



# Distinct Brain Mechanisms for Conflict Adaptation within and across Conflict Types

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## Abstract

■ Cognitive conflict, like other cognitive processes, shows the characteristic of adaptation, that is, conflict effects are attenuated when immediately following a conflicting event, a phenomenon known as the conflict adaptation effect (CAE). One important aspect of CAE is its sensitivity to the intertrial coherence of conflict type, that is, behavioral CAE occurs only if consecutive trials are of the same conflict type. Although reliably observed behaviorally, the neural mechanisms underlying such a phenomenon remains elusive. With a paradigm combining the classic Simon task and Stroop task, this fMRI study examined neural correlates of conflict adaptation both within and across conflict types. The results revealed that when the conflict type repeated (but not when it alternated), the CAE-like neural

activations were observed in dorsal ACC, inferior frontal gyrus (IFG), superior parietal lobe, and so forth (i.e., regions within typical task-positive networks). In contrast, when the conflict type alternated (but not when it repeated), we found CAE-like neural deactivations in the left superior frontal gyri (i.e., a region within the typical task-negative network). Network analyses suggested that the regions of ACC, IFG, superior parietal lobe, and superior frontal gyrus can be clustered into two antagonistic networks, and the ACC–IFG connection was associated with the within-type CAE. This evidence suggests that our adaptation to cognitive conflicts within a conflict type and across different types may rely on these two distinct neural mechanisms. ■

## INTRODUCTION

Adaptation is an important property of many cognitive and neural processes, which can occur at different cognitive levels when we are repetitively exposed to the same type of stimuli (Clifford & Palmer, 2018; Thompson & Burr, 2009; Zinke, Schweinberger, Kaufmann, & Kawahara, 2009). At higher levels of cognition, adaptation has been used as a research tool to probe the process of cognitive control, typically via adaptations in conflict processing. The conflict effect decreases after encountering an incongruent event relative to encountering a congruent event, a phenomenon known as the conflict adaptation effect (CAE; Duthoo, Abrahamse, Braem, Boehler, & Notebaert, 2014; Gratton, Coles, & Donchin, 1992). Importantly,

behavioral CAEs are highly sensitive to the coherence of the conflict type in adjacent trials, that is, CAEs happen only when consecutive trials belong to the same conflict type (e.g., a Stroop type of conflict vs. a Simon type of conflict). For instance, in a typical Stroop–Simon task (Egner, Delano, & Hirsch, 2007), the Stroop conflict could be better resolved (with a smaller conflict effect) if the previous trial is a Stroop incongruent (StI) condition, but not if the previous trial is a Simon incongruent (SmI) condition. Although this sensitivity of the CAE has been extensively reported and discussed at behavioral level (for a review, see Braem, Abrahamse, Duthoo, & Notebaert, 2014), the corresponding neural mechanisms are still unclear.

There has been strong evidence that CAE reflects the adjustment of cognitive control (Kerns, 2006; Kerns et al., 2004). It is believed that the monitoring of a conflict trial could act as an alerting signal and trigger higher level of control execution in the following trials (Botvinick, Cohen, & Carter, 2004; Botvinick, Braver, Barch, Carter, & Cohen, 2001). Therefore, in the subsequent trials, more attention will be biased to the task-relevant stimulus and less to the task-irrelevant stimulus (Egner, 2007). This explains the decrease of post-incongruent conflict effect. It is worth noting that some researchers argue that the CAE could reflect the stimulus-based feature integration instead, because the repetition of congruency usually co-occur with the repetition of stimulus and/or response (Hommel, Proctor, & Vu, 2004; Mayr, Awh, & Laurey,

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2003). Nevertheless, a number of studies have shown robust CAEs when the stimulus-based influences were eliminated (Schmidt & Weissman, 2014; Weissman, Jiang, & Egner, 2014). The type-sensitive CAE has also been proven to be unaffected whether containing or removing the stimulus-related factors (Weissman, 2020; Akcay & Hazeltine, 2011).

A behavioral CAE is commonly defined as the RT difference between the conflict effect after a congruent trial and the conflict effect after an incongruent trial, as described by the following equation:

$$CAE = (RT_{CI} - RT_{CC}) - (RT_{II} - RT_{IC}) \quad (1)$$

where C and I are the abbreviations of congruent and incongruent, respectively (Nieuwenhuis et al., 2006). To investigate sensitivity of the CAE to intertrial coherence on conflict type, the CAE-related brain activities in both within-type and across-type conditions need to be examined and compared (eight conditions). However, previous studies have examined brain areas showing a CAE-like neural activation (i.e., neural activities of the four conditions are submitted to Equation 1, and a CAE-like neural activation is detected when this calculation yields a significant effect) mainly within the same conflict type (Chun, Park, Kim, Kim, & Kim, 2017; Chechko, Kellermann, Schneider, & Habel, 2014; Egner & Hirsch, 2005b; Carter et al., 2000), and the neural mechanisms understanding the loss of CAE in across-type conditions have rarely been examined. Therefore, in this study, to explore the full picture of the neural correlates of CAEs, especially the neural mechanisms underlying sensitivity to conflict type, it was necessary to perform the analysis based on its definition in both conflict type repetition and alternation conditions (see Methods for details).

To date, there have been only a limited number of ERP studies and ROI studies attempting to reveal the mechanisms underlying the conflict-type sensitivity. N2 and P3, two components corresponding to the mental processing of conflict detection and attention allocation (Clayson & Larson, 2011), were found to show a CAE only when the consecutive conflict sequences were repeated (Q. Li et al., 2015; Z. Li et al., 2021). In addition, an ROI-based fMRI study observed the conflict-type sensitivity functions that focused on the conflict detection region (i.e., ACC) and executive control regions (i.e., premotor cortex and dorsolateral pFC; Kim, Chung, & Kim, 2010, 2012). These studies together implied that the lack of behavioral CAEs in conflict alternation conditions might reflect the absence of conflict detection, attention allocation, and executive control mechanisms in alternating conflict-type sequences. However, the low spatial resolution of ERP technology (Q. Li et al., 2015; Z. Li et al., 2021) and the ROI-based method (Kim et al., 2010, 2012) cannot describe the whole picture of neural processing in CAEs sensitive to conflict types. It remains possible that other CAE-related brain areas reported in previous studies, such as the superior

parietal lobe (SPL; Egner et al., 2007) and inferior frontal gyrus (IFG; Egner, 2011), may also show conflict-type-sensitive CAE.

Moreover, previous studies showed that the CAE is also related to functional connectivity between key regions. For example, the connectivity between ACC and the prefrontal regions has been linked to the CAE (Chen et al., 2008; Kerns et al., 2004). Another study also showed that the CAE involves the functional connectivity between ACC and the salience network (such as the insula and anterior frontal regions), as well as the connectivity between posterior parietal cortex and the central executive network (such as the anterior and middle frontal cortex); moreover, these connectivities predicted the behavioral CAE performances (Wang et al., 2015). However, it is not clear how functional connectivity is related to the type sensitivity of CAE. Hence, in this study, we analyzed connectivity among key brain regions that are related to CAE, characterized their potential network properties, and tested the correlation between such functional connectivity and behavioral CAE.

The current study aimed to elucidate the neural mechanisms of the sensitivity of the CAE to conflict type with a whole-brain exploratory method. We adopted a Stroop–color–Simon paradigm and collected fMRI data during the task performance. This paradigm has been reported to be valid in producing robust behavioral and neural conflict-type-sensitive CAEs (Wang, Li, Zheng, Wang, & Liu, 2014; Liu, Park, Gu, & Fan, 2010). Stroop and Simon are usually regarded as two dissociated paradigms in cognitive control mechanisms. According to a dimensional overlap structure, Stroop conflict effect derives from the overlap between task-relevant and task-irrelevant stimuli and thus belongs to the so-called stimulus–stimulus type; in comparison, the Simon conflict effect derives from the overlap between task-irrelevant stimulus and response and thus belongs to the so-called stimulus–response type (Kornblum, Hasbroucq, & Osman, 1990). We hypothesize that the conflict processing-related brain areas, such as the cingulo-opercular and frontoparietal regions (Q. Li et al., 2017), would show CAE-like neural activities (mirroring behavioral CAEs, with a significant interaction between previous congruency and current congruency conditions) only in conflict-type repetition (hereafter, Repetition) but not in conflict-type alternation (hereafter, Alternation) conditions. Additionally, we predict that the brain networks showing conflict-type-sensitive CAEs could predict the behavior.

## METHODS

### Participants

Twenty right-handed volunteers took part in the experiment. One participant was removed from the statistical analysis because of excessive head motion (rotation  $>2^\circ$  in two runs). The final sample consisted of 19 participants

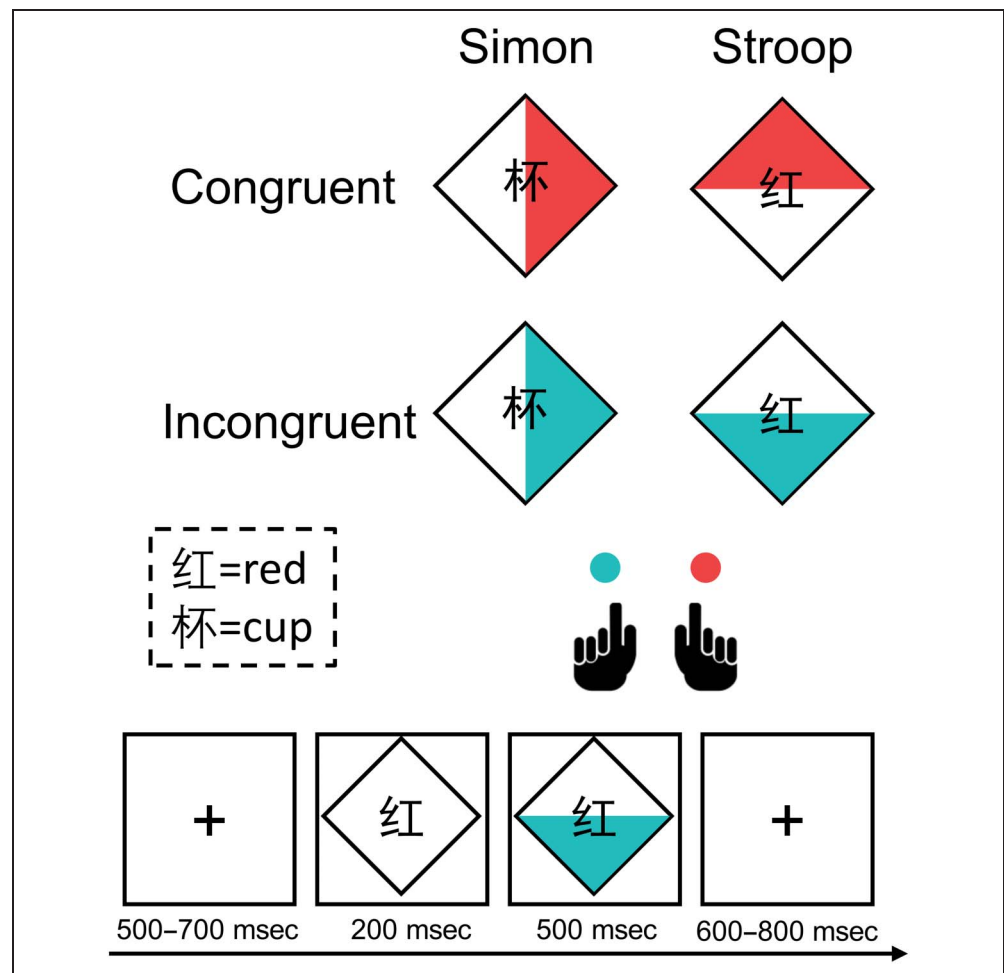
(11 women, aged  $19.9 \pm 1.8$  years). The sample size was decided based on previous fMRI studies detecting similar CAE effects (Chun et al., 2017; Purmann & Pollmann, 2015; Kim et al., 2012). All participants were healthy, with normal or corrected-to-normal visual acuity, and were free of psychiatric or neurological history. Before the experiment, all participants signed an informed consent form that was approved by the institutional review board of the Institute of Psychology, Chinese Academy of Sciences. All participants received a small fee for their participation.

### Apparatus, Stimuli, and Procedure

The paradigm was adopted from previous studies (Wang et al., 2014; Liu et al., 2010) and modified for the fMRI experiment (Figure 1). Stimulus presentation was controlled by E-Prime 2.0 (Psychological Software Tools, Inc.). The stimulus was a center-displayed diamond (visual angle  $4.9^\circ \times 4.9^\circ$ ), with half (a rectangular triangle) painted either red or blue. The triangle pointed in one of four directions (left, right, up, and down). A Chinese character indicating a color (i.e., “红” [red], or “蓝” [blue]) or having a neutral meaning (i.e., “杯” [a cup], and “莫” [do not]) displayed in black ink

was overlaid in the center of the diamond. There are several reasons for the selection of these two neutral words. First, we would like to generate “pure” Simon conditions, in which the overlaid word in the Simon condition should not be “red” or “blue”; second, we did not select other color words (e.g., “yellow”) as neutral words because they may introduce a kind of semantic interference with the color naming task (Liu, Banich, Jacobson, & Tanabe, 2006; Milham et al., 2001); third, we selected the Chinese characters “杯” and “莫” because they had similar structures with “红” (with left and right components) and “蓝” (with top, middle, and bottom components), respectively, and thus avoided a salience effect if the neutral words looked very different with the color words. All stimuli were presented on a gray background. The participants were instructed to make a left or right key press based on the color of the triangle (red or blue) while ignoring the other information and to respond as quickly and accurately as possible. Before scanning, the participants were trained to become familiar with the task. The participants were allowed to enter the scanner to perform a formal test when their training accuracy reached 90%. Color response mapping was counterbalanced across participants.

**Figure 1.** Experimental design and procedures. Participants were asked to respond to the color of the triangle and ignore any other information.



There were two types of conflicts (i.e., Stroop and Simon conflicts) during the test. In the Stroop conflict, the overlaid word was randomly chosen from “red” and “blue.” When the word matched the color of the triangle (e.g., the word is “red,” and the triangle color is also red), it would be the Stroop congruent (StC) condition; otherwise (e.g., the word is “red” but the triangle color is blue), it would be the StI condition. In addition, to avoid a mixture of Simon conflict (see below), the direction of the triangle in the Stroop conditions was always vertical (i.e., up or right). In the Simon conflict, the direction of the colored triangle was randomly chosen from left and right. The consistency between the orientation of the triangle and the response hand (left or right) determined the Simon congruency, that is, Simon congruent (SmC; e.g., a left-oriented red triangle that maps to the left response) or SmI (e.g., a right-oriented red triangle that maps to the left response). In addition, to avoid a mixture of Stroop conflict, the overlaid word in the Simon conditions were always neutral meaning (i.e., “cup” or “do not”). Note that the physical features are totally matched between the incongruent and congruent conditions for both Stroop and Simon conflicts, so the conflict effect (i.e., incongruent condition minus congruent condition) and CAE (i.e., Equation 1) could counteract the possible influence of physical stimuli. Therefore, our analyses are free from stimulus difference. Moreover, despite the seeming distinction between Stroop and Simon conditions, we kept the task (i.e., to judge the color of the triangle) the same across the two conflicts, so that the participants were free from task switching.

The participants performed four test sessions. Each session consisted of 162 trials listed in a pseudorandom fashion, with equal numbers of StI, StC, SmI, and SmC trials intermixed randomly and equal probability of each secondary trial sequence (e.g., StC–SmI, SmC–StC). The pseudorandom lists were generated with the TransGen function of AFNI software. Each trial lasted 2000 msec, with a prestimulus fixation icon presented centrally for 100–300 msec, followed by a white diamond with a character in the middle (700 msec); 200 msec after the onset of the diamond, the task stimulus (a colored triangle) appeared and lasted for 500 msec, after which a poststimulus fixation icon was presented for 600–800 msec. The participants were allowed a maximum of 1500 msec from the onset of the target display to respond. In addition, to better estimate the event-related fMRI signals, 55 blank trials with only the fixation icon, each lasting 2000 msec, were inserted into each session, dividing each long run into multiple miniblocks. The number of fixation trials between miniblocks followed the exponential distribution. There was no intertrial interval.

### Behavioral Data Analysis

Data were analyzed with dependent variables of both RT and error rate (ER). To avoid misleading potential

conflicting RT and ER results, we also calculated the linear integrated speed–accuracy score (LISAS), an index that has been proven to efficiently account for the variance in behavioral measures (Vandierendonck, 2017). The LISAS was calculated with the following equation:

$$\text{LISAS} = \text{RT} + \frac{\text{SD}_{\text{RT}}}{\text{SD}_{\text{ER}}} \times \text{ER} \quad (2)$$

in which the RT and ER denote the mean RT and ER of a certain condition (e.g., StC) in a certain participant, and the  $\text{SD}_{\text{RT}}$  and  $\text{SD}_{\text{ER}}$  denote the overall standard deviation (*SD*) of the same participant computed with RT and ER data, respectively.

The first trial of each miniblock (10.5%), error trials (3.7%), correct trials after an error trial (3.2%), and trials with RTs beyond 3 *SD*s of the mean or shorter than 200 msec (0.4%) were excluded before analyzing the interaction between previous congruency and current congruency (i.e., the CAE). We conducted three-way repeated-measures ANOVAs of Consecutive Conflict Type (2, Repetition vs. Alternation)  $\times$  Previous Congruency (2, Congruent vs. Incongruent)  $\times$  Current Congruency (2, Congruent vs. Incongruent) with RT, ER, and LISAS, respectively. The interaction between Consecutive Conflict Type and CAE was our major analysis of interest. Figure 2 illustrates how the CAE is calculated from different conditions and the hypothesized behavioral CAE results.

### Image Acquisition

Functional imaging was performed on a 3-T Trio scanner (Siemens Medical Systems) using EPI sensitive to BOLD contrast (in-plane resolution of  $3.4 \times 3.4 \text{ mm}^2$ ,  $64 \times 64$  matrix, 32 slices with a thickness of 3 mm and an interslice skip of 0.99 mm, repetition time of 2000 msec, echo time of 30 msec, and a flip angle of  $90^\circ$ ). In addition, a sagittal T1-weighted anatomical image was acquired as a structural reference scan, with a total of 128 slices at a thickness of 1.33 mm with no gap and an in-plane resolution of  $1.0 \times 1.0 \text{ mm}^2$ .

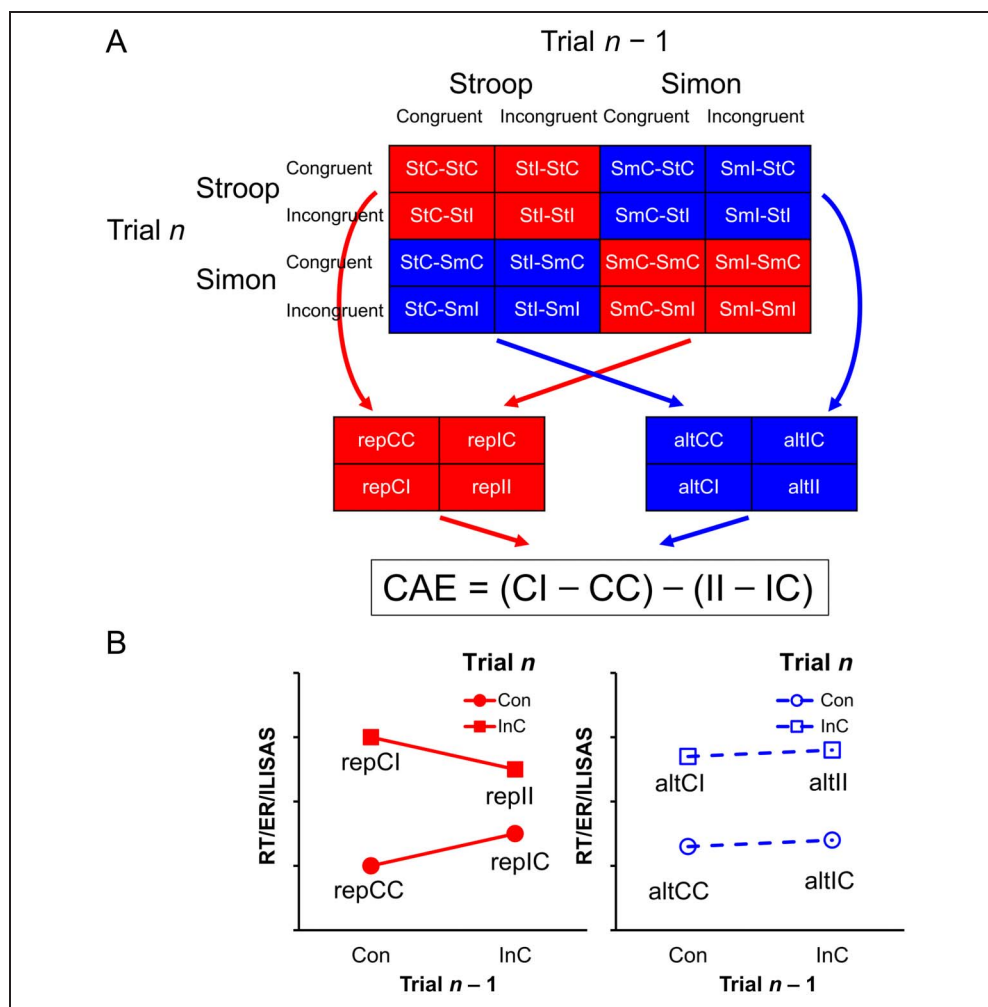
### Image Processing

#### Preprocessing

The acquired images were processed using SPM12 software ([www.fil.ion.ucl.ac.uk/spm/](http://www.fil.ion.ucl.ac.uk/spm/)). For each participant and for each functional run, the first five volumes were discarded. The remaining images were corrected for head movement between scans by an affine registration. In one of the 20 participants, head movements of rotation within two of four functional runs exceeded  $2^\circ$  and therefore was excluded from further analyses. The T1 image was segmented into gray matter, white matter, cerebrospinal fluid, skin, skull, and air. The head-motion-corrected functional images were aligned to the T1-weighted anatomical image through rigid body registration. Then, the EPI images were spatially normalized to standard Montreal Neurological Institute (MNI) space using the spatial



**Figure 2.** An illustration of the different conditions in our design. (A) Structure of the sequence conditions defined by the combinations of the trial  $n - 1$  and trial  $n$  congruency conditions. The Stroop–Stroop (both trial  $n - 1$  and trial  $n$  are Stroop) and Simon–Simon conditions are further grouped as the Repetition condition, whereas the Stroop–Simon and Simon–Stroop conditions are grouped as the Alternation condition. CAE could be calculated in both conditions. (B) Hypothesized results of the Repetition and Alternation conditions. St = Stroop; Sm = Simon; C/Con = congruent; I/InC = incongruent; rep = Repetition; alt = Alternation.



normalization parameters that mapped the structural image to the MNI space template. Normalized data were smoothed using an 8-mm FWHM Gaussian kernel.

### Whole-brain Analysis

For statistical analysis, fMRI data were analyzed using a two-level hierarchical general linear model. The first-level design matrix modeled fixed effects over the four sessions of smoothed data. Each session was modeled using eight event-related regressors, one for each of the conflict sequence conditions (repeated, altered, incongruent, and congruent components represented by rep, alt, I, and C, respectively, to define the conditions as repCC, repCI, repIC, repII, altCC, altCI, altIC, and altII). In addition, another regressor modeled errors/missed trials, and six regressors of no interest contained the realignment parameters to correct for motion artifacts. The eight conditions and the error regressors were convolved with a canonical hemodynamic response function in SPM. Low-frequency signal drifts were filtered using a cutoff period of 128 sec. Linear  $t$ -contrasts for CAE (CI-CC vs. II-IC) as

well as the reverse contrast in Repetition and Alternation conditions were tested. We also examined the first-order contrasts (I vs. C and its reverse contrast) on average for all conditions, as well as that for Repetition and Alternation conditions separately (Table 2). In the second level, one-sample  $t$  tests of the above contrasts were analyzed. To explore the whole-brain activities, we adopted the threshold-free cluster enhancement (TFCE) method (Smith & Nichols, 2009), which avoids an arbitrary selection of voxel-level and cluster-level thresholds. A family-wise error threshold of  $p < .05$  (two tails) was then adopted to control the multiple comparison error (Chen et al., 2019). The contrast images in volume were transferred into surface and visualized with Connectome Workbench software (Van Essen et al., 2013).

### Post Hoc Visualizations of CAE-like Neural Activities

To further clarify the specific activation patterns in Repetition and Alternation conditions, we extracted the neural signals from the regions reported in the whole-brain analysis. We tested whether each region showed a type-

sensitive CAE activation (i.e., difference of the CAE-like activities between the Repetition and Alternation conditions) with paired *t* tests and then extracted beta estimation values of each region (for the eight conditions) to illustrate the exact activation patterns.

### Connectivity Analysis

The CONN toolbox (Version 19.c; Whitfield-Gabrieli & Nieto-Castanon, 2012) was used to compute the functional connectivity of different brain areas activated in different conditions. The first peak coordinates of task-positive and task-negative areas reported in the whole-brain analysis (Table 1) were selected as ROIs. The weighted general linear model method was used. By convolving the hemodynamic response function of the temporal BOLD signal, the 10 events (eight task conditions, one error/missing condition, and one rest condition) regressors and their first-order derivatives were included. In addition, six head motions as well as their first-order derivatives, the white matter and the cerebrospinal fluid, were regressed out. The residuals were then used to calculate task-based functional connectivity. The connectivity values of the eight conditions of interest (i.e., repII, repIC, repCI, repCC, altII, altIC, altCI, and altCC) were averaged and then entered into the second-level analysis. The TFCE method built in the CONN toolbox was applied to examine the clusters of functional network connectivity.

## RESULTS

### Behavioral Results

For the RT, we observed a significant main effect of Current Congruency,  $F(1, 18) = 153.37, p < .001, \eta_p^2 = .90$ . Participants' responses were slower in incongruent conditions (445 msec) than in congruent conditions (416 msec), indicating a conflict effect (Figures 3). The main effect of Previous Congruency was also significant,  $F(1, 18) = 7.40, p = .014, \eta_p^2 = .29$ . Participants responded more slowly in post-incongruent conditions (432 msec) than in post-congruent conditions (429 msec), indicating a postconflict slowing effect (Verguts, Notebaert, Kunde, & Wuhr, 2011). We also observed an interaction between Previous Congruency and Current Congruency (i.e., CAE),  $F(1, 18) = 16.17, p = .001, \eta_p^2 = .47$ , suggesting that the conflict effect (incongruent vs. congruent) was significantly smaller after incongruent trials (445 msec vs. 413 msec) than after congruent trials (444 msec vs. 420 msec). Moreover, the interaction among Consecutive Conflict Type, Previous Congruency, and Current Congruency was significant,  $F(1, 18) = 12.15, p = .003, \eta_p^2 = .40$ . Simple effect analyses revealed that there was a significant CAE only in the Repetition condition (16 msec),  $F(1, 18) = 26.19, p < .001$ , but not in the Alternation condition (0 ms),  $F(1, 18) < 0.01, p = .986$ . No other main effects or interactions were observed (Figure 2A).

For the ER, there was a significant main effect of Current Congruency (i.e., conflict effect),  $F(1, 18) = 27.06, p < .001, \eta_p^2 = .60$ . Participants had a higher ER in incongruent conditions (4.2%) than in congruent conditions (1.6%). Importantly, the interaction among consecutive conflict type, Previous Congruency, and Current Congruency was significant,  $F(1, 18) = 4.96, p = .039, \eta_p^2 = .22$ . Simple effect analyses revealed that there was a significant CAE only in the Repetition condition (2.3%),  $F(1, 18) = 4.91, p = .040$ , but not in the Alternation condition (-1.3%),  $F(1, 18) = 2.65, p = .121$ . No other significant main effects or interactions were found (Figure 2B).

For the LISAS, there was a significant main effect of Current Congruency (i.e., conflict effect),  $F(1, 18) = 123.73, p < .001, \eta_p^2 = .87$ . Participants responded more slowly in incongruent conditions (458 LISAS units) than in congruent conditions (421 LISAS units). The interaction between Previous Congruency and Current Congruency (i.e., CAE) was significant,  $F(1, 18) = 13.76, p = .002, \eta_p^2 = .43$ , suggesting that the conflict effect (incongruent vs. congruent) was smaller after incongruent trials (459 LISAS units vs. 417 LISAS units) than after congruent trials (457 LISAS units vs. 425 LISAS units). Moreover, the interaction among Consecutive Conflict Type, Previous Congruency, and Current Congruency conditions was significant,  $F(1, 18) = 20.56, p < .001, \eta_p^2 = .53$ . Simple effect analyses revealed that there was a significant CAE only in the Repetition condition (24 LISAS units),  $F(1, 18) = 26.10, p < .001$ , but not in the Alternation condition (-3 LISAS units),  $F(1, 18) < 1$ . No other main effects or interactions were observed (Figure 2C).

### fMRI Results

#### *Brain Activation Correlates of CAEs: When Conflict Type Repeats versus When It Changes*

When the previous trial was of the same conflict type, the CAE (i.e., greater conflict effect [activation in incongruent condition minus activation in congruent condition] after a congruent trial than the conflict effect after an incongruent trial) is reflected in the activation of the bilateral inferior occipital cortices (IOCs), right SPL, right ACC, right IFG, bilateral caudate, and right fusiform gyrus (Table 1). In contrast, when the conflict type changes between consecutive trials, the conflict effect (incongruent activation minus congruent activation) after a previous congruent trial was found to be greater than that after a previous incongruent trial in the left superior frontal gyri (SFG), also showing CAE-like activities (Figures 4).

#### *Brain Activation Correlates of Conflict Effects*

The average conflict effect was associated with brain areas commonly reported in conflict tasks (Q. Li et al., 2017), including the SMA, inferior parietal lobe, thalamus, precuneus, insula, and IFG. Further analyses showed that the activations were driven by the conflict type repetition condition (see Table 2).

**Table 1.** Brain Activations for CAE Effects in Repetition and Alternation Conditions

Region	L/R	MNI Coordinate (mm)			Volume (No. of Voxels)	Peak Z	BA
		x	y	z			
<i>(CI - CC) &gt; (II - IC), Repetition condition</i>							
Inferior occipital cortex	L	-18	-96	-2	3482	5.98	18
Inferior occipital cortex	R	38	-74	-4	771	4.58	19
Caudate	R	16	2	26	281	4.13	-
SPL	R	20	-50	50	277	4.45	7
Fusiform gyrus	R	38	-44	-10	205	4.49	19
Caudate	L	-16	0	26	109	4.22	-
IFG	R	46	10	18	108	4.43	9
Caudate	L	-14	30	-4	93	3.95	11
Dorsal ACC	R	12	20	48	78	4.00	32
Caudate	L	-18	22	14	69	3.98	-
<i>(II - IC) &gt; (CI - CC), Repetition condition</i>							
None							
<i>(CI - CC) &gt; (II - IC), Alternation condition</i>							
SFG	L	-12	42	44	428	4.33	9
<i>(II - IC) &gt; (CI - CC), Alternation condition</i>							
None							
<i>(CI - CC) &gt; (II - IC), Repetition condition &gt; Alternation condition</i>							
Inferior occipital cortex	L	-18	-100	-4	30	5.23	17
<i>(CI - CC) &gt; (II - IC), Repetition condition &lt; Alternation condition</i>							
None							

L = left; R = right; BA = Brodmann's area; C = congruent; I = incongruent.

### Post Hoc Visualizations of CAE-like Neural Activities

Two-tailed paired *t* tests of the neural-level CAEs revealed a tendency of dissociations between the Repetition and Alternation conditions (Figure 5, bar plots). On the one hand, three of the brain areas showing CAE-like neural activities in the Repetition condition (i.e., SPL, ACC, and caudate) showed significantly decreased activation in the Alternation condition,  $ps < .05$  (Bonferroni-corrected). The other three regions (IOC, fusiform gyrus, and IFG) also showed similar decreased tendencies. In effect, none of these regions showed CAE-like neural activities in the Alternation condition at all,  $ps > .20$ . On the other hand, the SFG region that showed CAE-like neural activity in the Alternation condition

was significantly less activated (and even reversed) in the Repetition condition,  $p = .004$  (Bonferroni-corrected). In addition, we extracted the activations for each of the eight basic conditions (e.g., repIC; Figure 5, line graphs). We found that the areas survived in the Repetition condition were generally positively activated, and the SFG area survived in the Alternation condition was generally negatively activated.

### Verifying the Involvement of Task-positive/Task-negative Networks

Among the brain regions we observed in the Repetition condition, ACC, IFG, and SPL are within the typical task-

**Table 2.** Brain Activations for the First-order Contrast Analysis

Region	L/R	MNI Coordinate (mm)			Volume (No. of Voxels)	Peak Z	BA
		x	y	z			
<i>I &gt; C, all conditions</i>							
SMA	R	10	-4	66	4444	5.22	6
Inferior parietal sulcus	L	-30	-52	36	2259	4.94	40
Inferior parietal sulcus	R	28	-54	44	489	4.3	7
Thalamus	L	-10	-22	14	123	5.25	-
Precentral cortex	L	-44	-2	34	107	4.15	6
Precuneus	R	8	-60	56	93	4	7
Insula	L	-28	24	0	78	5.08	47
IFG	L	-38	12	20	31	3.94	48
<i>I &lt; C, all conditions</i>							
None							
<i>I &gt; C, Repetition condition</i>							
SMA	R	12	-6	72	12260	5.53	6
Inferior parietal sulcus	L	-24	-56	38	7095	4.93	7
Inferior parietal sulcus	L	-38	-56	-32	4792	5.12	39
Inferior occipital gyrus	R	38	-74	-4	3556	4.63	19
IFG	L	-56	16	-2	235	3.96	48
Precentral cortex	L	-52	2	22	42	3.16	6
Postcentral cortex	R	18	-34	-72	22	2.89	4
<i>I &lt; C, Repetition condition</i>							
None							
<i>I &gt; C, Alternation condition</i>							
None							
<i>I &lt; C, Alternation condition</i>							
None							

positive network, whereas the region SFG we observed in the Alternation condition is within the typical task-negative network. To examine whether these task-positive and task-negative brain areas functioned as networks, we computed the functional connectivity between these ROIs. Connectivity analysis revealed two closely connected clusters. One cluster was the negative connections between SFG and

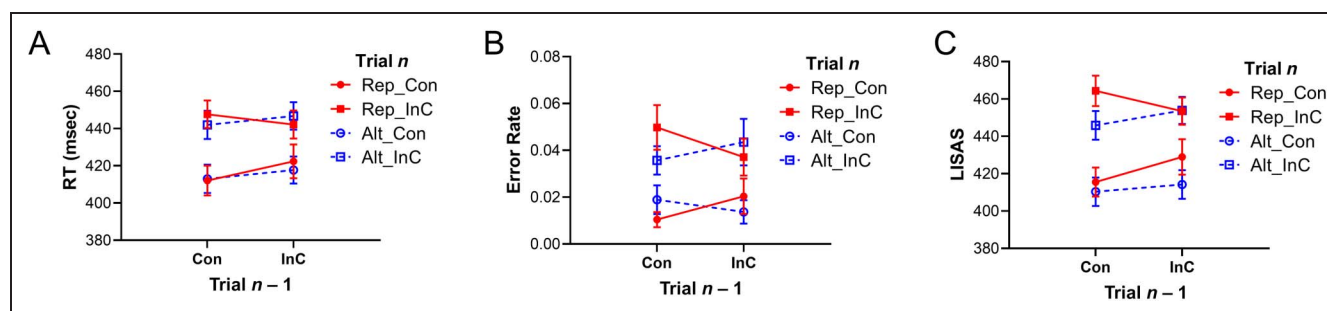
ACC, IFG, and SPL,  $TFCE = 231.83$ ,  $p < .001$ . All three ROI-to-ROI connections (i.e., SFG-ACC, SFG-IFG, SFG-SPL) were significant,  $ps < .001$ . The other cluster constituted the within-network connectivity for the brain areas activated in the Repetition condition, namely, ACC, IFG, and SPL,  $TFCE = 109.18$ ,  $p < .001$ . These three ROI-to-ROI connections were all significant,  $ps < .001$ .



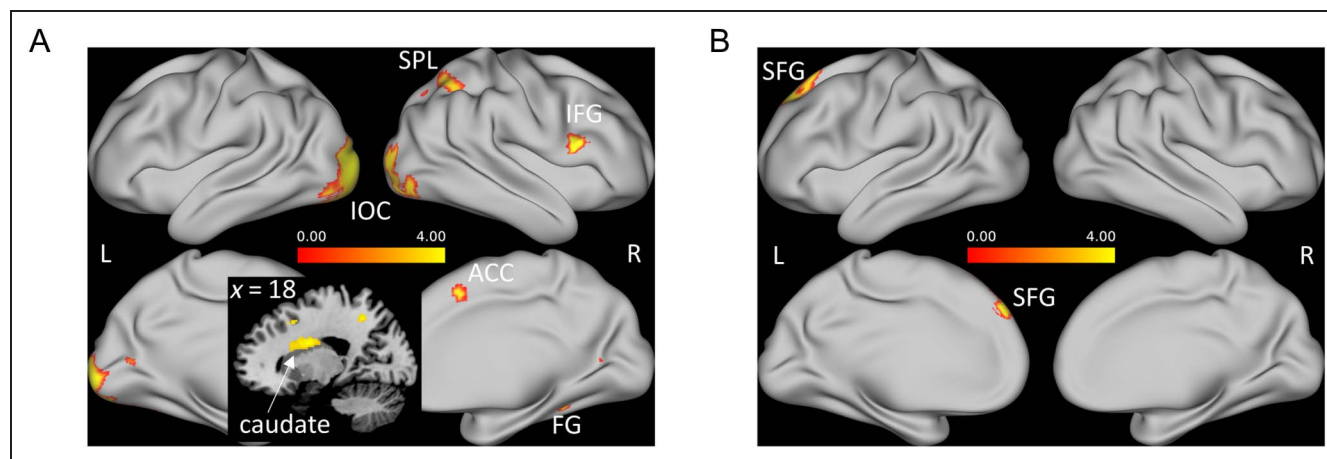
**Table 2.** (continued)

Region	L/R	MNI Coordinate (mm)			Volume (No. of Voxels)	Peak Z	BA
		x	y	z			
<i>I &gt; C, Repetition &gt; Alternation condition</i>							
SMA	R	10	-6	72	1252	4.22	6
Calcarine	L	-24	-56	14	115	3.94	17
Inferior occipital gyrus	L	-32	-70	2	52	3.83	19
Cuneus	R	2	-74	24	39	4.16	18
Inferior occipital gyrus	L	-24	-78	12	11	3.66	19
<i>I &gt; C, Repetition &lt; Alternation condition</i>							
None							

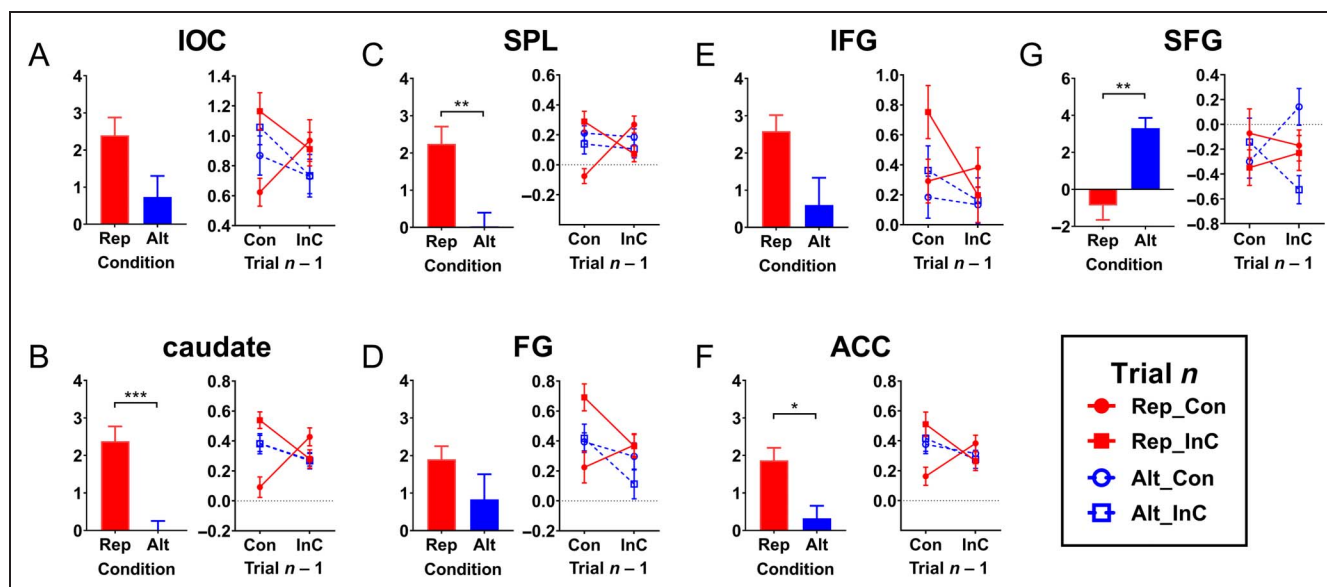
L = left; R = right; BA = Brodmann's area; C = congruent; I = incongruent.



**Figure 3.** Behavioral CAE as measured by RT, ER, and LISAS. When adjacent trials are of the same conflict type, CAE can be observed, that is, an incongruent previous trial leads to a smaller conflict effect than a congruent previous trial does. In contrast, when adjacent trials are of different conflict types, no CAE is observed. Error bars indicate standard errors. Con = congruent; InC = incongruent; Rep = repetition of conflict type; Alt = alternation of conflict type.



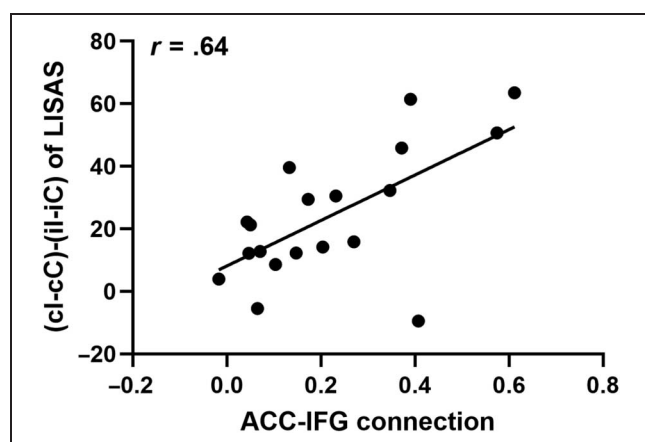
**Figure 4.** Brain correlates of the CAE for (A) Repetition and (B) Alternation conditions, respectively. The displayed brain regions are those survived multiple comparison corrections of the CAE contrast ( $[CI - CC] - [II - IC]$ ). The color scales indicate the Z scores derived from one-sample *t* test of the CAE-like neural activations. IOC = inferior occipital cortex; FG = fusiform gyrus; L = left; R = right.



**Figure 5.** The visualization of the CAE-like brain activities for regions observed in the Repetition condition (A–F) and the Alternation condition (G). The bar plots show the type-sensitive CAE-like neural activities. The line graphs show the beta values as a function of congruent and incongruent conditions for both current and previous trials and their relationship (conflict-type repetition or alternation). The points above the dashed lines denote positive activations. Error bars stand for standard errors. Note that the IOC and the caudate were the mean of their own bilateral subregions.  $*p < .05$ ,  $**p < .01$ ,  $***p < .001$ . Con = congruent; InC = incongruent; Rep = repetition of conflict type; Alt = alternation of conflict type.

#### Correlations between Brain Activities/Connections and Behaviors

Correlation analyses were conducted to examine whether the activities and connections among task-positive and task-negative areas modulated the CAE size. The activated regions within task-positive (ACC, IFG, and SPL) and task-negative (SFG) networks were selected as ROIs. The beta estimates and the connections among ACC, IFG, SPL, and SFG (six connections) were extracted for each participant. We did not find significant correlations between the beta estimations of these areas and the behavioral results. However, we did observe a significant positive correlation between the ACC–IFG connection and the behavioral performance in the Repetition condition,  $r = .643$ ,  $p = .036$  (Bonferroni-corrected; Figure 6).



**Figure 6.** Scatter plot and the fitting line of the correlation between ACC–IFG connection and the behavioral CAE in the Repetition condition.

#### DISCUSSION

With the Stroop–color–Simon paradigm, which discreetly combines the two distinct types of conflict, this study aimed to examine the neural mechanisms underlying the sensitivity of the CAE to the coherence of conflict types. We demonstrated that, with an adequate analytic strategy, CAE-like neural activities can be observed both within a conflict type and between distinct conflict types. Specifically, when the conflict type repeated (but not when it alternated), CAE-like neural activities were manifested as an activation pattern in regions within task-positive networks (i.e., ACC, IFG, and SPL). Whereas when the conflict type alternated (but not when it repeated), CAE-like neural activities were associated with a deactivation pattern in a region within task-negative network (i.e., the SFG). Network analyses suggest that ACC, IFG, and SPL showed synchronous within-network activity; on the other hand, these regions showed antagonistic activity with the SFG. ACC–IFG is also correlated with the behavioral within-type CAE. To our knowledge, this is the first report on the task-negative network correlates of the sensitivity of CAEs in relation to conflict types. These findings extended our understanding of the conflict type-sensitive CAE processing.

#### CAE-like Neural Activities in Task-negative Regions When Conflict Type Alternates

One novel finding of this study is that when conflict type alternates, our neural adaptation to conflicts is related to deactivation of regions within the task-negative network (i.e., the default mode network, DMN), that is, after a

conflict trial of another type, these regions tend to be more deactivated in the current incongruent condition than they do in the current congruent condition.

The DMN was originally characterized as a network of regions consistently being deactivated in non-self-referential, goal-directed tasks, though later, it was better known as a network that becomes active during conscious rest (Raichle, 2015). Meanwhile, many DMN regions can be activated by tasks involving certain implicit processes, such as introspection, and was considered to be the source of “mind wandering” (Andrews-Hanna, 2012). Therefore, the deactivation of the DMN is regarded as a way to reduce internal distraction, which may act as a resource compensation mechanism in demanding tasks (Rajan et al., 2019; Anticevic et al., 2012). Considering these facts, the CAE pattern we observed that, after a conflict trial of another type, DMN regions tend to deactivate further for the current conflict event, may reflect the way how our brain reacts to successive control demand of another cognitive type.

Our network analysis further suggests that activity within these DMN regions tend to be synchronous and are antagonistic to activity of the task-positive network. It seems that the adaptive reaction of our neural system to alternating conflict events is primarily manifested as the deactivation in DMN region rather than reconfiguration in task positive regions.

### CAE-like Activities in Task-positive Regions When Conflict Type Repeats

When a conflict type repeats, the same conflict resolution mechanism is supposed to be involved. Therefore, participants needed to, in real time, mobilize the conflict-processing mechanism that resides in task-positive regions, causing activation in these regions, which were captured by fMRI signals (Kerns et al., 2004; Botvinick et al., 2001).

The task-positive regions (i.e., ACC, IFG, and SPL) we observed well replicated previous studies (Sheth et al., 2012; Egner, 2011; Egner et al., 2007; Kerns, 2006; Egner & Hirsch, 2005a; Kerns et al., 2004). ACC is believed to play a key role in conflict detection during dynamic conflict adjustment (Botvinick et al., 2001; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999), the right IFG is believed to act as the source of online cognitive control in dynamically resolving conflicts (Egner, 2011), and the SPL is believed to bias attention resources toward task-relevant stimuli (Purmann & Pollmann, 2015; Egner et al., 2007; Egner & Hirsch, 2005a). Moreover, we found strong intrinsic connectivity between ACC, IFG, and SPL areas, indicating that the CAE was probably attributable to a broader conception of task-positive networks, which had been largely concealed in previous studies. This idea is consistent with a recent finding that conflict resolution involves widely distributed brain areas (Q. Li et al., 2017). This network view is strengthened by the results that a stronger ACC–IFG connection was associated with a larger behavioral CAE. We thus argue

that the connections between these brain areas are critical for the successful adjustment of control processing.

Akin to the behavioral performance, these task-positive areas showed a conflict-type-sensitive feature, that is, the CAE-like neural activities were not found in these areas when conflict type alternated. These results nicely replicated a previous ERP study (Q. Li et al., 2015) that found conflict type sensitivity on the neural CAE of the N2 component, but we localized the source of domain-specific CAE with a higher spatial resolution. The inactivation of the task-positive areas in the Alternation condition may provide a direct explanation for the loss of the CAE when conflict type alternated. In comparison with the previous perspectives that the dissociated cognitive control mechanisms underlying Stroop and Simon conflicts prevented the CAE from occurring (Kim et al., 2012; Egner, 2008; Egner et al., 2007; Egner & Hirsch, 2005b), we shed light on the dynamic mechanisms underlying the loss of cross-conflict CAEs.

### Type-sensitive CAE-like Activities in Other Regions

In addition to the task-positive areas, we also observed similar conflict-type-sensitive activities in the caudate. The caudate has been reported to play an important role in predicting the forthcoming control demand by linking the stimulus to control sets (Chiu & Egner, 2019; Jiang, Beck, Heller, & Egner, 2015). This mechanism may also underlie the successful CAE when a predicted control type matches that in need in the Repetition condition. Importantly, we found that the caudate was not activated in the Alternation condition, suggesting that the disappearance of CAE when the conflict type mismatch might reflect a failure of control prediction. The finding is consistent with an emerging account of control learning, which regards the adjustment of control as a kind of associative learning, although control itself is at the abstract level (Abrahamse, Braem, Notebaert, & Verguts, 2016; Egner, 2014). This finding extended our understanding of type-sensitive CAE beyond the dissociation of control mechanisms for Stroop and Simon conflicts (Wang et al., 2014; Egner, 2008).

Another brain area we observed is the visual area (i.e., IOC and fusiform gyrus). This may help to resolve discrepancies regarding how cognitive control modulates sensory inputs in conflict processing. Generally speaking, conflict resolution can be achieved by either facilitating task-relevant stimuli or suppressing task-irrelevant stimuli (Z. Li, Goschl, & Yang, 2020). With a face-name Stroop task, a previous study found that the fusiform face area showed a CAE-like neural activity (similar to the results of the IOC in the Repetition condition in our study) when the face was task-relevant, but not when the face was task-irrelevant (Egner & Hirsch, 2005a). Egner and Hirsch (2005a) thus proposed that the conflict resolution was achieved by facilitating task-relevant information. However, this explanation was challenged by the findings of

several behavioral studies (Yang et al., 2017; Lee & Cho, 2013); these researchers observed a loss of cross-conflict CAEs when task-relevant information was kept constant while task-irrelevant information changed, which was unexpected because the repetition of task-relevant information should have produced the CAE. However, our results implied that the repetition of task-relevant information may not produce the CAE when the conflict type alternated, because the task-relevant facilitation control mechanism that supports a CAE was absent, as shown by the inactivation of task-positive and visual areas. We thus propose that the facilitation of task-relevant information does underlie the conflict processing when the conflict type repeats, but it is turned down when the conflict type alternated.

### Limitations and Future Directions

There has been some debate on whether the CAE reflects control adjustment or instead the bottom-up learning effect, such as feature integration. According to the feature integration theory (Hommel et al., 2004), in the congruent-congruent (CC) condition of the color Stroop task, the consecutive task-relevant and task-irrelevant stimuli are totally repeated (e.g., RED<sub>R</sub>-RED<sub>R</sub>, with the subscript letter R denoting printed color red) or totally alternated (e.g., RED<sub>R</sub>-BLUE<sub>B</sub>, with the subscript letter B denoting printed color blue); in the incongruent-incongruent (II) condition, they are also totally repeated (e.g., BLUE<sub>R</sub>-BLUE<sub>R</sub>) or totally alternated (e.g., RED<sub>B</sub>-BLUE<sub>R</sub>). However, in the congruent-incongruent and incongruent-congruent conditions, the sequences are partially repeated (e.g., BLUE<sub>B</sub>-BLUE<sub>R</sub> or RED<sub>B</sub>-RED<sub>R</sub>). The feature integration theory proposes that two simultaneously displayed stimuli are bound together, so that a presentation of one stimulus will evoke the other. Thus, the total repetition trials will be faster because of the priming effect. On the other hand, the partial repetition trials will suffer from a mismatch between the evoked stimulus and the presented stimulus and will become slower. The total alternation trials will not be affected by the above two effects, so its RT will be between the above two conditions. With respect to the CAE, when the equation  $CAE = (CI - CC) - (II - IC)$  is rewritten as  $CAE = (CI + IC) - (II + CC)$ , it turns out to be that the CAE is the partial repetition condition minus the total repetition/total alternation condition, which yields a positive effect. By removing the feature binding biased trials (for details, see Appendix, Section A.1), the results showed very similar pattern of type-specific CAE. In addition, we also excluded the possible influence of response repetition effect by removing the response repetition (see Appendix, Section A.2). Therefore, our results have not been influenced by the bottom-up factors.

Given that the behavioral results are not affected by the bottom-up factors, we did not remove these trials in the fMRI results analysis, and we mainly discussed the results

from the top-down control perspective. Another reason for not deleting these trials was to avoid a significant power loss in the fMRI data analysis. However, because the neural effects might be different than the behavioral effects, we regard this as a limitation of our study design. To better examine the pure cognitive control mechanisms, future studies could be designed by increasing the stimulus-response sets (Braem et al., 2014, 2019; Duthoo et al., 2014).

### Conclusion

Our study found that there are different brain areas involved in the CAEs within and across conflict types. On the one hand, when conflict type repeated (rather than when it alternated), the activation of task-positive areas, such as ACC, IFG, and SPL, contributed to the within-conflict CAE. On the other hand, when the conflict type alternated (rather than when it repeated), the deactivation of task-negative area (i.e., SFG) contributed to the absence of the cross-conflict CAE. These two anticorrelated networks collectively modulated the conflict-type-sensitive CAE. We also found the important role of caudate in the type-specific CAE.

## APPENDIX

### A.1 Behavioral Results after Deleting Feature Binding Biased Trials

In our experimental design, three dimensions of stimuli (i.e., the triangle color, the overlaid word, and the orientation of the triangle) determined whether the consecutive trials contained stimulus repetition. When all three dimensions match across the consecutive trials, the current trial is labeled as the total repetition condition. When all three dimensions mismatch, the current trial is labeled as the total alternation condition. The remaining trials are labeled the partial repetition condition. For the conflict type Alternation condition, the final sequence yielded the same ratio of partial repetition and total alternation trials for the four consecutive conditions (i.e., altCI, altCC, altII, and altIC), so the CAE contrast cancels out the influence of feature binding. However, for the conflict type Repetition condition, the repCI and repIC conditions contained only partial repetition trials, but the repII and repCC conditions included 41.6% partial repetition trials, 11.1% total repetition trials, and 47.2% total alternation trials. Therefore, the CAE calculation in the conflict type Repetition condition cannot fully cancel out the feature binding influences. To test whether the feature binding has influenced the results, we removed the total repetition and total alternation trials in the Repetition condition and conducted the three-way ANOVA as we reported in the article. We report the results below.

For the RT, there was a significant main effect of Current Congruency,  $F(1, 18) = 113.56, p < .001, \eta_p^2 = .86$ .



Participants responded more slowly in incongruent conditions (445 msec) than in congruent conditions (417 msec), indicating a conflict effect. The interaction between Previous Congruency and Current Congruency (i.e., CAE) was significant,  $F(1, 18) = 4.78, p = .042, \eta_p^2 = .23$ , suggesting that the conflict effect (incongruent vs. congruent) was significantly smaller after incongruent trials (445 vs. 420 msec) than after congruent trials (445 vs. 415 msec).

For the ER, there was a significant main effect of Current Congruency,  $F(1, 18) = 21.42, p < .001, \eta_p^2 = .54$ . Participants had a higher ER in incongruent conditions (3.0%) than in congruent conditions (1.3%). The main effect of Consecutive Conflict Type was also significant,  $F(1, 18) = 6.92, p = .017, \eta_p^2 = .28$ . No other significant main effects nor interactions were found.

For the LISAS, there was a significant main effect of Current Congruency,  $F(1, 18) = 100.09, p < .001, \eta_p^2 = .85$ . Participants responded more slowly in incongruent conditions (458 LISAS units) than in congruent conditions (422 LISAS units). Interaction between Previous Congruency  $\times$  Current Congruency (CA effect) was significant,  $F(1, 18) = 7.33, p = .014, \eta_p^2 = .29$ , suggesting that the conflict effect (incongruent vs. congruent) was smaller after incongruent trials (457 vs. 425 LISAS units) than after congruent trials (459 vs. 418 LISAS units). Moreover, the interaction among Consecutive Conflict Type, Previous Congruency, and Current Congruency conditions was significant,  $F(1, 18) = 13.65, p = .002, \eta_p^2 = .43$ . Simple effect analyses revealed that there was a significant CAE only in the Repetition condition (20 LISAS units),  $F(1, 18) = 17.22, p = .001$ , but not in the Alternation condition ( $-3$  LISAS units),  $F(1, 18) < 1$ . No other main effects or interactions were observed.

## A.2 Behavioral Results after Deleting Response Repetition Trials

The response repetition might also influence the results, because repetition of a response could make the response faster and possibly more accurate. Therefore, we reported the results when the response repetition trials were deleted.

For the RT, there was a significant main effect of Current Congruency,  $F(1, 18) = 169.85, p < .001, \eta_p^2 = .90$ . Participants responded more slowly in incongruent conditions (441 msec) than in congruent conditions (410 msec), indicating a conflict effect. The main effect of Previous Congruency was also significant,  $F(1, 18) = 12.12, p < .01, \eta_p^2 = .40$ . Participants responded more slowly in post-incongruent conditions (428 msec) than in post-congruent conditions (423 msec), indicating a postconflict slowing effect. The interaction between Previous Congruency and Current Congruency (i.e., CAE) was significant,  $F(1, 18) = 12.69, p = .002, \eta_p^2 = .41$ , suggesting that the conflict effect (incongruent vs. congruent) was significantly smaller after incongruent trials (442 vs. 414 msec) than after congruent trials (441

vs. 406 msec). Moreover, the interaction among Switch, Previous Congruency, and Current Congruency was significant,  $F(1, 18) = 21.12, p < .001, \eta_p^2 = .54$ . Simple effect analyses revealed that there was a significant CAE only in the Repetition condition (19 msec),  $F(1, 18) = 32.05, p < .001$ , but not in the Alternation condition ( $-3$  msec),  $F(1, 18) < 1$ . In addition, we observed significant interaction between Consecutive Conflict Type and Current Congruency,  $F(1, 18) = 6.06, p < .05, \eta_p^2 = .25$ . No other main effects or interactions were observed.

For the ER, there was a significant main effect of Current Congruency,  $F(1, 18) = 6.69, p < .05, \eta_p^2 = .27$ . Participants had a higher ER in the incongruent condition (2.1%) than in the congruent condition (1.2%). No other significant main effects nor interactions were found.

For the LISAS, there was a significant main effect of Current Congruency,  $F(1, 18) = 119.70, p < .001, \eta_p^2 = .87$ . Participants responded more slowly in incongruent conditions (450 LISAS units) than in congruent conditions (414 LISAS units). We also observed significant main effects of Previous Congruency,  $F(1, 18) = 5.56, p = .030, \eta_p^2 = .24$ . Participants responded more slowly in post-incongruent conditions (430 LISAS units) than in post-congruent conditions (434 LISAS units), indicating a post-conflict slowing effect. Interaction between Previous Congruency and Current Congruency (CA effect) was significant,  $F(1, 18) = 6.93, p = .017, \eta_p^2 = .28$ , suggesting that the conflict effect (incongruent vs. congruent) was smaller after incongruent trials (450 vs. 410 LISAS units) than after congruent trials (450 vs. 419 LISAS units). Moreover, the interaction among Consecutive Conflict Type, Previous Congruency, and Current Congruency conditions was significant,  $F(1, 18) = 20.36, p < .001, \eta_p^2 = .53$ . Simple effect analyses revealed that there was a significant CAE only in the Repetition condition (23 LISAS units),  $F(1, 18) = 17.22, p = .001$ , but not in the Alternation condition ( $-4$  LISAS units),  $F(1, 18) = 1.39, p = .253$ . No other main effects or interactions were observed.

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## Author Contributions

Guochun Yang: Formal analysis; Methodology; Visualization; Writing—Original draft; Writing—Review & editing. Kai Wang: Conceptualization; Data curation; Formal analysis; Methodology; Validation; Writing—Original draft; Writing—Review & editing. Weizhi Nan: Data curation; Writing—Review & editing. Qi Li: Conceptualization; Writing—Review & editing. Ya Zheng: Writing—Review & editing. Haiyan Wu: Writing—Review & editing. Xun Liu: Conceptualization; Funding acquisition; Project administration; Resources; Supervision; Writing—Review & editing.



## Funding Information

The work was supported by the National Natural Science Foundation of China and the German Research Foundation, grant number: NSFC 62061136001/DFG TRR-169 to X. L. Guangdong Philosophy and Social Science Planning Project, grant number: GD21CXL02 to K. W., Guangdong Basic and Applied Basic Research Foundation, grant number: 2021A1515011259 to K. W., the National Natural Science Foundation of China, grant number: 31571161 to Q. L., Key project of Beijing Education Science Planning, Reevaluation and cognitive training to treat College students with Internet addiction, grant number: BEAA21046 to Q. L., Open Research Fund of the CAS Key Laboratory of Behavioral Science, Institute of Psychology to Q. L., and China Postdoctoral Science Foundation (<https://dx.doi.org/10.13039/501100002858>), grant number: 2019M650884 to G. Y.

## Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were  $M(\text{an})/M = .407$ ,  $W(\text{oman})/M = .32$ ,  $M/W = .115$ , and  $W/W = .159$ , the comparable proportions for the articles that these authorship teams cited were  $M/M = .549$ ,  $W/M = .257$ ,  $M/W = .109$ , and  $W/W = .085$  (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows:  $M/M = .842$ ;  $W/M = .026$ ;  $M/W = .079$ ;  $W/W = .053$ .

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