

# Dissociable Networks Control Conflict during Perception and Response Selection: A Transcranial Magnetic Stimulation Study

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Current models of conflict processing propose that cognitive control resolves conflict in the flanker task by enhancing task-relevant stimulus processing at a perceptual level. However, because conflicts occur at both a perceptual and a response selection level in that task, we tested the hypothesis of conflict-specific control networks for perceptual and response selection conflicts using transcranial magnetic stimulation (TMS). TMS of the presupplementary motor area selectively disrupted the processing of response selection conflict, whereas TMS of the posterior intraparietal sulcus/inferior parietal lobule interfered with perceptual conflict processing. In more detail, the presupplementary motor area seems to resolve response selection conflict mainly when no conflicts have occurred in the previous trial. In contrast, the posterior intraparietal sulcus/inferior parietal lobule may resolve perceptual conflicts selectively when a conflict has occurred in the previous trial. The current data show the need for revising models of cognitive control by providing evidence for the existence of conflict-specific control networks resolving conflict at different processing levels.

## Introduction

Cognitive control enables successful goal-directed behavior by adjusting information processing in response to changing task demands. Research on cognitive control has often focused on control adjustments in interference paradigms in which conflicts between task-relevant and distracting information occur. A parsimonious and elegant model of the role of cognitive control in conflict resolution is the conflict-monitoring account (Botvinick et al., 2001). However, whereas this model assumes that conflicts in interference paradigms occur at the response selection stage, empirical studies using the Stroop or flanker paradigm found that conflicts occur at both a perceptual and a response selection level (De Houwer, 2003; van Veen and Carter, 2005). Findings from neuroimaging studies suggest that perceptual conflict is correlated with superior/middle frontal and posterior parietal cortex (PPC) activity, whereas response selection conflict is associated with medial and inferior frontal activity (van Veen and Carter, 2005; Liston et al., 2006; Nigbur et al., 2012). However, because the results of neuroimaging studies are correlative in nature, it remains unclear whether these regions are *causally* involved in the active resolution (instead of passive processing) of

conflict. Using transcranial magnetic stimulation (TMS), the present study tested the hypothesis of conflict-specific control networks for perceptual and response selection conflict. Because the existence of conflict-specific control networks is still a matter of controversy (Egner, 2008), the potential finding that the resolution of perceptual and response selection conflict can be impaired selectively by TMS of dissociable brain regions would not only clarify the roles of these regions in conflict processing, but would also provide evidence for the existence of distinct control networks for the resolution of perceptual and response selection conflict.

Resolution of response selection conflict may be related to the presupplementary motor area (pre-SMA). A combined TMS-EEG study by Taylor et al. (2007) showed that pre-SMA TMS modulates the lateralized readiness potential in incongruent trials of a flanker task, suggesting that the pre-SMA exerts top-down control over the motor cortex to resolve response selection conflict. Consistent with this interpretation, other studies reported a causal role of the pre-SMA in action reprogramming and response inhibition (Mars et al., 2009; Neubert et al., 2010). Based on these findings, we hypothesized that pre-SMA TMS interferes selectively with the processing of response selection conflict.

In contrast, resolution of perceptual conflict may be linked to the PPC. Although previous studies suggesting PPC involvement in conflict control did not distinguish between different conflict-processing levels (Egner et al., 2007; Luks et al., 2007; Wang et al., 2010), subregions of the PPC close to the intraparietal sulcus (IPS) and the inferior parietal lobule (IPL) have been related to top-down regulation of attention (Rushworth and Taylor, 2006; Green and McDonald, 2008) and may thus contribute selectively to resolving perceptual conflict.

Received Oct. 9, 2012; revised Jan. 21, 2013; accepted Feb. 19, 2013.

Author contributions: A.S., P.C.J.T., and T.S. designed research; A.S. and P.C.J.T. performed research; A.S. analyzed data; A.S., P.C.J.T., H.J.M., and T.S. wrote the paper.

This work was supported by a the German Research Foundation (to T.S.) and Cognition for Technical Systems (CoTeSys Grant #439 to T.S.). A.S. was supported by doctoral scholarships from the Bavarian Elite Aid Act and the Munich Center for Neurosciences, Mind and Brain.

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DOI:10.1523/JNEUROSCI.4768-12.2013

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We tested the hypothesized roles of pre-SMA and IPS/IPL in resolving perceptual and response selection conflict in two separate experiments using a flanker task that permits these different types of conflicts to be dissociated.

## Materials and Methods

### Experiment 1: pre-SMA TMS

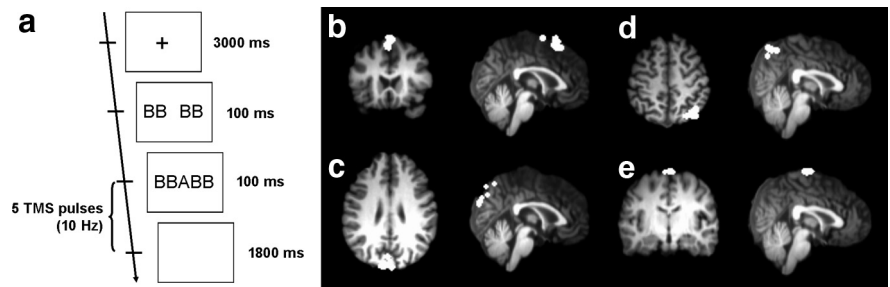
**Participants.** Thirty-one right-handed volunteers (mean age, 24.03 years; range, 20–29; 22 female) who were recruited at the Ludwig-Maximilians-Universität participated in Experiment 1. All volunteers had normal or corrected-to-normal vision, gave informed consent before participating in the study, and were paid 10 Euros per hour for their participation.

**Task design.** Participants performed a letter variant of the Eriksen flanker paradigm that allowed dissociating conflicts at the perceptual and at the response selection stage. Participants had to decide whether a centrally presented target letter surrounded by four distractor letters was either a vowel (“A” or “E”) or a consonant (“B” or “K”). We instructed them to respond to the target letter by pressing the left control key on a keyboard for vowels and the right control key for consonants, using the left and right index finger, respectively. The targets and distractors were either congruent (C), stimulus-incongruent (SI), or response-incongruent (RI). In C trials, target and distractor letters were identical (e.g., “AAAA”). In SI trials, target and distractor letters were different but linked to the same response alternative (e.g., “EEAEE”), resulting in conflict at the perceptual processing level. In RI trials, target and distractors were additionally associated with different response alternatives (e.g., “BBABB”). Therefore, conflicts occurred both at the perceptual and the response selection stage in RI trials because targets and distractors were represented by different stimuli (perceptual conflict) and were also associated with different response alternatives (response selection conflict). Using subtraction logic, we defined perceptual conflict as the difference between SI and C trials and response selection conflict as the difference between RI and SI trials (van Veen and Carter, 2005). Hereafter, the terms “perceptual conflict” and “response selection conflict” will refer to the SI-C and RI-SI contrasts, respectively.

Every block contained 60 trials that were divided into equal numbers of C, SI, and RI trials. In every block, TMS was applied in half of the trials of each condition. Trial order was randomized, with the only constraint that we never applied more than three consecutive TMS trials.

**Procedure.** On each trial, first a white fixation cross was presented for 3000 ms on a black background, followed by a stimulus array comprising only the four distractors for the flanker task (Fig. 1*a*). After 100 ms, the target stimulus was also presented in addition to the distractors and the whole stimulus array disappeared after 100 ms. Participants had to respond within an interval of 1800 ms after stimulus presentation.

**TMS.** We applied TMS in half of the trials of a block, starting with target onset and ending 300 ms after target offset (five pulses at 10 Hz and 110% resting motor threshold) using a figure-eight coil with an internal diameter of 7 cm (MagPro R30 machine with MC-B70 Butterfly Coil; Medtronic). On TMS trials, TMS was applied blockwise either to the pre-SMA or to a control site to test our hypothesis that the pre-SMA plays a causal role in resolving response selection conflict. The pre-SMA TMS site was 4 cm anterior to the vertex, whereas the control TMS site was at electrode position Pz according to the 10–20 international system (Taylor et al., 2007). Previous studies have shown that this procedure provides reliable stimulation of the pre-SMA (Rushworth et al., 2002; Taylor et al., 2007; Mars et al., 2009). After the recording session, coil positioning was confirmed for six subjects by using optical tracking via theBrainsight frameless stereotaxy system (Rogue Research) to determine Montreal Neurological Institute (MNI) coordinates of the stimulation sites based on their structural magnetic resonance images. Mean MNI coordinates of the pre-SMA TMS ( $x = 0, y = 21, z = 62$ ) and the control TMS ( $x =$



**Figure 1.** *a*, Schematic illustration of a flanker task trial in which participants had to respond to the central target letter of an array of five letters. On TMS trials, five TMS pulses were applied with a frequency of 10 Hz starting with target onset. Stimulation sites in the pre-SMA (*b*) and the control (*c*) condition of Experiment 1 and in the IPS/IPL (*d*) and control (*e*) condition of Experiment 2. Each white circle represents the stimulated site in one participant.

$1, y = -79, z = 40$ ) condition suggested that the coil was placed over the pre-SMA and over the parietooccipital cortex, respectively, for active and control sites (Fig. 1*b,c*).

**Analysis.** We analyzed reaction times (RTs) and error rates. For the RT analysis, we excluded error and posterror trials from the dataset. Note that cognitive control may resolve conflicts both on a within-trial and a trial-by-trial level (Boy et al., 2010). Because TMS may affect within-trial and/or trial-by-trial control processes, we conducted separate within-trial and trial-by-trial analyses (for details, see below). For tests of significance, we calculated ANOVAs and paired-samples *t* tests with a significance threshold of 5%. The *p* values of the ANOVAs were adjusted using Huynh-Feldt corrections (Huynh and Feldt, 1976).

### Experiment 2: IPS/IPL TMS

**Participants.** Twenty-seven right-handed volunteers (mean age, 24.85 years; range, 19–29 years; 22 female), who were recruited at the Ludwig-Maximilians-Universität and had normal or corrected-to-normal vision, participated in Experiment 2 after having given informed consent. Eight of these volunteers had also participated in Experiment 1.

**TMS.** We applied TMS blockwise either to the IPS/IPL or to a control site. Our hypothesis was that IPS/IPL TMS should interfere selectively with the resolution of perceptual conflict. The IPS/IPL TMS site was at electrode position P4 to target the posterior IPS/IPL region previously found to affect tasks requiring attentional reupdating (Rushworth and Taylor, 2006). Following previous studies that had stimulated the IPS/IPL region, we used electrode position Cz as the control TMS site (Muggleton et al., 2008; Silvanto et al., 2009). After the recording session, coil positioning was confirmed for six subjects using frameless (optical-tracking) stereotactic registration of individuals' structural MRIs into standard space (Brainsight; Rogue Research). Mean MNI coordinates for the IPS/IPL TMS ( $x = 39, y = -67, z = 54$ ) and the control TMS ( $x = 1, y = -16, z = 76$ ) condition suggested that the coil was placed over the posterior IPS/IPL in the vicinity of the right angular gyrus in the IPS/IPL condition (Fig. 1*d,e*).

**Task design and analysis.** We used the same task design and statistical analyses as in Experiment 1.

## Results

### Experiment 1: pre-SMA TMS

#### Within-trial effects

First, we tested the effects of pre-SMA TMS on perceptual and response selection conflict processing in the present trial. If our hypothesis is correct and the pre-SMA is causally involved in the resolution of response selection, pre-SMA TMS should increase the magnitude of response selection conflict selectively (i.e., the RT difference between RI and SI trials). We analyzed congruency effects in RTs with a  $3 \times 3$  repeated-measures ANOVA including the factors TMS (no TMS, pre-SMA TMS, control TMS) and congruency (C, SI, RI). The significant main effect of TMS ( $F_{(2,60)} = 18.01, p < 0.001, \eta_p^2 = 0.375$ ) indicated that RTs were speeded in the pre-SMA TMS (429 ms) and control TMS (433 ms) condition

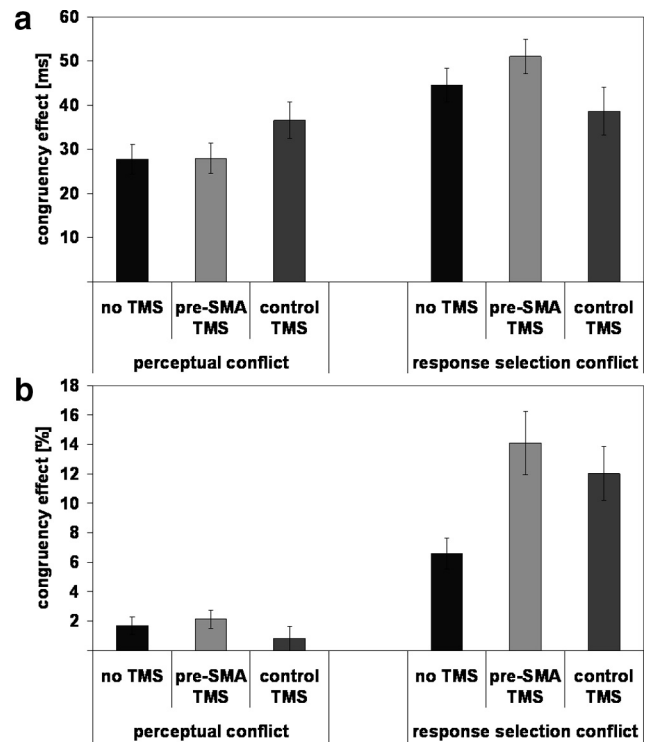
**Table 1. Mean RTs and error rates in Experiment 1**

	No TMS	Pre-SMA TMS	Control TMS
RT (ms)			
C	416 (11)	393 (12)	396 (12)
SI	444 (12)	421 (12)	433 (12)
RI	488 (11)	472 (12)	471 (12)
Error rate (%)			
C	1.5 (0.4)	2.5 (0.8)	3.0 (0.6)
SI	3.1 (0.5)	4.7 (0.8)	3.8 (0.7)
RI	9.7 (1.2)	18.8 (2.4)	15.9 (1.9)

Numbers in parentheses indicate SEM.

relative to the no TMS (449 ms) condition (both  $p < 0.001$ ; Table 1). In addition, we found a significant congruency effect ( $F_{(2,60)} = 235.64$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.887$ ), indicating that RTs differed between the congruency conditions (i.e., C, SI, and RI trials): RTs were slowest in RI trials (477 ms), followed by SI trials (433 ms) and, finally, C trials (402 ms; all  $p < 0.001$ ). Therefore, both perceptual (SI-C: 31 ms;  $p < 0.001$ ) and response selection conflict (RI-SI: 45 ms;  $p < 0.001$ ) occurred. The congruency effect was modulated by the factor TMS ( $F_{(4,120)} = 2.46$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.076$ ), suggesting that the TMS conditions had dissociable effects on perceptual versus response selection conflict. To examine the effects of TMS on perceptual and response selection conflict in more detail, we computed two separate ANOVAs with the factor TMS (no TMS, pre-SMA TMS, control TMS), one on perceptual conflict and the other on response selection conflict. The ANOVA on perceptual conflict did not yield a significant main effect of TMS ( $F_{(2,60)} = 1.81$ ,  $p > 0.17$ ,  $\eta_p^2 = 0.057$ ), indicating that perceptual conflict did not differ among the pre-SMA TMS (28 ms), no TMS (28 ms), and control TMS trials (37 ms) (all  $p > 0.1$ ). In contrast, the ANOVA on response selection conflict revealed the main effect of TMS to be significant ( $F_{(2,60)} = 5.42$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.153$ ). Consistent with our hypothesis, response selection conflict was increased significantly in the pre-SMA TMS condition (51 ms) compared with the no TMS (44 ms;  $t_{(30)} = 2.18$ ,  $p < 0.05$ ) and the control TMS condition (39 ms;  $t_{(30)} = 3.25$ ,  $p < 0.01$ ), whereas no significant difference was found between the control TMS and the no TMS condition ( $t_{(30)} = 1.35$ ,  $p > 0.18$ ; Fig. 2).

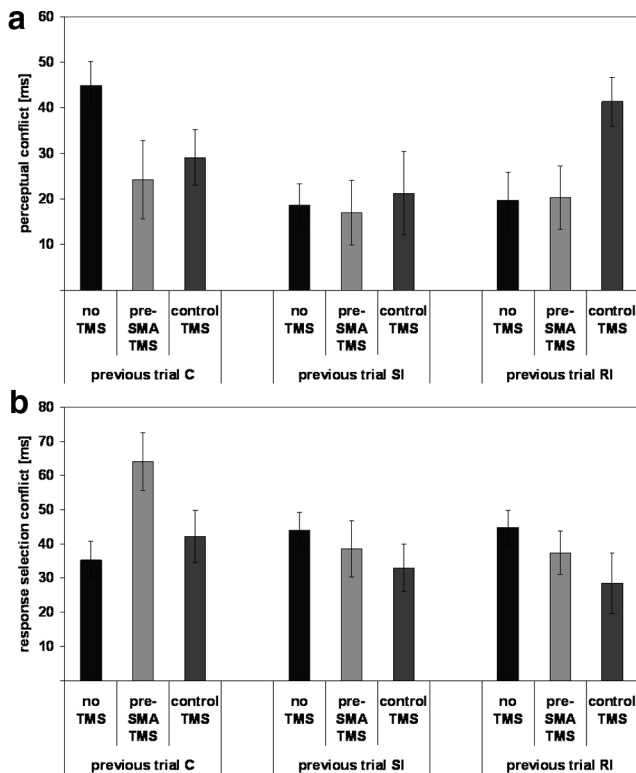
The ANOVA on the error rates revealed a significant main effect of congruency ( $F_{(2,60)} = 56.79$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.654$ ), with the highest error rate in RI trials (14.8%), followed by SI (3.9%) and C (2.3%) trials (all  $p < 0.01$ ). The main effect of TMS was also significant ( $F_{(2,60)} = 19.03$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.388$ ): participants committed more errors in pre-SMA TMS (8.7%) and control TMS (7.6%) compared with no TMS (4.8%) trials ( $p < 0.001$ ). The significant TMS  $\times$  C interaction ( $F_{(4,120)} = 8.16$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.214$ ) suggested that, similar to the RT analysis, the size of perceptual and/or response selection conflict was modulated by TMS. An additional ANOVA on perceptual conflict with the factor TMS yielded no significant result ( $F_{(2,60)} = 1.08$ ,  $p > 0.34$ ,  $\eta_p^2 = 0.035$ ), indicating that the magnitude of perceptual conflict did not differ among the pre-SMA TMS (2.1%), no TMS (0.8%), and control TMS trials (1.3%) trials (all  $p > 0.17$ ). In contrast, the ANOVA on response selection conflict proved the main effect of TMS to be significant ( $F_{(2,60)} = 8.96$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.230$ ). Planned comparisons revealed a larger response selection conflict in the pre-SMA (14.1%) and the control TMS condition (12.0%) compared with the no TMS condition (6.6%; both  $p < 0.01$ ), whereas the difference between the pre-SMA and the control TMS condition was not significant ( $p > 0.16$ ).



**Figure 2.** pre-SMA TMS effects on perceptual and response selection conflict in RTs (in ms; *a*) and error rates (in %; *b*). Error bars indicate SEM.

#### Trial-by-trial effects

In addition to the previous analyses, we also tested for potential effects of pre-SMA TMS on trial-by-trial modulations of the congruency effects. Several previous studies had found that congruency effects in the current trial are reduced after the occurrence of a conflict in the previous trial (Kerns et al., 2004; Ullsperger et al., 2005; Verbruggen et al., 2006; Egner, 2007). Because this sequential modulation of congruency effects is thought to reflect the activation of enhanced cognitive control processes, we investigated whether the observed effects of pre-SMA TMS on response selection conflict would relate to this mechanism. There is evidence that conflict adaptation improves conflict processing at the perceptual, rather than the response selection, level (Verbruggen et al., 2006). Therefore, we expected the effects of pre-SMA TMS on response selection conflict not to be related to the reduction of conflict after previously incongruent trials (which should affect conflict at the perceptual processing level). For the analysis of sequential modulations, we removed all repetition trials from the dataset to control for priming effects on conflict adaptation (Mayr et al., 2003; Hommel et al., 2004), leaving a mean total trial number of 487 per subject. We computed two separate ANOVAs involving the factors TMS (no TMS, pre-SMA TMS, control TMS) and previous trial congruency (C, SI, RI) on perceptual and response selection conflict (Fig. 3). The analysis of perceptual conflict revealed only a significant main effect of previous trial congruency ( $F_{(2,60)} = 3.74$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.112$ ), suggesting the occurrence of conflict adaptation. Perceptual conflict was significantly reduced after previous encounters of SI (19 ms) compared with C (33 ms) trials ( $t_{(30)} = 3.17$ ,  $p < 0.01$ ), whereas the reduction of perceptual conflict after RI (27 ms) compared with C trials failed to reach statistical significance ( $t_{(30)} < 1$ ). Similarly to the results of the within-trial analysis, we found no effect of pre-SMA TMS on the sequential modulation of perceptual conflict: the TMS  $\times$  previous trial congruency interaction ( $F_{(4,120)} = 2.07$ ,  $p >$



**Figure 3.** pre-SMA TMS effects on perceptual (*a*) and response selection conflict (*b*) separately for after previously congruent (C), stimulus-incongruent (SI), and response-incongruent trials (RI). Error bars indicate SEM.

0.09,  $\eta_p^2 = 0.064$ ) and the main effect of TMS ( $F_{(2,60)} = 1.54, p > 0.22, \eta_p^2 = 0.049$ ) were not significant.

In contrast, the ANOVA on response selection conflict revealed a significant effect of TMS ( $F_{(2,60)} = 3.92, p < 0.05, \eta_p^2 = 0.115$ ). Because the main effect of previous trial congruency was not significant ( $F_{(2,60)} = 1.92, p > 0.15, \eta_p^2 = 0.060$ ), no conflict adaptation effect occurred at the response selection level. However, the significant TMS  $\times$  previous trial congruency interaction ( $F_{(4,120)} = 2.74, p < 0.05, \eta_p^2 = 0.084$ ) indicated that the effects of pre-SMA TMS on response selection conflict depended on the congruency of the previous trial. Planned comparisons revealed that response selection conflict was significantly increased in the pre-SMA TMS compared with both the no TMS and the control TMS condition only after previous C trials (both  $t_{(30)} > 3.31, p < 0.01$ ), whereas no significant differences manifested after SI and RI trials (all  $p > 0.11$ ). Therefore, the effects of pre-SMA TMS on response selection conflict were most pronounced when no conflict had occurred in the preceding trial.

#### Conflict monitoring

Whereas the previous analyses suggest that the pre-SMA is engaged in resolving response selection conflict, an alternative account of pre-SMA functioning claims an involvement of pre-SMA in conflict-monitoring processes. According to this account, pre-SMA activity may be related to the detection of response selection conflicts in the stream of information processing, which results in adjustments of cognitive control and improved conflict resolution in subsequent trials (Ullsperger and von Cramon, 2001; Garavan et al., 2003). If this assumption is correct, then pre-SMA TMS in incongruent trials should interfere with conflict-monitoring processes, and thus with conflict adaptation in subsequent trials. To test this alternative account,

**Table 2. Mean RTs and error rates in Experiment 2**

	No TMS	IPS/IPL TMS	Control TMS
RT (ms)			
C	430 (12)	403 (12)	409 (13)
SI	450 (11)	444 (16)	436 (13)
RI	497 (10)	475 (13)	480 (13)
Error rate (%)			
C	1.9 (0.6)	2.6 (0.8)	2.7 (0.8)
SI	3.2 (0.7)	4.0 (0.9)	4.1 (0.6)
RI	10.4 (1.9)	16.7 (2.7)	18.2 (2.7)

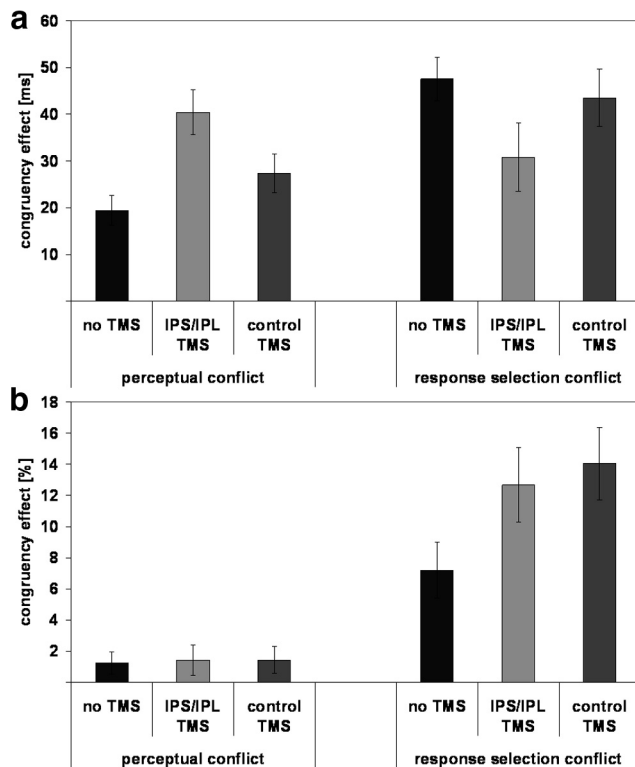
Numbers in parentheses indicate SEM.

we conducted two separate ANOVAs on perceptual and response selection conflict involving the factors previous trial TMS (no TMS, pre-SMA TMS, control TMS) and previous trial congruency (C, SI, RI). We excluded repetition trials and, importantly, because we intended to test the effects of TMS in incongruent previous trials on conflict resolution in current trials, we analyzed only trials in which currently no TMS had been applied. This allowed us to avoid possible interaction effects between the delivery of TMS in the previous and the current trial on the sequential modulation of congruency effects. On average, 244 trials per participant were entered into this analysis. Consistent with the above reported trial-by-trial analysis, the ANOVA on perceptual conflict revealed a main effect of previous trial congruency ( $F_{(2,60)} = 4.93, p < 0.01, \eta_p^2 = 0.141$ ), indicative of the occurrence of conflict adaptation at the perceptual level. Neither the main effect of previous trial TMS nor the previous trial TMS  $\times$  previous trial congruency interaction was significant (both  $F < 1.41$ ); that is, the conflict adaptation effect was not modulated by the application of TMS in the previous trial. The ANOVA on response selection conflict did not reveal any significant effects (all  $F < 1.43, p > 0.22$ ). This pattern does not tally with the conflict-monitoring hypothesis of the pre-SMA, because we failed to find an effect of pre-SMA TMS in the previous trial on the sequential modulation of congruency effects.

#### Experiment 2: IPS/IPL TMS

##### Within-trial effects

As for Experiment 1, we first tested for effects of IPS/IPL TMS on perceptual and response selection conflict processing in the current trial. A 3 (TMS)  $\times$  3 (C) ANOVA on the RTs revealed a significant main effect of TMS ( $F_{(2,52)} = 14.15, p < 0.001, \eta_p^2 = 0.352$ ): RTs were faster in both IPS/IPL TMS (441 ms) and control TMS (442 ms) relative to no TMS (459 ms) trials ( $p < 0.001$ ; Table 2). The main effect of C ( $F_{(2,52)} = 118.38, p < 0.001, \eta_p^2 = 0.820$ ) showed that RTs were slowest in RI trials (484 ms), followed by SI trials (443 ms) and, finally, C trials (414 ms; all  $p < 0.001$ ). Because congruency effects were modulated by the factor TMS ( $F_{(4,104)} = 4.36, p < 0.01, \eta_p^2 = 0.143$ ), we performed, as in Experiment 1, two separate ANOVAs with the factor TMS on perceptual and, respectively, response selection conflict. The ANOVA on perceptual conflict revealed the main effect of TMS to be significant ( $F_{(2,52)} = 8.63, p < 0.001, \eta_p^2 = 0.249$ ). Consistent with our hypothesis, perceptual conflict was significantly increased in the IPS/IPL TMS condition (40 ms) compared with the no TMS condition (19 ms;  $t_{(26)} = 3.78, p < 0.001$ ) and with the control TMS (27 ms) condition ( $t_{(26)} = 2.24, p < 0.05$ ; Fig. 4). Therefore, IPS/IPL TMS interfered with the resolution of perceptual conflict. In addition, perceptual conflict was larger in control TMS than in no TMS trials ( $t_{(26)} = 2.16, p < 0.05$ ). Likewise, the ANOVA on response selection conflict yielded a significant effect of TMS ( $F_{(2,52)} = 4.28, p < 0.05, \eta_p^2 = 0.141$ ). The response selection conflict



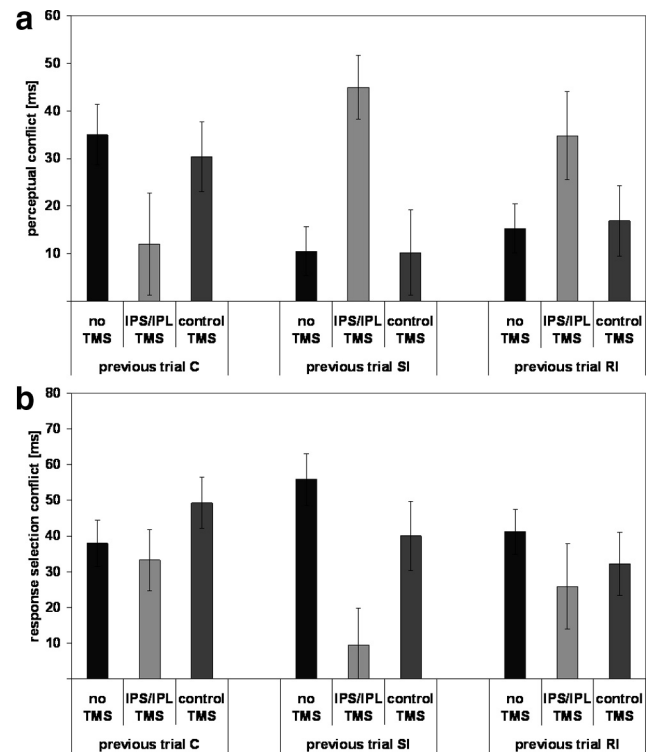
**Figure 4.** IPS/IPL TMS effects on perceptual and response selection conflict in RTs (in ms; *a*) and error rates (in %; *b*). Error bars indicate SEM.

was significantly decreased in the IPS/IPL TMS (31 ms) relative to the no TMS condition (48 ms;  $t_{(26)} = 2.69$ ,  $p < 0.05$ ) and to the control TMS condition (44 ms;  $t_{(26)} = 2.17$ ,  $p < 0.05$ ). No difference was evident between the no TMS and the control TMS condition ( $t_{(26)} < 1$ ).

The ANOVA on the error rates revealed a significant effect of TMS ( $F_{(2,52)} = 14.37$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.356$ ), indicating that more errors were committed in the IPS/IPL TMS (7.8%) and control TMS (8.3%) trials relative to no TMS trials (5.2%;  $p < 0.001$ ). We also found a significant congruency effect ( $F_{(2,52)} = 33.71$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.565$ ). Participants showed the highest error rate in RI trials (15.1%), followed by SI trials (3.8%), and the lowest error rate in C trials (2.4%; all  $p < 0.01$ ). This error congruency effect was modulated by the factor TMS ( $F_{(4,104)} = 9.50$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.268$ ). Although an additional ANOVA on perceptual conflict did not yield a significant result ( $F_{(2,52)} < 1$ ,  $p > 0.98$ ), an ANOVA on response selection conflict revealed the main effect of TMS to be significant ( $F_{(2,52)} = 12.43$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.323$ ): Response selection conflict was significantly larger in both the IPS/IPL TMS (12.7%) and the control TMS (14.0%) relative to the no TMS (7.2%) condition ( $p < 0.01$ ), whereas response selection conflict did not differ between the IPS/IPL TMS and the control TMS condition ( $t_{(26)} < 1$ ). Given that similar effects of TMS on response selection conflict on the error rates had also been observed in Experiment 1, these unspecific TMS effects on response speed, be attributable to the alerting effects of TMS (Marzi et al., 1998).

#### Trial-by-trial effects

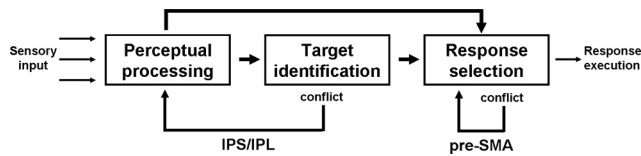
Next, we tested for potential effects of IPS/IPL TMS on sequential trial-by-trial modulations of the congruency effects. Because conflict adaptation in the flanker paradigm appears to affect



**Figure 5.** IPS/IPL TMS effects on perceptual (*a*) and response selection conflict (*b*) separately for after previously congruent (C), stimulus-incongruent (SI), and response-incongruent trials (RI). Error bars indicate SEM.

mainly the perceptual processing level (see Experiment 1), it is possible that the effects of IPS/IPL TMS on perceptual conflict are related to the modulation of conflict processing after incongruent trials. For that analysis, we again excluded all repetition trials, resulting in a mean trial number of 486 per subject. As for Experiment 1, we analyzed perceptual and response selection conflict in two separate ANOVAs involving the factors TMS and previous trial congruency (Fig. 5). The ANOVA on perceptual conflict revealed only a significant TMS  $\times$  previous trial congruency interaction ( $F_{(4,104)} = 4.26$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.141$ ), suggesting that the sequential modulation of perceptual conflict (i.e., the conflict adaptation effect) differed between the TMS conditions. To specify this interaction, we calculated the conflict adaptation effect in each TMS condition separately for the reduction of perceptual conflict after previous encounters of SI trials (i.e., perceptual conflict after C trials – perceptual conflict after SI trials) and after RI trials (i.e., perceptual conflict after C trials – perceptual conflict after RI trials). We found that conflict adaptation after SI trials was significantly reduced in the IPS/IPL TMS compared with both the no TMS condition ( $t_{(26)} = 4.48$ ,  $p < 0.001$ ) and the control TMS condition ( $t_{(26)} = 3.39$ ,  $p < 0.01$ ). In addition, conflict adaptation after RI trials was also significantly reduced in the IPS/IPL TMS relative to the no TMS condition ( $t_{(26)} = 2.08$ ,  $p < 0.05$ ), whereas the difference between the IPS/IPL TMS and the control TMS condition was only marginally significant ( $t_{(26)} = 1.91$ ,  $p < 0.07$ ). These findings suggest that IPS/IPL TMS interferes with the sequential modulation of perceptual conflict—that is, with conflict adaptation.

The trial-by-trial analysis of response selection conflict revealed a significant main effect of TMS ( $F_{(2,52)} = 6.93$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.210$ ), reflecting the fact that response selection conflict was decreased in IPS/IPL TMS (23 ms) relative to both no TMS



**Figure 6.** Architecture of control suggested by the current findings. Conflicts at the response selection level are resolved by the pre-SMA. If the cognitive system detects the occurrence of perceptual conflict in the previous trial, the IPS/IPL improves perceptual processing by directing increased attention to task-relevant stimuli.

(45 ms) and control TMS trials (41 ms; both  $p < 0.01$ ). Neither the effect of previous trial congruency ( $F_{(2,52)} < 1.05$ ,  $p > 0.35$ ,  $\eta_p^2 = 0.039$ ) nor the TMS  $\times$  previous trial congruency interaction was significant ( $F_{(4,104)} = 2.13$ ,  $p > 0.08$ ,  $\eta_p^2 = 0.076$ ). Therefore, our results again provide no evidence of conflict adaptation at the response selection level.

#### Between-experiment analysis

The results of Experiments 1 and 2 suggested dissociable roles of the pre-SMA and the IPS/IPL in resolving response selection conflict and perceptual conflict, respectively. To provide additional support in favor of this hypothesis, we entered the data of both experiments into a common, mixed-design ANOVA with the magnitude of the congruency effect as the variable and with conflict (perceptual vs response selection), TMS (no TMS, active TMS, control TMS), and experiment (between-subject factor: Experiment 1 vs Experiment 2) as independent variables. The factor level “active TMS” represented a combination of the conditions pre-SMA TMS and IPS/IPL TMS from Experiments 1 and 2, respectively. The only significant effect involving the factor experiment was the experiment  $\times$  conflict  $\times$  TMS interaction ( $F_{(2,112)} = 8.68$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.134$ ), indicating that the conflict-specific effects of TMS on perceptual and response selection conflict did differ between Experiment 1 and Experiment 2. In addition, to examine whether the TMS conditions had dissociable effects in the two experiments on perceptual and response selection conflict, we conducted two additional ANOVAs with the factors experiment and TMS, one on perceptual and the other on response selection conflict. Both ANOVAs revealed a significant experiment  $\times$  TMS interaction (both  $F_{(2,112)} = 5.46$ ,  $p < 0.01$ ). The results of these between-experiment analyses support the findings of the previous single-experiment analyses, suggesting that the effects of TMS on perceptual and response selection conflict differed between Experiment 1 and Experiment 2.

## Discussion

The present study provided evidence for the hypothesis of conflict-specific control networks selectively resolving conflicts at the perceptual processing and response selection levels, respectively. Whereas TMS of the pre-SMA interfered selectively with the processing of response selection conflict, IPS/IPL TMS disrupted the processing of perceptual conflict. Therefore, we conclude that the pre-SMA is causally involved in the resolution of conflict at the response selection level, whereas the posterior IPS/IPL is part of a control network adjusting attentional processes to resolve conflicts at a perceptual level. Interestingly, our data also suggest that these networks resolve conflicts at different time scales. Pre-SMA TMS disrupted response selection conflict only after previously congruent trials, that is, when—according to the conflict-monitoring account of Botvinick et al. (2001)—the level of conflict-triggered control could be assumed to be low. In contrast, IPS/IPL TMS disrupted perceptual conflict processing only

when a conflict had occurred in the previous trial. Note that one of the core assumptions of the conflict-monitoring account proposes that the detection of a conflict leads to improved perceptual processing in subsequent trials (Botvinick et al., 2001; Egner and Hirsch, 2005; Verbruggen et al., 2006). The current data support this assumption and additionally suggest that the posterior IPS/IPL represents a central part of this reactive control network that enables attention to be focused on the task-relevant stimulus dimension.

The current data are consistent with previous findings on pre-SMA and PPC functioning. Several studies have related pre-SMA activity to conflict resolution (Taylor et al., 2007; Forstmann et al., 2008) and action reprogramming (Mars et al., 2009; Neubert et al., 2010). Our results specify the role of the pre-SMA in conflict processing by showing that it is causally involved in the resolution of conflict specifically at the response selection level. The pre-SMA may support response selection under conflict by facilitating the processing of the task-relevant response alternative (Mars et al., 2009; Neubert et al., 2010). Moreover, the pre-SMA resolves response selection conflict predominantly when the level of activated cognitive control is low—that is, when no conflict has arisen in the previous trial. Therefore, the pre-SMA is mainly active when conflicts have to be resolved under circumstances in which the cognitive system is not prepared for the occurrence of a conflict.

Furthermore, the current data do not support the conflict-monitoring hypothesis of pre-SMA functioning, because disrupting pre-SMA activity had no significant impact on conflict processing in subsequent trials (note, though, that this non-significant result does not necessarily imply that the conflict-monitoring hypothesis of pre-SMA functioning must be rejected). The conflict-monitoring hypothesis of the pre-SMA has been tested in functional imaging studies that found a correlation between pre-SMA activity and the occurrence of conflict in the current trial (Ullsperger and von Cramon, 2001; Garavan et al., 2003). In contrast to these correlation studies, the present study provides causal evidence for an active role of the pre-SMA in conflict resolution, because disrupting pre-SMA activity resulted in increased response selection conflict, but not in impaired conflict adaptation.

An involvement of the posterior IPS/IPL in conflict resolution has already been suggested by previous studies (Egner et al., 2007; Luks et al., 2007; Wang et al., 2010). Our findings specify current accounts of the role of the IPS/IPL region in conflict processing and show that the posterior IPS/IPL resolves conflict selectively at a perceptual processing level. This conclusion is consistent with previous results suggesting that parts of the PPC, including the posterior IPS/IPL and the right angular gyrus, are related to the top-down regulation of attentional processes (Rushworth et al., 2001; Chambers et al., 2004; Rushworth and Taylor, 2006; Green and McDonald, 2008; Silvanto et al., 2009; Taylor et al., 2011). Posterior IPS/IPL activity appears to be related to attention-regulated biasing of perceptual processing to facilitate target identification. In addition, our findings also suggest that the posterior IPS/IPL is mainly active when the level of cognitive control is enhanced after the detection of a conflict, because IPS/IPL TMS suppressed conflict adaptation. This proposal is supported by a study of Egner et al. (2007), which found that IPS/IPL activity was correlated with conflict adaptation in the Stroop task. Therefore, when the cognitive system is prepared for the potential occurrence of a conflict, it may inhibit the impact of distracting information by focusing on task-relevant stimulus attributes.

An unexpected finding was that disrupting posterior IPS/IPL activity resulted in reduced response selection conflict. Therefore, although IPS/IPL TMS impaired the resolution of perceptual conflict, it seemed to facilitate the processing of response selection conflict. However, this finding can be accounted for by assuming that perceptual target identification and response selection processes are performed in parallel (Hübner et al., 2010). Target and distractors may activate the corresponding response alternatives at the response selection level before the task-relevant target has been fully identified, on the basis of a preliminary draft of perceptual processing. Therefore, in trials in which IPS/IPL TMS impairs the identification of the task-relevant target, response selection processes might have more time for processing the task-relevant response even before the target identification process has been completed, resulting in the decreased response selection conflict observed. According to this account, the IPS/IPL region is not involved directly in the resolution of response selection conflict (if it were, IPS/IPL TMS should have increased, and not decreased, response selection conflict); rather, it influences the processing of response selection conflict processing in only an indirect manner by increasing the time required to identify the task-relevant target on a perceptual level.

Our data provide further support for the idea of conflict-specific control processes (Egner et al., 2007; Egner, 2008), challenging the assumption of a domain-unspecific general control mechanism (Botvinick et al., 2001; Freitas et al., 2007; Davelaar, 2008; Niendam et al., 2012). For example, the original conflict-monitoring model of Botvinick et al. (2001) assumes that the detection of a conflict at the response selection level activates control processes, which then resolve conflict at a perceptual level. Our data suggest that this correctly describes the mechanism underlying conflict adaptation (but note that conflict adaptation seems to occur also after SI trials, i.e., in the absence of response selection conflict; see also Verbruggen et al., 2006). Conversely, though, the conflict-monitoring model maintains that control processes at the response selection stage are triggered only by performance errors, whereas our data provide evidence for the operation of control mechanisms resolving response selection conflict after trials with correct responses (recall that post-error trials were excluded from the analyses).

Our data suggest that these conflict-specific control mechanisms may operate at different time scales (Fig. 6). When reactive control processes are activated in preparation for potential upcoming conflicts—that is, when a conflict has occurred in the previous trial—the cognitive system allocates enhanced attentional resources to task-relevant stimulus information. Therefore, it can reduce the amount of conflict already at a perceptual processing level and suppress the impact of distracting information on cognition. However, if the probability of a conflict in the next trial is anticipated to be low (e.g., after previously congruent trials), the system is not prepared for upcoming conflicts. In this processing mode, conflicts cannot be resolved at a perceptual, but only at a response selection level, probably due to the time required to activate control processes after the detection of a conflict (Ridderinkhof, 2002). Similar assumptions regarding cognitive control processes operating on different time scales have been formulated within the dual-mechanisms framework of control, which draws a distinction between a proactive and a reactive control mode (Braver, 2012; Jiménez and Méndez, 2013; but note that it is still a matter of debate whether conflict adaptation is triggered by proactive or by reactive control processes). The assumption that within-trial control affects the response selection level whereas between-trial control affects the perceptual

level is also supported by a study by Boy et al. (2010), which revealed that subliminal priming affects the flanker congruency effect in the current trial but does not modulate conflict adaptation. From these findings, the authors concluded that there may be a distinction between reactive control mechanisms resolving conflict after its occurrence (poststimulus control) and anticipatory control mechanisms that are modulated on a trial-by-trial basis (prestimulus control). Our present data support this distinction between prestimulus and poststimulus control and also show that these two control mechanisms affect different processing levels, are implemented in dissociable neural networks, and operate at different time scales.

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