing was not significant ($p > 0.05$).

Moreover, the ROI analysis of raw stimuli and the activation changes of traditional Stroop effects between the early and late stages showed that the activations of the raw stimuli and Stroop conflict processing were declined, suggesting that the whole conflict-related cognitive resources were decreased after practice. Thus, the increased activations under RI-SI may be stemming from the proportional increase of conflict-related cognitive resources for response conflict; the practice effects of response conflict may be a proportional resource reallocation. Furthermore, as mentioned above, the strengthened S–R mapping of stimulus and key-pressing response would make the vocal-level response conflict components, which were contained in the early stage semantic conflict effects, to be translated to the key-pressing response conflict effects after practice. These

findings indicated that the purification of semantic and response conflicts during the practice also made a contribution to the increased activations of the response conflict.

On the other hand, the interactions between practice stage and conflict type were associated with activity in the DLPFC, dmFC (ACC and pre-SMA), PPC, TPJ, medial temporal lobes, cerebellum, basal ganglia, and so on. The TPJ is related to alerting and stimulus driven attention (Corbetta and Shulman, 2002; Matsuyoshi et al., 2010; Todd et al., 2005). The medial temporal lobes, cerebellum and basal ganglia are associated with responding to the implicit perceptual and motor skills learning of task-relevant S–R mapping (Ashby et al., 2010; Doya, 2000; Packard and Knowlton, 2002; Rose et al., 2011). Therefore, these interactions provided differential practice effects between semantic and response conflict for conflict monitoring, resolution, memory and the top-down attentional modulation of the perception of conflict stimuli.

Additionally, the conjunction analysis revealed common areas of brain activation for semantic and response conflict within the DLPFC, ACC and PPC of the left hemisphere, all of which are implicated in the fronto-parietal attentional network (Wang et al., 2010). As the ACC has been related more to the monitoring of response conflict (Liu et al., 2006; Milham et al., 2001, 2003a; Paus, 2001; Swick and Jovanovic, 2002), the common activation in the ACC may be an indication that some components of the response conflict effect were contained within the semantic conflict effect at the early stage of practice. The common activation within the DLPFC and PPC may indicate that both conflict types are associated with top-down modulation from the DLPFC to the PPC in the regulation of attentional processing (Brass et al., 2005b; Liu et al., 2004; Miller and Cohen, 2001; Wang et al., 2010). These also suggest that some response conflict effects were contained in the semantic conflict effects in the early stage.

As a consequence, separating the semantic conflict and response conflicts using the subtraction strategy may not adequately conform to the pure insertion or linear additivity principles (Price and Friston, 1997), as the semantic and response conflicts are not independent of each other during the early portions of the experiment. And the use of the subtraction method for the exploration of semantic and response conflicts may need to be reviewed. What deserves to be mentioned here is that the task which was used by Kim et al. (2012) might give us some advice to exclude the confusion of semantic and response conflicts.

In summary, associating with Erickson et al. (2004), our findings further support the suggestion that the decrease in activity within the ACC was attributable to the automation of conflict detection for semantic conflict, and that the rise in activity within the DLPFC was associated with the increased allocation of cognitive resources to attentional control for response conflict. The practice effects in our study could be defined as the practice-related concentration of conflicts to the response conflict, which was accompanied by the reduction and reallocation of conflict resolution resources. These findings demonstrate that the nature of Stroop effect is response conflict rather than semantic conflict and there are two kinds of response conflicts that are contained in the key-pressing Stroop paradigm, namely, the vocal-level response conflict (mainly in the early stage) and the key-pressing response conflict (mainly in the late stage). This distinction should be taken into consideration in the future key-pressing Stroop research.

Conclusions

The present study revealed differential practice effects for semantic and response conflicts. However, there were also some common brain activations, suggesting shared mechanisms for these two conflict types. These findings can further our understanding of the neural mechanisms underlying semantic and response conflicts, and the

practice-related effects associated with these conflicts. It would be interesting for future studies to address the different practice effects between response conflict and semantic conflict in other subject groups, such as the elderly, and patients with dysfunction of attentional control. If the practice effects of such groups were different from normal subjects, we would also want to know whether the inflexibility of cognitive control associated with these groups (Edwards et al., 2010; Lesh et al., 2011; Milham et al., 2002) was caused by difficulties in automatic processing or in the reallocation of cognitive resources. In addition, simultaneous EEG-fMRI will be utilized to investigate the dynamical organization of the practice-related effects associated with semantic and response conflicts (Lei et al., 2011a,b). Our study would provide some important comparative findings for such researches.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2012.10.028>.

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