The Neural Dynamics of Conflict Adaptation within a Look-to-Do Transition

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Abstract

Background: For optimal performance in conflict situations, conflict adaptation (conflict detection and adjustment) is necessary. However, the neural dynamics of conflict adaptation is still unclear.

Methods: In the present study, behavioral and electroencephalography (EEG) data were recorded from seventeen healthy participants during performance of a color-word Stroop task with a novel look-to-do transition. Within this transition, participants looked at the Stroop stimuli but no responses were required in the ‘look’ trials; or made manual responses to the Stroop stimuli in the ‘do’ trials.

Results: In the ‘look’ trials, the amplitude modulation of N450 occurred exclusively in the right-frontal region. Subsequently, the amplitude modulation of sustained potential (SP) emerged in the posterior parietal and right-frontal regions. A significantly positive correlation between the modulation of reconfiguration in the ‘look’ trials and the behavioral conflict adaptation in the ‘do’ trials was observed. Specially, a stronger information flow from right-frontal region to posterior parietal region in the beta band was observed for incongruent condition than for congruent condition. In the ‘do’ trials, the conflict of ‘look’ trials enhanced the amplitude modulations of N450 in the right-frontal and posterior parietal regions, but decreased the amplitude modulations of SP in these regions. Uniquely, a stronger information flow from centro-parietal region to right-frontal region in the theta band was observed for il condition than for cl condition.

Conclusion: All these findings showed that top-down conflict adaptation is implemented by: (1) enhancing the sensitivity to conflict detection and the adaptation to conflict resolution; (2) modulating the effective connectivity between parietal region and right-frontal region.

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Introduction

Cognitive control is the basis of goal-directed behaviors, through which people can effectively utilize the limited cognitive resources to optimize the performance, especially when facing difficulty or interference [1,2]. Conflict adaptation, often used to investigate the cognitive and neural mechanisms of cognitive control, refers to the conflict-driven sequential modulations of congruency effects in congruency task, e.g., Stroop task [3]. The congruency effects, indexed by the performance differences between incongruent and congruent conditions, are often smaller following incongruent compared to congruent condition [4]. Although conflict adaptation may be confounded by the antergic influence from bottom-up repetition priming [5,6], as a top-down modulation, it will occur under appropriate experimental environments [7,8,9]. In terms of the popular conflict monitoring model [10], cognitive control consists of two basic components: evaluation of conflict occurrence and regulation of control, which have been universally acknowledged in the relevant studies [7,11,12,13]. With regard to the neural architecture of cognitive control, three brain areas have been implicated: the anterior cingulate cortex (ACC), dorsal lateral prefrontal cortex (DLPFC), and posterior parietal cortex (PPC) [see [14] for an overall review].

However, there are some disputes concerning their particular functions in cognitive control. According to the conflict monitoring model [10], the ACC detects the occurrence of conflict, and then the DLPFC, which is activated by the signal from the ACC, implements a top-down adjustment to optimize performance [15,16,17,18,19]. In terms of the ACC-regulative account [20], the DLPFC evaluates conflict detection, and then the ACC regulates the control [21,22]. Cognitive control studies also report modulations in the PPC [18,23,24], which has been shown to play a role in the resolution of stimulus-based conflict [7,25] or motor preparatory activity [26]. Clearly, the two main accounts emphasize the role of the ACC, which can be corroborated by the findings from lesion studies which find evidence for impaired conflict adjustment in patients with ACC damage [19,27]. However, other lesion studies in patients or animals indicate that...
the ACC is not specifically involved in interference processes, but is involved in motor preparation processes [28,29,30,31]. Since lesion studies are able to demonstrate the necessity of one brain area for a particular cognitive function, the different results indicated that the role of the ACC in cognitive control is seriously questioned.

Since conflict adaptation refers to a sequential trial-to-trial modulation in the temporal course, event-related potentials (ERPs), which have millisecond resolution, can provide unique neural activation data for understanding this phenomenon in the time-domain studies. Some researches indicate that two ERP modulations primarily associate with the resolution of Stroop-type interference [3]: N450 and sustained potential (SP).

The N450 is a phasic negativity in the fronto-central region that reverses polarity in the fronto-lateral region, and is elicited about 400–550 ms following the presentation of a stimulus with non-response or response conflict [32,33,34,35]. It may arise from the activity of a neural generator in the ACC [36] or anterior frontal cortex [21,35,37]. Recent research of conflict adaptation indicated that the N450 amplitude indexed current-trial congruency (greater amplitude for incongruent compared to congruent condition), but did not vary as a function of previous-trial congruency [38]. This finding suggests the amplitude modulations of N450 reflect conflict detection in the current trials [35,39]. However, it is still unclear whether conflict detection is related to the fronto-central N450 or fronto-lateral N450.

The SP is a sustained parietal positivity or fronto-lateral negativity starting nearly 500 ms post-stimulus onset [37,40]. The SP may be associated with general preparation [35], conflict processing [36,37,41,42], or response selection [39]. Recent study found that the parietal SP amplitude not only indexed current-trial congruency (greater amplitude for incongruent compared to congruent condition), but also varied as a function of previous-trial congruency (greater amplitude for cI compared to iI condition) in the Stroop task. The result suggests that the amplitude modulations of parietal SP reflect conflict adaptation [38].

As a typical trial-to-trial regulation of cognition, conflict adaptation involves top-down information exchange among different brain areas (e.g., DLPFC, ACC, and PPC) [15]. However, the neural mechanisms of information exchange involved in conflict adaptation among these areas are not well understood. Recently, effective connectivity analysis [43] has been confirmed to provide a way to directly discuss the causal relationships between different brain areas, the results of which can reveal the basic mechanisms of high cognitive information communication [44]. The theoretical basis of it is the Granger causality [45]. Specifically, if previous values of X1 help to predict the future values of X2, a signal X1 is thought to cause a signal X2. Previously, the method based on the Granger causality has been applied to the study of cognitive information processing in the human brain [46,47].

Traditionally, conflict adaptation is investigated within a do-to-do transition, where participants are required to execute a response in each trial (‘do’ trial). Specially, to execute a response in an incongruent trial, both conflict detection and resolution are necessary [48]. Since the intertrial intervals between these ‘do’ trials are normally short (e.g., range from 800 ms to 1,200 ms), the cortical processing evoked by the response execution in the previous ‘do’ trials will unavoidably impaired the trial-to-trial conflict adaptation in the current ‘do’ trials. Therefore, it is necessary to exclude the influence of response execution in the previous trials to investigate the unimpaired conflict adaptation in the current trials.

In the present study, we designed a novel look-to-do transition based on the Stroop task. Namely, ‘look’ trials were cued with asterisk (*) which informed participants just to look at the color of forthcoming word but not make any (overt or covert) response; ‘do’ trials were cued with cross (+) which informed participants to respond to the color of forthcoming word. Using the novel look-to-do transition design, the present study is able to examine unimpaired conflict adaptation when the proportion of congruent vs. incongruent trials is 50:50 [49,50,51,52,53] and the neural dynamics of it. In terms of ERP modulations, we will focus on the amplitudes of N450 and SP both in the ‘look’ trials and ‘do’ trials. In addition, to demonstrate how the brain evaluates conflict and implements control, we examine the effective connectivity from right-frontal region to posterior parietal region for incongruent and congruent conditions in the ‘look’ trials, and from centro-parietal region to right-frontal region for iI and cI conditions in the ‘do’ trials, respectively.

Materials and Methods

Ethics Statement

Approval of the study was made by the Human Research Ethics Committee of the Southwest University of China, and all participants provided written informed consent.

Participants

Seventeen self-report right-handed healthy undergraduates (9 females, aged from 20 to 24 years, 21.71 ± 1.27, mean ± SD) with normal or corrected-to-normal vision and normal color perception took part in the study. They were paid for their participation. All were unaware of the purposes of the experiment.

Stimuli

The stimuli consisted of four words RED, YELLOW, BLUE, and GREEN [in Chinese, Song Ti No. 28 1.4 (horizontal) × 1.4" (vertical)], and were displayed in the center of a 17-in. screen using E-Prime software (Psychology Software Tools, Inc. Pittsburgh, PA). The viewing distance (between the participants and the computer screen) was approximately 60 cm. Responses were registered using a standard QWERTY keyboard. The words were colored in red, yellow, blue or green. The RGB values for the stimulus colors were 255, 0, 0 (red); 255, 255, 0 (yellow); 0, 0, 255 (blue); and 0, 255, 0 (green).

The trials were pseudo-random sequenced according to the congruency (congruent, incongruent) of ‘look’ trials and the congruency (congruent, incongruent) of ‘do’ trials. That resulted in an equal proportion of: cC trials (congruent ‘do’ trials preceded by congruent ‘look’ trials), cI trials (incongruent ‘do’ trials preceded by congruent ‘look’ trials), iC trials (congruent ‘do’ trials preceded by incongruent ‘look’ trials), and iI trials (incongruent ‘do’ trial preceded by incongruent ‘look’ trial) within the look-to-do transition. Trials, in which the ‘look’ trial was followed by the ‘do’ trial, were categorized in this way, whereas all other trials were discarded for the following analysis. All the transitions were based on two successive feature change trials where there were not (semantic) distractor-to-distractor, distractor-to-target (color), target-to-distractor, and target-to-target repetitions.

Procedure and Task

Fig. 1A depicts part of the trial sequence and the timing of one trial. All trials started with a fixation for 500 ms, followed by a blank screen for 500–800 ms (interval varied randomly) from offset of fixation to target onset. A colored word was then presented until a key was pressed or for 1,500 ms, whichever came
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Electrophysiological Recording and Analyses

Electroencephalography (EEG) was recorded using a 64-channel system (Brain Products GmbH, Germany), with references on the left and right mastoids (average mastoid reference). The electrocorticogram (EOG) was recorded with electrodes placed above and below the left eye. All interelectrode impedance was maintained below 5 kΩ during recording. The EEG and EOG were continuously sampled at 500 Hz with 0.01–100 Hz bandpass and the 50 Hz notch filter on. Trials contaminated with EOG artifacts (mean EOG voltage exceeding ±80 µV) or those with artifacts due to amplifier clipping, bursts of electromyographic (EMG) activity, or peak-to-peak deflection exceeding ±80 µV were excluded from averaging. ERP analysis epochs were extracted offline from −200 ms (pre-stimulus onset) to 1,000 ms (post-stimulus onset). ERPs were averaged for the ‘look’ trials where no response was executed, and for the ‘do’ trials where the responses were correct and response time (RT) was less than 1,500 ms.

Based on previous researches [32,38,40,54,55,56] and the scalp topography distributions of the difference waves in the present study, the following scalp region-of-interests (ROIs) and time windows were defined. In the ‘look’ trials, we chose the left-frontal (F1, F3, FC1, FC3, and FC5), right-frontal (F2, F4, FC2, FC4, and FC6), fronto-central (C1, Cz, C2, and FC2), and posterior parietal (Pz, P2, P4, PO4, and POz) scalp regions, where the time windows of N450 (480–550 ms) and SP (700–800 ms and 800–900 ms) were respectively defined. In the ‘do’ trials, we chose the left-frontal (F1, F3, FC1, FC3, and FC5), right-frontal (F4, FC2, and FC4), fronto-central (FC2, FC4, Cz, and C2), and centro-parietal (P2, P1, POz, and CPz) scalp regions, where the time windows of N450 (400–450 ms) and SP (700–800 ms) were respectively defined.

In the ‘look’ trials, we compared the amplitudes of N450 and SP between incongruent and congruent conditions, respectively. To clarify whether ERP modulations in the ‘look’ trials predicted behavioral conflict adaptation in the post-‘look’ ‘do’ trials, we examined the correlations between the amplitudes of N450(I–C), SP(I–C) in the ‘look’ trials and the RT(cI–cC)–(iI–iC) [57,58,59] in the post-‘look’ ‘do’ trials by conducting the Pearson’s correlation analysis (two-tailed) [60,61]. Then, the casual relationship between right-frontal region and posterior parietal region was assessed using a time-varying effective connectivity [62], which is based on the concept of Granger causality [63]. This time-varying effective connectivity analysis was recently developed to capture fast changing information flows between neural activation from high-density EEG recordings [62]. The same analysis strategy, demonstrated in Hu et al [62], has been adopted in the present study. First, a time-varying multivariate autoregressive (tvMVAR) model was used to describe the evolution of single-trial variations of brain responses and a Kalman smoother was used to identify the tvMVAR model. The Kalman smoother had been proved to provide an accurate estimation of the tvMVAR coefficients. Second, the effective connectivity patterns (presented as time-varying partial directed coherence, tvPDC, in the time-frequency domain) were calculated from the Kalman smoother-based tvMVAR coefficient estimates [64] for both congruent and incongruent conditions. The significance of the tvPDC was sub-

Figure 1. Experimental procedure and behavioral data. Panel A illustrates the timing parameters of one trial (above) and part of the trial sequence within the look-to-do transition design (below); the asterisk preceding the colored words informed participants only to look at the color of the forthcoming word (‘look’ trial), the cross informed participants to respond to the color of the forthcoming stimulus (‘do’ trial). Panel B illustrates the mean RT in the ‘do’ trials as a function of congruency in the ‘look’ trials. The RT(iI–iC) was significantly smaller than RT(cI–cC) (error bars were SEM). NB. ‘c’ or ‘C’ are the congruent condition; ‘i’ or ‘I’ are the incongruent condition. doi:10.1371/journal.pone.0057912.g001
Results

Behavioral Data

Two-way repeated-measure ANOVAs were respectively conducted with the following variables for the mean amplitudes of N450 and SP with the following variables: the congruency of ‘look’ trials (congruent, incongruent) and the congruency of ‘do’ trials (congruent, incongruent). To assess the neural activities of conflict adaptation in the post-‘look’ ‘do’ trials, the amplitudes of N450(aI–cI) and SP(aI–cI) were calculated. Second, the usual relationship between right-frontal region and centro-parietal region was assessed using the time-varying effective connectivity for il and ic conditions, the steps of which are same as what mentioned before. For the obtained PDC values, a paired sample t-test was conducted between il condition and ic condition.

For the N450 (480–550 ms post-stimulus onset), the mean amplitude was more negative for congruent condition than for incongruent condition in the right-frontal region, t(15) = −2.27, p<.05; no significant differences were found in the other regions, ps >.05. For the SP, the mean amplitudes for congruent and incongruent conditions were significantly different: (1) from 700 ms to 900 ms in the posterior parietal region only, t(15) = −2.07, p<.05; (2) from 800 ms to 900 ms in the left-frontal region, t(15) = −2.05, p<.05; right-frontal region, t(15) = −1.97, p<.05; centro-frontal region, t(15) = −2.23, p<.05; and posterior parietal region, t(15) = −2.32, p<.05.

We tested whether the amplitudes of N450(aC) and SP(aC) in the ‘look’ trials predicted the RT(aI–cI)–(aI–cI) in the post-‘look’ ‘do’ trials by calculating Pearson’s correlation (two-tailed). A significantly positive correlation between the amplitude of SP(aC) (800–900 ms) in the posterior parietal region and RT(aI–cI)–(aI–cI), r = 5.4, p<.03, was found (Fig. 2C). No other significant correlations were found, ps >.1.

Fig. 2D shows the time-frequency regions that exhibited significantly increased tvPDC values [68], in both incongruent and congruent conditions, as revealed using time-varying effective connectivity. To determine the information flow between the right-frontal and posterior parietal scalp regions, significantly increased tvPDC values [p<.01, false discovery rate (FDR) corrected, bootstrap analysis] were summarized via separation into two temporally distinct groups. In the two time windows (300–500 ms and 700–900 ms), significant increases in effective connectivity were observed from right-frontal scalp region to posterior parietal scalp region in beta-band (20–21 Hz) for incongruent condition (p<.02), but the connectivity was weaker (p>.05) for congruent condition.

ERP results and effective connectivity analysis in the ‘do’ trials. The grand-averaged waveforms of cC, cI, iC, and iI trials for the four ROIs are illustrated in Fig. 3A. The mean amplitudes of the N450 and SP for the right-frontal and centro-parietal regions are illustrated in Fig. 3B. The scalp topographies of difference wave for the N450 and SP are illustrated in Fig. 3C. Table 1 illustrates the results of two-way repeated-measure ANOVAs to the mean amplitudes of N450 and SP for the four ROIs.

As displayed in Fig. 3C, the topographies of N450(aI–cI)–(aI–cI) (400–450 ms) and SP(aI–cI)–(aI–cI) (700–800 ms) revealed that conflict adaptation resulted in highly similar scalp activity distributions. Specifically, both the right-frontal and the centro-parietal regions were activated during the two time windows (400–450 ms, 700–800 ms). These are consistent with the findings that significant amplitude interactions between the congruency of ‘look’ trials and the congruency of ‘do’ trials were found in these regions (Fig. 3B). Further analyses indicated that the congruency (congruent, incongruent) of ‘look’ trials led to contrasting influences on the N450 and SP. The amplitude of N450(aI–cI) compared to N450(aI–cI) showed stronger activation in the right-frontal and centro-parietal regions (Fig. 3C, left); however, the amplitude of SP(aI–cI) compared to SP(aI–cI) indicated weaker activation in these regions (Fig. 3C, right).

Fig. 3D illustrated the time-frequency regions that exhibited remarkable increase of tvPDC values (FDR corrected) for il condition than for ic condition. A significant increase in effective connectivity was observed from centro-parietal scalp region to right-frontal scalp region in the theta-band (180–330 ms, 6–7 Hz) for il condition than for il condition, t(15) = 2.17, p<.05. However, the connectivity was comparable in the theta-band (600–1,000 ms, 6–7 Hz) between il and ic conditions, t(15) = 1.58, p>.1.

Electrophysiological Data

ERP results and effective connectivity analysis in the ‘look’ trials. The grand-averaged waveforms of incongruent and congruent conditions for the four ROIs are illustrated in Fig. 2A. The scalp topographies of difference wave for the N450 and SP are illustrated in Fig. 2B.
Discussion

In a standard Stroop task where the proportion of congruent trials is equal to that of incongruent trials, we found significant neural and behavioral conflict adaptation within a novel look-to-do transition design. The RT pattern of conflict adaptation (Fig. 1B) was manifested in smaller RT\(_{(iI–iC)}\) compared with RT\(_{(cI–cC)}\), which was consistent with the previous observations [4,65,66,67]. The electrophysiological data of present study revealed intriguing neural dynamics of conflict detection and control implementation. In the ‘look’ trials, the activity of amplitude of N450\(_{(I–C)}\) implicated the right-frontal region; but that of SP\(_{(I–C)}\) implicated the right-frontal, fronto-central, and posterior parietal regions (Fig. 2A and 2B). In the ‘do’ trials, the activity of amplitude of N450\(_{(I–C)}\) implicated the left-frontal, right-frontal, fronto-central, and centro-parietal regions, but that of SP\(_{(I–C)}\) was limited to the centro-parietal region (Fig. 3A and 3C). Specially, effective connectivity revealed that the cortical information was consistently flowed from right-frontal region to posterior parietal region in the beta band in the ‘look’ trials (Fig. 2D), and from centro-parietal region to right-frontal region in the theta band in the ‘do’ trials (Fig. 3D). All these results suggest that conflict adaptation mediates the cortical processing involving in the interaction of multiple functionally specialized cortical regions.

In the ‘look’ trials, the right-frontal N450 was a reverse polarity N450 (more negative amplitudes in congruent compared to incongruent condition), which was also found in the fronto-lateral regions by West and colleagues [33,35]. Since the N450 has been related to conflict detection, primarily observed in Stroop-type conflict [35,39], the reverse polarity N450 should reflect conflict detection in the ‘look’ trials. Besides, since the response executions which will result in strong activation in the fronto-central region, such as the ACC [30], have been excluded in the ‘look’ trials, the conflict detection has not been contaminated by them in these trials. Therefore, the reverse polarity N450 may reflect that the brain recruits more resources to process colors when facing the interruption from incongruent color-word codes in incongruent condition than in congruent condition. Indeed, evidence from patients with ACC damage [28] and monkeys with ACC lesions [29] show the intact conflict adjustment. However, it disappears entirely following DLPFC lesions [29]. These results indicate that the DLPFC plays a critical role in conflict adjustment.

The amplitude modulation of SP in the posterior parietal region started at 700 ms post-stimulus onset. The latency difference between N450 and SP may reflect the minimal time requirement (about 200 ms) between conflict detection and reconfiguration of
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Figure 3. Electrophysiological results in the ‘do’ trials. Panel A illustrates the stimulus-locked grand-averaged ERP waveforms for cc, cl, IC, and il conditions in the left-frontal (F1, F3, FC1, FC3, and FC5), right-frontal (F4, FC2, and FC4), fronto-central (FC2, FC4, Cz, and C2), and centro-parietal (P2, P1, POz, and CPz) scalp regions. Panel B illustrates the mean amplitudes of N450 (400–450 ms) and SP (700–800 ms) for cc, cl, IC, and il conditions in the right-frontal and centro-parietal regions. Significant interactions between the congruency of ‘look’ trials and the congruency of ‘do’ trials are found for the amplitude modulations of both N450 and SP, which index neural adaptation. Panel C shows that the topographies of the N450 are different from those of the SP. Although the activated topography distributions of N450 and N450 were contrasting with the SP and SP, those of the SP and SP are similar. The patterns suggest that the amplitude modulations of SP and N450 in the right-frontal and centro-parietal scalp regions reflect neural adaptation. Panel D illustrates the time-frequency distributions of the effective connectivity from centro-parietal scalp region to right-frontal scalp region for il and cl conditions. X-axis, time (ms); Y-axis, frequency (Hz). Significant increase of effective connectivity from centro-parietal scalp region to right-frontal scalp region is observed in the theta band (180–330 ms, 6–7 Hz) for il compared to cl condition. The white vertical bars indicate the stimulus onset. NB. ‘c or C’ are the congruent condition, ‘i or I’ are the incongruent condition; cl, IC, il, and ilC respectively refer to incongruent trials preceded by congruent trials, congruent trials preceded by congruent trials, incongruent trials preceded by incongruent trials, and incongruent trials preceded by congruent trials. ‘PDC’ is partial directed coherence. doi:10.1371/journal.pone.0057912.g003

the cognitive system for conflict adjustment [69,70]. Previous studies have indicated that the amplitude modulation of SP in the posterior parietal region was associated with conflict adaptation [38,55,61] or response selection [39]. Whereas there is no response execution in the ‘look’ trials, we propose that the amplitude modulation of posterior parietal SP may reflect the processing of information reconfiguration or control preparation [35].

In general, a activated brain area will favor its function execution in completing the forthcoming task [15]. In fact, the significantly positive correlation between the amplitude of SP and the RT in the posterior parietal region in the ‘look’ trials and the RT in the ‘do’ trials (Fig. 2D) suggested that the larger amplitude of SP predicts the stronger conflict adaptation. Since the PPC has been shown to play a role in the resolution of stimulus-based conflict [23] or motor preparatory activity [26], the amplitude modulation of SP in the posterior parietal region may reflect the resolutions of stimulus conflict or imaginary response conflict. In addition, the amplitude modulations of SP in the right-frontal region indicate that the conflict information may be maintained in the DLPFC [29].

About in the N450 and SP time windows in the ‘look’ trials, the effective connectivity results showed a stronger cortical information flow from right-frontal scalp region to posterior parietal scalp region in the beta band (20–21 Hz, 300–500 ms and 700–900 ms) for incongruent than for congruent condition (Fig. 2C). Although the spatial resolution limitations of using EEG/ERP methods, it suggests that the information related to conflict detection may have been effectively transferred from right-frontal region to posterior parietal region. These results can be explained by the proposes that the beta-band modulation supports the maintenance of the current sensorimotor or cognitive state [71].

In the ‘do’ trials, the interaction between the congruency of ‘look’ trials and the congruency of ‘do’ trials for N450 amplitude was significant in the right-frontal and centro-parietal regions (Fig. 3B). The topographies showed that larger amplitude for N450 than for N450 were evoked in these regions; but the left-frontal or fronto-central regions were not affected by the incongruent-look context. Furthermore, the topography clearly indicated the right-frontal and centro-parietal distributions of N450 (Fig. 3C). Recent studies in healthy human and individuals with mild and moderate-to-severe traumatic brain injury [38,30,54,55,72,73] also did not show conflict adaptation for the fronto-central N450. The present study found that down conflict adaptation was embodied in the amplitude modulations of N450 in the right-frontal and centro-parietal regions, which corroborated and expanded the previous studies. Thus, we think that the larger N450 amplitude suggests that the conflict of ‘look’ trials may have enhanced the sensitivity of the brain to the conflict occurrence. In addition, the latency of N450 was shorter in the ‘do’ trials than in the ‘look’ trials, maybe implying that the conflict detection is easier and earlier in the ‘do’ trials.

Interestingly, in the ‘do’ trials, the interaction between the congruency of ‘look’ trials and the congruency of ‘do’ trials for SP...
amplitude was significant in the right-frontal and centro-parietal regions (Fig. 3B). Furthermore, the topography distribution of SP\(_{cI\rightarrow cC}\) mainly implicated the right-frontal and centro-parietal regions (Fig. 3C, right), which was driven by stronger SP\(_{cI\rightarrow cC}\) compared to SP\(_{iI\rightarrow iC}\) activation in the centro-parietal region. In the literature, the SP has been associated with multiple functions, including general preparation [35], conflict processing [36,37,41,42], response selection [39], and conflict adaptation [38]. The focused activation in the centro-parietal region indicates that executing responses in the ‘do’ trials may need the brain to recruit most of cognitive resources to conduct the response-related processing (e.g., response selection or response-conflict resolution). Accordingly, we suggest that the amplitude modulations of SP in the ‘do’ trials are affected by the ‘look-trial’ congruency, and therefore reflect conflict adaptation.

It is worth noting that there was no significant RT difference between il and cl conditions in the ‘do’ trials. However, as revealed by effective connectivity in the ‘do’ trials, the cortical information is more consistently flowed from centro-parietal scalp region to right-frontal scalp region in the theta band (6–7 Hz, 180–330 ms) for il compared to cl condition. This performance-invariant neural difference in effective connectivity may reflect the basic neural mechanisms of conflict adaptation. Namely, the evaluation of conflict occurrence and regulation of control can be reflected in the theta-band modulation in human brain. Therefore, the present result provides novel evidence for understanding the course of information exchange between different brain areas related to conflict detection and potential conflict resolution in cognitive control.

In conclusion, using the novel look-to-do transition design, the profile of conflict adaptation can be clearly determined. In the ‘look’ trials, the amplitude modulation of N450 (480–550 ms) in the right-frontal region reflects conflict detection. A more effective information flow is transferred from right-frontal region to posterior parietal region in incongruent compared to congruent condition. The amplitude modulation of SP appears in the posterior parietal region (700–800 ms), frontal- and parietal-regions (800–900 ms). In the post-‘look’ ‘do’ trials, conflict adaptation is reflected in the amplitude modulations of N450 and SP in the right-frontal and parietal regions. Moreover, a more effective information flow is transferred from centro-parietal region to right-frontal region for il compared to cl condition. The present findings reveal that conflict adaptation mediates the cortical processing involving in the interaction of multiple functionally specialized cortical regions by enhancing the sensitivity to conflict detection and the adaptation to conflict resolution.

**Author Contributions**
Conceived and designed the experiments: DT AC QZ HL. Performed the experiments: DT. Analyzed the data: DT LH AC. Contributed reagents/materials/analysis tools: LH. Wrote the paper: DT AC.
References

1. Miller EK, Cohen JD (2001) An integrative theory of prefrontal cortex function. Annual review of neuroscience 24: 167–202.

2. Posner MI, Snyder CRR (1975) Attention and cognitive control. In R.L. Solso (Ed.) Information processing and cognition: The Loyola symposium pp.455-83. Hildale, NJ: Erlbaum.

3. Stroop JH (1933) Studies of interference in serial verbal reactions. Journal of Experimental Psychology 18: 643–662.

4. Gratton G, Coles MG, Donchin E (1992) Optimizing the use of information: Strategic control of activation of responses. Journal of Experimental Psychology: General 121: 480–506.

5. Mayr U, Awh E, Laurey P (2003) Conflict adaptation effects in the absence of cognitive control: Nature Neuroscience 6: 450–452.

6. Hommel B, Proctor RW, Vu KPL (2004) A feature-integration account of sequential effects in the Simon task. Psychological research 68: 1–17.

7. Egner T, Raas M (2007) Cognitive control processes and hypothesis. Hypnosis and conscious states: the cognitive neuroscience perspective 29.

8. Mayr U, Awh E (2009) The elusive link between conflict and conflict adaptation. Psychological research 73: 794–802.

9. Liu P, Chen A, Li G, Li H, West R (2012) Conflict adaptation is reflected by response interference. Journal of Cognitive Psychology 24: 457–467.

10. Bovtvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD (2001) Conflict monitoring and cognitive control. Psychological review 108: 624–652.

11. Botvinick MM, Cohen JD, Carter CS (2004) Conflict monitoring and anterior cingulate cortex: an update. Trends in Cognitive Sciences 8: 339–346.

12. Carter CS, van Veen V (2007) Anterior cingulate cortex and conflict detection: an update of theory and data. Cognitive, Affective, & Behavioral Neuroscience 7: 367–379.

13. Verguts T, Notteboert W (2008) Hebbian learning of cognitive control: Dealing with specific and nonspecific adaptation. Psychological review 115: 518–525.

14. Monsour AF, Tanaka K, Buckley MJ (2009) Conflict-induced behavioral adjustment: a clue to the executive functions of the prefrontal cortex. Nature Reviews Neuroscience 10: 141–152.

15. Kim CS, Matalon S, Hare TA, Davidson MC, Casey B (2006) Anterior cingulate conflict monitoring and adjustments in control. Science 303: 1023–1026.

16. Egner T, Hirsch J (2005) The neural correlates and functional integration of cognitive control in a Stroop task. NeuroImage 24: 539–547.

17. Egner T, Hirsch J (2005) Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. Nature Neuroscience 8: 1784–1790.

18. Liston C, Matalon S, Hare TA, Davidson MC, Casey B (2006) Anterior cingulate and posterior parietal cortices are sensitive to dissociable forms of conflict in a task-switching paradigm. Neuron 50: 643–653.

19. di Pellegrino G, Ciaramelli E, Ladavas E (2007) The regulation of cognitive control following rostral anterior cingulate cortex lesion in humans. Journal of Cognitive Neuroscience 19: 273–286.

20. Posner MI, DiGirolamo GJ (1988) Executive attention: Conflict, target detection, and cognitive control. The Royal Society 353: 1915–1927.

21. Markela-Lerenc J, Ille N, Kaiser S, Fiedler P, Mundt C, et al. (2004) Prefrontal–dorsolateral prefrontal cortex in conflict-induced behavioral adjustment. Science 303: 1784–1790.

22. Sauseng P, Klimesch W (2008) What does phase information of oscillatory brain activity tell us about cognitive processes? Neuroscience & Biobehavioral Reviews 32: 1001–1013.

23. Granger CWJ (1969) Investigating causal relations by econometric models and cross-spectral methods. Econometrica: Journal of the Econometric Society: 424–438.

24. Huang K, Vrakasova K, Luca B (2010) Strengthening of top-down frontal cognitive control networks underlying the development of inhibitory control: a functional magnetic resonance imaging effective connectivity study. The Journal of Neuroscience 30: 15353–15354.

25. Peng W, Hu L, Zhang Z, Yang H (2012) Causality in the Association between P300 and Alpha Event-Related Desynchronization. PLoS One 7: e34163.

26. Bruce D, Wagner AD (2004) Selection, Integration, and Conflict Monitoring: Assessing the Nature and Generality of Prefrontal Cognitive Control Mechanisms. Neuron 41: 473–487.

27. Donohue SE, Liston C, Perez R, Woldorff MG (2011) Is conflict monitoring supramodal? Spatiotemporal dynamics of cognitive control processes in an auditory Stroop task. Cognitive, Affective, & Behavioral Neuroscience: 1–15.

28. Larson MJ, Glassco A, Clayson PE, South M (2012) Cognitive Control and Conflict Adaptation Similarities in Children and Adults. Developmental Neurobiology 37: 343–357.

29. Akay C, Hazeleline E (2007) Conflict monitoring and feature overlap: Two routes of sequential modulations. Psychonomic bulletin & review 14: 742–748.

30. Purnam S, Babde S, Wendt M (2009) Adjustments to recent and frequent conflict reflect two distinguishable mechanisms. Psychonomic bulletin & review 16: 350–355.

31. Hazeleline E, Lighteman E, Schwarz H, Schumacher EH (2011) The boundaries of sequential modulations: Evidence for set-level control. Journal of Experimental Psychology: Human Perception and Performance 37: 1898–1914.

32. Larson MJ, Farrow TJ, Clayson PE (2011) Cognitive control in mild traumatic brain injury: Conflict monitoring and conflict adaptation. International Journal of Psychophysiology 82: 69–78.

33. Larson MJ, Kaufman DAS, Perlstein WM (2009) Conflict adaptation and cognitive control adaptations following traumatic brain injury. Journal of the International Neuropsychological Society 15: 927–937.

34. Chen A, Bailey K, Tiernan BN, West R (2011) Neural correlates of stimulus and nonresponse conflict. Psychophysiology 48: 1621–1630.
62. Hu L, Zhang Z, Hu Y (2012) A time-varying source connectivity approach to reveal human somatosensory information processing. NeuroImage 62: 217–228.
63. Granger CWJ (1969) Investigating causal relations by econometric models and cross-spectral methods. Econometrica 37: 424–438.
64. Baccala LA, Sameshima K (2001) Partial directed coherence: a new concept in neural structure determination. Biol Cybern 84: 463–474.
65. Freitas AL, Bahar M, Yang S, Banai R (2007) Contextual adjustments in cognitive control across tasks. Psychological Science 18: 1040–1043.
66. Lamers MJM, Roelofs A (2011) Attentional control adjustments in Eriksen and Stroop task performance can be independent of response conflict. The Quarterly Journal of Experimental Psychology 64: 1056–1081.
67. Uliger M, Bylsma LM, Botvinick MM (2005) The conflict adaptation effect: It’s not just priming. Cognitive, Affective, & Behavioral Neuroscience 5: 467–472.
68. Milde T, Leistritz L, Astolfi L, Mittner WHR, Weiss T, et al. (2010) A new Kalman filter approach for the estimation of high-dimensional time-variant multivariate AR models and its application in analysis of laser-evoked brain potentials. NeuroImage 50: 960–969.
69. Muller HJ, Rabhiit PM (1989) Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. Journal of Experimental Psychology: Human Perception and Performance 15: 315–330.
70. Notebaert W, Gevers W, Verbruggen F, Liefooghe B (2006) Top-down and bottom-up sequential modulations of congruency effects. Psychonomic bulletin & review 13: 112–117.
71. Engel AK, Fries P (2010) Beta-band oscillations-signalling the status quo? Current Opinion in Neurobiology 20: 156–165.
72. Larson MJ, Clayson PE, Farrer TJ (2012) Performance Monitoring and Cognitive Control in Individuals with Mild Traumatic Brain Injury. Journal of the International Neuropsychological Society 18: 323–333.
73. Larson MJ, Clayson PE, Baldwin SA (2012) Performance monitoring following conflict: Internal adjustments in cognitive control? Neuropsychologia 50: 426–433.