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Alertness function of thalamus in conflict adaptation☆

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ABSTRACT

Conflict adaptation reflects the ability to improve current conflict resolution based on previously experienced conflict, which is crucial for our goal-directed behaviors. In recent years, the roles of alertness are attracting increasing attention when discussing the generation of conflict adaptation. However, due to the difficulty of manipulating alertness, very limited progress has been made in this line. Inspired by that color may affect alertness, we manipulated background color of experimental task and found that conflict adaptation significantly presented in gray and red backgrounds but did not in blue background. Furthermore, behavioral and functional magnetic resonance imaging results revealed that the modulation of color on conflict adaptation was implemented through changing alertness level. In particular, blue background eliminated conflict adaptation by damping the alertness regulating function of thalamus and the functional connectivity between thalamus and inferior frontal gyrus (IFG). In contrast, in gray and red backgrounds where alertness levels are typically high, the thalamus and the right IFG functioned normally and conflict adaptations were significant. Therefore, the alertness function of thalamus is determinant to conflict adaptation, and thalamus and rIFG are crucial nodes of the neural circuit subserving this ability. Present findings provide new insights into the neural mechanisms of conflict adaptation.

1. Introduction

Conflict adaptation manifests an improved conflict resolution driven by previously experienced conflict (Botvinick et al., 1999; Gratton et al., 1992), which subserves our goal-directed behaviors and therefore is crucial for success in work and everyday life. Specifically, individuals send conflict information detected on previous situation to the top-down control system, which subsequently bias the perceptual processing toward to task-relevant information and away from task-irrelevant information on current situation. A newly prominent model accounting for conflict adaptation, the Hebbian learning model (Verguts and Notebaert, 2009), suggests that the conflict monitoring system triggers an arousal response in a neuromodulatory system, which increases Hebbian learning acting on task-relevant representations and accordingly conflict control would be improved. The neuromodulatory system is mainly located in the subcortical areas (Hobson and Pace-Schott, 2002; Pace-Schott and Hobson, 2002; Pessoa, 2008); however, the activation in these areas is not typically reported in conflict adaptation fMRI (functional magnetic resonance imaging) studies (Verguts and Notebaert, 2009). In fact, knowledge of the mechanisms underlying conflict adaptation is still very limited.

A dominant viewpoint of the Hebbian learning model is that the arousal level modulates conflict adaptation. Usually, to obtain an optimal performance, individuals have to maintain a high arousal/alertness level in experimental conditions. Relationship between alertness and executive control has been detected in the literature (Weinbach and Henik, 2012), with one study suggested that response conflict could induce generalized alertness (Kahneman, 1973). A recent study reported that the alertness level correlated positively with the conflict adaptation effect (Liu et al., 2013). However, as alertness level was not effectively manipulated in previous studies, the critical hypothesis of Hebbian learning model could not be directly examined. Interestingly, color has been suggested to be able to modulate alertness level. As one kind of basic information input, color ubiquitously influences our cognition and behavior (Elliot et al., 2007, 2009; Green et al., 1982). It had been mentioned that red, relative to blue, induces primarily the avoidance motivation, which makes people more vigilant and risk-averse; while, differently from red, blue is often associated with openness, peace, and tranquility (Mehta and Zhu, 2009). Common sense, when individuals perform the task needed to keep more vigilant, they would be in high alertness level. Braun and Silver (1995) examined the effect of color on perceptions of hazard, which may support the hypothesis that the color may exert influence on the alertness level. In their experiment, participants assessed the perceived hazard of signal words printed in specific hazard colors. Results showed that red was linked to the highest level of perceived hazard, followed by orange, black, green and blue. Therefore, once the hypothesis is established, we can

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change the background color of current experiments to examine the influence of color on conflict adaptation.

Gray, blue and red were separately used as the screen background color in current study. Because background color is generally monochrome (i.e., gray, white or black) in previously related studies, the results in gray background can provide a comparison baseline. Blue and red are primary colors when examining the effect of color on cognition and behavior (Jalil et al., 2012). Moreover, they have been found to induce opposite associations: blue is often associated with openness, peace, and tranquility (NAz and Epps, 2004), which may decrease alertness level; in contrast, red is often associated with dangers and mistakes (Elliot et al., 2007), which may induce high alertness. If alertness modulates conflict adaptation, as predicted by the Hebbian learning model, it could be expected to observe distinct influences of blue and red on conflict adaptation.

In the present study, we first used an Attentional Networks Test (ANT) (Fan et al., 2002) to confirm the modulation of background color on alertness level (Experiment 1). The ANT is developed to measure the efficiency of the attentional networks, and it can provide scores for alerting, orienting and executive control (Fan et al., 2005; Petersen and Posner, 2012). In this experiment, we evaluated the alerting score differences across the gray, blue, and red backgrounds through the ANT. Based on Experiment 1, we then employed a letter Flanker task to investigate the color effect on conflict adaptation in Experiment 2. In this task, participants were required to respond to central letter while ignoring flanking letter that may suggest the same response as the target (congruent trial, C) or an opposite response to the target (incongruent trial, I) (Wang et al., 2014). Conflict adaptation is defined as the reduced conflict effect (I − C) following an incongruent trial relative to a congruent trial (Egner, 2007). And then we repeated and extended the investigation about conflict adaptation by combining behavioral and fMRI measurements (Experiment 3). Accordingly, we could obtain the influences of color on alertness and conflict adaptation on both behavioral and fMRI levels, which allows us to analyze whether those brain areas regulating alertness level are modulated by background colors during conflict adaptation, and how these areas interact with cognitive control network (Cole and Schneider, 2007; Power and Petersen, 2013). The event-related fMRI data allows us to address the neural mechanisms of how alertness modulates conflict adaptation. Especially, we will utilize the psychophysiological interaction (PPI) analysis (Friston et al., 1997) to examine the neural network underlying the modulation of color on conflict adaptation.

In general, neuroimaging studies have demonstrated that alertness is associated with the norepinephrine system, including the thalamus, prefrontal cortex and the parietal cortex (Marrocco and Davidson, 1998; Coull et al., 2000 范). The thalamic neurons could mediate the shift between alert and nonalert states (Cano et al., 2006), whilst the anterior and posterior cortical sites and the thalamic area consist of the alerting network (Fan et al., 2005). Meanwhile, conflict adaptation is subserved by a set of prefrontal and parietal regions, involving the anterior cingulate cortex, the prefrontal cortex, and the posterior parietal cortex (Wang et al., 2015; Egner et al., 2011; Kerns et al., 2004). Therefore, in the present study, we expected to observe the color modulated activation of the alertness-related regions, such as the thalamus. And we further hypothesized that the color effect on conflict adaptation is achieved by influencing the interaction between the altering and conflict control systems.

2. Materials and methods

2.1. Experiment 1: Behavioral modulation of color on alertness level

2.1.1. Subject

Forty-two (22 females) volunteers, between the age of 17 and 26 years (20 ± 4.76, mean ± SD), took part in Experiment 1. All participants were right-handed, had normal or corrected-to-normal vision, and normal color perception. Informed consent was acquired from each participant, and the study was approved by Southwest University Human Ethics Committee for the Human Research.

2.1.2. Stimuli and procedure

Participants performed a standard ANT task. Stimuli consisted of five horizontal arrows, with arrowheads pointing leftward or rightward within gray, blue, or red backgrounds. This central target arrowhead was flanked on either side by two arrows in congruent direction, or in incongruent direction, or by lines (neutral condition). The participants were inquired to identify the orientation of the target by pressing different keys. Participants viewed the stimuli from a distance of about 60 cm, and the visual angle of stimulus was 3.08°. The color of the computer screen was manipulated using RGB (red–green–blue) scheme (gray: $R = 128$, $G = 128$, $B = 128$; blue: $R = 0$, $G = 0$, $B = 255$; red: $R = 255$, $G = 0$, $B = 0$).

At the beginning of each trial, a fixation cross was presented for a random duration ranging between 400 and 1600 ms, followed by the appearance of a cue for 100 ms. There were four cue conditions: no cue, center cue, double cue, and spatial cue. In the no-cue condition, only the fixation cross was presented in the center of the screen for 100 ms. In the center-cue condition, an asterisk was presented in the center of the screen for 100 ms. In the last two conditions, the fixation cross was always presented in the center of the screen. In addition, in the double-cue condition, two asterisks were presented simultaneously at two possible target positions for 100 ms; in the spatial-cue condition, an asterisk was presented at the target position for 100 ms. After cue presentation, the fixation cross was again presented for 400 ms followed by the appearance of the target at a visual angle of 0.96° above or below the cross. Target location was always uncertain except on spatial-cue trials. Participants were instructed to focus on the centrally located fixation cross throughout the task.

Participants were instructed to respond as quickly and accurately as possible by pressing a key on the keyboard in correspondence to the target after the appearance of the target. Specifically, half of the participants were instructed to press F with the left index finger if the target oriented left and to press J with the right index finger if the target oriented right. The finger-to-key mapping was reversed in the remainder of the participants. Each participant firstly completed 24 full-feedback practice trials. There were three blocks in this experiment, each of which was randomly set as one of three background colors (gray, blue and red). Each block has 96 ANT trials (4 cue conditions × 2 target locations × 2 target directions × 3 flanker conditions × 2 repetitions).

2.2. Experiment 2: Behavioral modulation of color on conflict adaptation

In this experiment, we asked the participants to complete the letter flanker task under three background screen colors (gray, blue, and red). Because conflict adaptation effect can be analyzed based on the letter flanker task, this experiment allows us to explore the influence of background color on conflict adaptation effect.

2.2.1. Subject

Thirty-six (22 females) right-handed volunteers, between the age of 19 and 26 years (21 ± 1.72, mean ± *SD*), took part in Experiment 2. All participants were right-handed, had normal or corrected-to-normal vision, and normal color perception. Informed consent was acquired from each participant, and the study was approved by Southwest University Human Ethics Committee for the Human Research.

2.2.2. Stimuli and procedure

Stimuli were presented on a computer screen placed at a distance of about 60 cm from participants. The color of the computer screen was manipulated using RGB (red-green-blue) scheme (gray: $R = 128$, $G = 128$, $B = 128$; blue: $R = 0$, $G = 0$, $B = 255$; red: $R = 255$, $G = 0$, $B = 0$). The letter flanker task was employed by using four letters (S,

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H, N, and P), and each letter could be a target or a flanker. In each trial, a five-letter array was presented: the central one was the target and the remaining ones were the flankers. The stimulus type consisted of the congruent stimuli, in which the flankers were identical to the target (e.g., NNNNN); and the incongruent stimuli, in which the flankers were mapped onto a different response from the target (e.g., PPNPP). Participants were asked to respond according to the central letter, regardless of the flankers. The four letters (S, H, N, and P) were separately mapped onto four different keys of the keyboard. Specifically, S was mapped onto key 1 (left middle finger), H was mapped onto key 2 (left index finger), N was mapped onto key 3 (right index finger), and P was mapped onto key 4 (right middle finger). They were told to respond as quickly as possible while avoiding errors. The visual angle between the letters was 0.09°.

There were three blocks in this experiment, each of which was set as one of three background colors (gray, blue, and red). The time intervals between blocks were 60,000 ms and the order of these three blocks was counterbalanced across subjects. Each trial started with a black fixation for 300 ms, followed by the random blank presented for 300–500 ms. After that, the stimulus was presented for 200 ms with a following response blank for 1500 ms. The next trial started before another random blank presented for 800–1200 ms. The participants received 24 practice trials before entering the experimental phase, which consisted of three blocks of 192 valid trials (i.e., the first trial of each block was eliminated in behavioral data analysis). Generally, conflict adaptation effect is analyzed based on the previous (c, i) and current (C, I) trial types, and is calculated as RT $[c(I - C) - i(I - C)]$ (RT refers to reaction time). In each block, the four trial types (cC, cI, iC, iI) were sequenced in a pseudorandom way in order to result in an equal proportion and to avoid repetition priming and feature integration effects (Mayr et al., 2003).

2.3. Experiment 3: Neural correlates of the modulation of color on conflict adaptation

We recorded the event-related fMRI data when the participants performed the letter flanker task. Accordingly, we can reach at three aims in Experiment 3. First, we can examine the reliability of the findings in Experiment 2, and then provide neural evidences for the involvement of alertness in the modulation of color on conflict adaptation. Finally, using the PPI analysis, we can address the neural mechanisms underlying the modulation of color on conflict adaptation.

2.3.1. Subject

Twenty-four (14 females) volunteers, between the age of 18 and 24 years (21 ± 1.90, mean ± SD), took part in Experiment 3. The data of one participants in this experiment was excluded due to excessive head movement artifacts. All participants were right-handed, had normal or corrected-to-normal vision, and had normal color perception. Informed consent was acquired from each participant, and the study was approved by Southwest University Human Ethics Committee for the Human Research.

2.3.2. Stimuli and procedure

Stimuli were presented on a computer screen placed at a distance of about 60 cm from participants. The color of the computer screen was manipulated using RGB (red–green–blue) scheme (gray: $R = 128$, $G = 128$, $B = 128$; blue: $R = 0$, $G = 0$, $B = 255$; red: $R = 255$, $G = 0$, $B = 0$). The letter flanker task was employed by using four letters (S, H, N, and P), and each letter could be a target or a flanker. In each trial, a five-letter array was presented: the central one was the target and the remaining ones were the flankers. The stimulus type consisted of the congruent stimuli, in which the flankers were identical to the target (e.g., NNNNN); and the incongruent stimuli, in which the flankers were mapped onto a different response from the target (e.g., PPNPP). Participants were asked to respond according to the central letter, regardless of the flankers. The four letters (S, H, N, and P) were separately mapped onto four different keys of the keyboard. Specifically, S was mapped onto key 1 (left middle finger), H was mapped onto key 2 (left index finger), N was mapped onto key 3 (right index finger), and P was mapped onto key 4 (right middle finger). They were told to respond as quickly as possible while avoiding errors. The visual angle between the letters was 0.09°.

The experiment was comprised of three runs (i.e., three blocks), for each of which the same screen color was arranged (i.e., gray, blue, and red runs), with the order of three runs counterbalanced across subjects. Each run started with a black fixation for 7500 ms to keep the signal stable and also ended with a black fixation for 7500 ms to make the signal back. There was 1-min rest in the middle of each run. Each run consisted of 194 trials (i.e., the first trial of each run and the first trial after rest in each run were eliminated in data analysis of conflict adaptation).

Each trial started with a black fixation for 1500 ms, followed by the stimuli presented for 1500 ms, during which subjects were asked to respond as quickly and accurately as possible. The inter-trial interval (ITI) was 3000 ms. Considered that a jittered ITI is likely being as a confounding factor to influence cognitive control processes by the meaningful but still unclear way (Wühr and Ansorge, 2005; Weissman et al., 2005), we employed the fast-event related designs with a constant ITI. Additionally, previous conflict adaptation fMRI studies which also adopt the fast constant ITI event-related design (Egner and Hirsch, 2005b; Kerns et al., 2004), therefore, it is adequate for the fast event-related design with a constant ITI to observe the conflict adaptation effect from imaging level.

2.3.3. Image acquisition

Imaging data were collected with a 3.0 Tesla Siemens scanner (Siemens Magnetom Trio TIM, Erlangen, Germany). T2*-weighted images were acquired using an echo-planar imaging (EPI) sequence of 25 contiguous axial slices [time repetition (TR) = 1500 ms; time echo (TE) = 29 ms; flip angle = 90°; field of view (FoV) = 192×192 mm^2; matrix size = 64×64; inter-slice gap = 0.5 mm] of 5 mm thickness and 3×3 mm^2 in-plane resolution. The functional data were acquired in three runs of 438 scans each. T1-weighted structural images were recorded with a total of 176 slices at a thickness of 1 mm and in-plane resolution of 0.98×0.98 mm^2 using magnetization prepared gradient echo sequence (TR = 1900 ms; TE = 2.52 ms; flip angle = 9°; FoV = 250×250 mm^2).

2.3.4. fMRI data preprocessing

All preprocessing and statistical analyses of imaging data were carried out by using Statistical Parametric Mapping 8 (Welcome Department of Cognitive Neurology, London, UK, http://www.fil.ion.ucl.ac.uk/spm/spm8). For each subject, the first five functional volumes of each run were discarded to acquire the magnet-steady images. The remaining functional images were slice-timing corrected and spatially realigned to estimate and modify the six parameters of head motion. Then, the structural image was co-registered to the mean functional volumes, which were acquired in the step of realignment, and served to calculate the transformation parameters for spatially warping the functional images into the Montreal Neurological Institute (MNI) template brain in $3 \times 3 \times 3$ mm^3 voxel sizes. Finally, normalized functional images were smoothed with a Gaussian kernel; the full width at half maximum (FWHM) was specified as $6 \times 6 \times 6$ mm^3. In order to remove low-frequency noise, the images were high-pass filtered with a 128 s cutoff period.

2.3.5. First-level analysis

At individual level, the five regressors (i.e., cC, cI, iC, iI, and the deleted trials in data analysis (i.e., the first trial and error and post-error trials)) from each run were modeled to construct the design matrix, and all runs were modeled into one general linear model (GLM) which was convolved with the Canonical Hemodynamic Response Function. The cC, cI, iC, and iI contrast images were entered into the group-level

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analysis. The eliminated trials of each run in data analysis were as a regressor of non-interest. The six realignment parameters for each subject were included in the model as nuisance covariates.

2.3.6. Activation analysis

At group level, the contrast estimates of cC, cI, iC, and iI within three backgrounds were submitted to the full factorial design using the random-effect analysis within the whole brain. In addition, we control the effect of covariate (i.e., gender variable) on the results. Within this design, the background color type (gray, blue and red), the previous trial congruency (congruent and incongruent), and the current trial congruency (Congruent and Incongruent) were identified as factors ($3 \times 2 \times 2$) to acquire the interaction effect. The statistical threshold of activation analysis was corrected at $p < 0.05$ cluster level according to the random field theory (Ashburner and Friston, 2000).

2.3.7. Region of interest analysis

Mean activation estimates of cC, cI, iC, and iI conditions in each color background were extracted from specific thalamic region of interest (ROI) identified in the three-way interaction effect described above, using the Marsbar software (http://marsbar.sourceforge.net/). Then, we presented the thalamic magnitudes for the cC, cI, iC, and iI conditions to compare the its activation patterns during conflict adaptation across the three backgrounds.

2.3.8. Psychophysiological interaction (PPI) analysis

In order to assess the modulations from the thalamus engaged in the three-way interaction during conflict adaptation across the three backgrounds, we carried out the PPI analysis, which can show the influence of one region on another under the manipulation of an experimental context, or the effect of an experimental variable on the target region when taking the input from the source region into account (Friston et al., 1997).

Firstly, in each subject, we extracted the raw time course of the seed (i.e., the thalamus) as the volume of interest (VOI). In order to exclude the effect of different conditions on the psychophysiological interaction, these time courses were adjusted by the *F*-contrasts of the cC, cI, iC, and iI conditions and the conditions non-interested before computing the PPI parameters. Then, we calculated the product of the time courses and the vector of physiological variable of interest (i.e., [the high conflict resolution trial (i.e., iI) − the low conflict resolution trial (i.e., cI)]) to construct the PPI term. Following that, the PPI parameters obtained and the six realignment parameters were entered into the new SPM GLM as the regressors to find the regions which indicated significant relationship with the interaction between the physiological signals of the seed and the psychological conditions. Finally, the individual PPI results across three backgrounds were entered into the full factorial design using the random-effect one-way ANOVA analysis within the whole brain to examine the effect of background color factor on the PPI results. In addition, we control the effect of covariate (i.e., gender variable) on the results. The PPI results were assessed at a combined threshold of voxel-wise $P < 0.005$ uncorrected with a cluster size of $k > 10$ voxels.

3. Results

3.1. Experiment 1: Behavioral modulation of color on alertness level

According to Fan et al. (2002), the efficiency of alerting was defined as $RT_{no\ cue} - RT_{double\ cue}$, with higher scores suggesting larger alerting effects due to the presentation of cues warning the participants of the upcoming target; the efficiency of executive control was defined as $RT_{incongruent\ trials} - RT_{congruent\ trials}$, with higher scores suggesting larger conflict interference and less efficiency; the efficiency of orienting was defined as $RT_{center\ cue} - RT_{spatial\ cue}$, with higher scores suggesting larger orienting effects based on the provision of exact spatial predictive information.

Then, we separately performed one-way ANOVAs on the alerting scores, executive control scores, and orienting scores across the three backgrounds. Importantly, as to the alerting score, one-way ANOVA showed that there was a significant difference across three color backgrounds, $F\ (2, 82) = 6.84$, $P < 0.01$, $\eta^2 = 0.14$. Post hoc test indicated that the gray and red backgrounds were associated with higher alerting scores than blue background ($P < 0.001$; $P < 0.05$; Fig. 1A). To elucidate the meaning of decreased alerting score in the blue background, we compared the separate components of the alerting score (i.e., the no cue RT and the double cue RT) across the three backgrounds. There were significant differences on no cue RT across the three backgrounds, $F_{(2,\ 82)} = 8.10$, $P = 0.001$, $\eta^2 = 0.17$. Post hoc test indicated that the no cue RT was longer in the blue background than the gray and red backgrounds ($Ps < 0.05$; Fig. 1B). There were also significant differences on double cue RT across them, $F_{(2,\ 82)} = 31.86$, $P < 0.001$, $\eta^2 = 0.44$. Post hoc test showed that the double cue RT was longer in the blue background than the gray and red backgrounds ($Ps < 0.001$; Fig. 1B). And the red background was associated with longer double cue RT than the gray background ($P < 0.05$; Fig. 1B). These results suggested that the reduced alerting score was mainly led by the increased double cue RT in blue background as compared to the gray and red backgrounds.

As to the executive control and orienting scores, one-way ANOVA also demonstrated that there were significant differences across three color backgrounds, $F_{(2,\ 82)} = 16.47$, $P < 0.001$, $\eta^2 = 0.29$, $F_{(2,\ 82)} = 16.09$, $P < 0.001$, $\eta^2 = 0.28$. Post hoc test indicated that the gray and red backgrounds were associated with higher conflict than the blue background ($Ps < 0.001$; Fig. 1A); the gray and red backgrounds were associated with lower orienting scores than the blue background ($Ps < 0.001$; Fig. 1A).

3.2. Experiment 2: Behavioral modulation of color on conflict adaptation

The background color type × previous trial congruency × current trial congruency repeated-measures ANOVA on RT data revealed a significant interaction effect, $F_{(2,\ 70)} = 4.19$, $P < 0.05$, $\eta^2 = 0.11$. Additionally, the three-way ANONA demonstrated a marginally significant main effect of background color type, $F_{(2,\ 70)} = 2.60$, $P = 0.08$, $\eta^2 =$

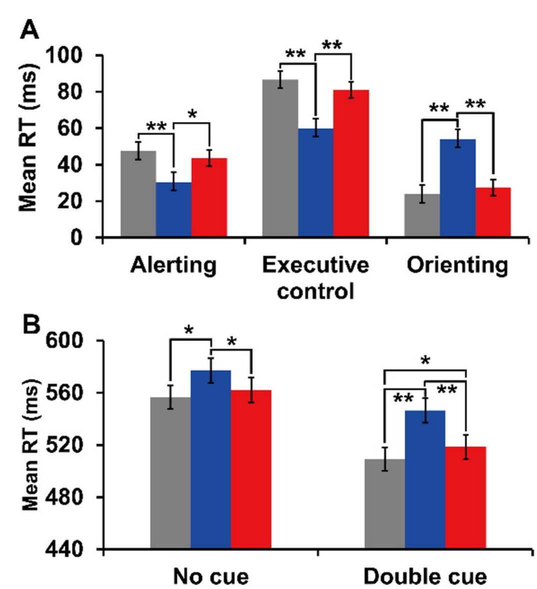

Fig. 1. Color modulated attentional network differences in Experimental 1. Alerting, executive control, and orienting scores (Panel A) and mean RTs for no cue and double cue conditions in three background colors (Panel B) (Note: the single and double asterisks represent $P < 0.05$ and $P < 0.01$, respectively; the ordinate scale is ms (millisecond); the colors of histograms represent to correspond with background colors (gray, blue, and red).). Error bars donate the standard error of the mean (SEM) across subjects.

0.07, as the blue background was associated with slower response than the gray backgrounds ($P < 0.05$). Furthermore, the previous × current trial type two-way ANOVA was performed to assess the conflict adaptation effects across the three backgrounds, respectively. For the gray background (Fig. 2A), the main effect of previous trial type was not significant, $F_{(1, 35)} < 1$, $P > 0.05$, $\eta^2 = 0.01$, however, the main effect of current trial type and the interaction between previous and current trial type were significant, $F_{(1, 35)} = 86.07$, $P < 0.001$, $\eta^2 = 0.71$, $F_{(1, 35)} = 13.56$, $P < 0.01$, $\eta^2 = 0.28$. Post hoc test showed that iC trials had slower response than cC trials ($P < 0.01$) and iI trials were processed faster than cI trials ($P < 0.05$). For the blue background (Fig. 2B), although the main effect of current trial type was significant $F_{(1, 35)} = 120.84$, $P < 0.01$, $\eta^2 = 0.78$, the main effect of previous trial type was not significant, $F_{(1, 35)} = 1.58$, $P > 0.05$, $\eta^2 = 0.04$, nor was the interaction between previous and current trial type, $F_{(1, 35)} < 0.04$, $P > 0.05$, $\eta^2 = 0.01$. For the red background (Fig. 2C), the main effect of previous trial was not significant, $F_{(1, 35)} < 1$, $P > 0.01$, $\eta^2 < 0.01$, while the main effect of current trial and the interaction effect were significant, $F_{(1, 35)} = 99.61$, $P < 0.01$, $\eta^2 = 0.74$, $F_{(1, 35)} = 11.08$, $P < 0.01$, $\eta^2 = 0.24$. Post hoc test showed that iC trials had slower response than cC trials ($P < 0.05$) and iI trials were processed faster than cI trials ($P < 0.05$). Thus, conflict adaptation effect was significantly present in the gray and red backgrounds, but not in the blue background. The corresponding analysis was carried out on the accuracy data. The accuracy data did not exhibit a significant three-way interaction effect, $F_{(2, 70)} < 1$, $P > 0.05$, $\eta^2 = 0.02$. However, the blue background was associated with lower accuracy than the gray backgrounds, corresponding to their RT data ($P = 0.05$).

3.3. Experiment 3: Neural correlates of the modulation of color on conflict adaptation

The background color type × previous trial congruency × current trial congruency repeated-measures ANOVA on RT data revealed a significant interaction effect, $F_{(2, 44)} = 3.53$, $P < 0.05$, $\eta^2 = 0.14$. Additionally, the three-way ANONA demonstrated a main effect of background color type, $F_{(2, 44)} = 16.06$, $P < 0.001$, $\eta^2 = 0.42$, as the blue background was associated with slower response than the gray/red backgrounds ($Ps < 0.001$). Furthermore, the previous × current trial type two-way ANOVA was performed to assess conflict adaptation effects across the three backgrounds, respectively. For the gray background (Fig. 2A), the main effect of previous trial type was not significant, $F_{(1, 22)} = 0.86$, $P > 0.05$, $\eta^2 = 0.04$, however, the main effect of current trial type and the interaction between previous and current trial type were significant, $F_{(1, 22)} = 128.89$, $P < 0.001$, $\eta^2 = 0.85$, $F_{(1, 22)} = 13.73$, $P = 0.001$, $\eta^2 = 0.38$. Post hoc test showed that iC trials had slower response than cC trials ($P = 0.05$) and iI trials were processed faster than cI trials ($P < 0.01$), indicating a typical conflict adaptation pattern. For the blue background (Fig. 2E), although the main effect of current trial type was significant, $F_{(1, 22)} = 212.66$, $P < 0.001$, $\eta^2 = 0.91$, the main effect of previous trial type was not significant, $F_{(1, 22)} = 0.51$, $P > 0.05$, $\eta^2 = 0.02$, nor was the interaction between previous and current trial type, $F_{(1, 22)} = 0.04$, $P > 0.05$, $\eta^2 < 0.01$. For the red background (Fig. 2F), the main effect of previous trial and current trial type and the interaction effect were significant, $F_{(1, 22)} = 15.72$, $P = 0.001$, $\eta^2 = 0.42$, $F_{(1, 22)} = 118.07$, $P < 0.001$, $\eta^2 = 0.84$, $F_{(1, 22)} = 8.28$, $P < 0.01$, $\eta^2 = 0.27$.

The corresponding analyses were carried out on the accuracy data. The accuracy data did not exhibit a significant three-way interaction effect, $F_{(2, 44)} < 1$, $P > 0.05$, $\eta^2 = 0.03$. Obviously, the accuracy data showed that there was no speed-accuracy tradeoff for conflict adaptation effects. The mean accuracy data of each condition display in Table 1.

Through the activation analysis, we found that the three-way interaction was associated with activation in the thalamus (Fig. 3A). Crucially, the thalamus displayed a background color type × previous trial congruency × current trial congruency interaction, as it showed opposite activity patterns between gray/red backgrounds and blue background, $F_{(2, 44)} = 5.19$, $P < 0.01$, $\eta^2 = 0.19$ (Fig. 3B, C, and D).

For the PPI analysis, we performed one-way ANOVA analysis (with three levels: gray, blue and red) to examine the effect of background color factor on the PPI results. Specifically, the left and right inferior frontal gyrus (lIFG, rIFG) showed a significant one-way ANOVA results across three backgrounds (Fig. 4A). Since the left IFG is associated with semantic processing (Rosen et al., 2000; Xiao et al., 2005), while the right IFG is engaged in inhibition control (Aron et al., 2004) and conflict adaptation (Egner, 2011), it seems to be more representative to further analyze the thalamus–rIFG coupling. In this way, to further

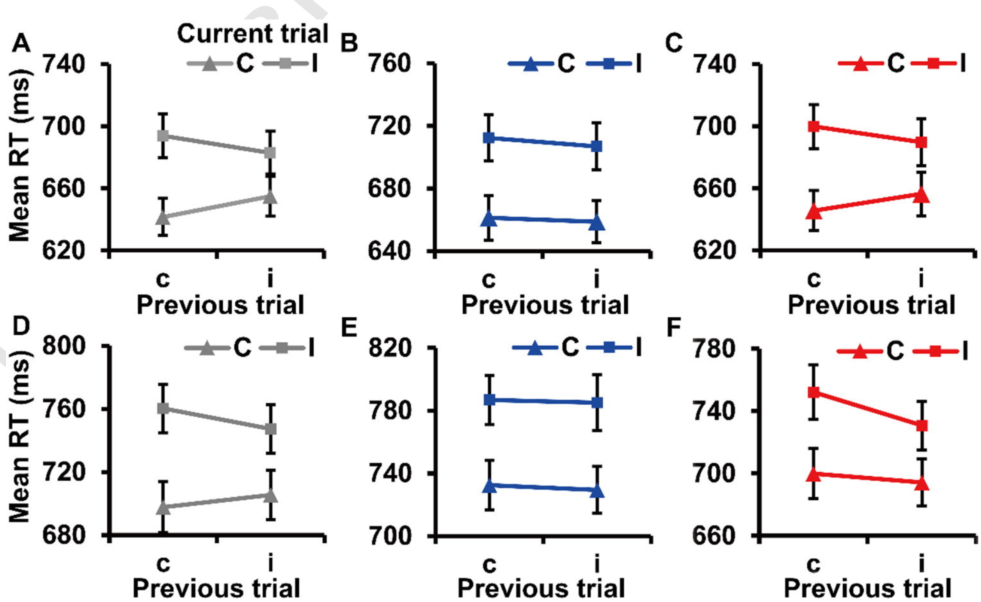

Fig. 2. Behavioral conflict adaptation effect under three background colors. Conflict adaptation previous trial × current trial interaction effect on mean RT (with standard error) in millisecond (ms) under the gray background (Panel A, CAE: 24.28), the blue background (Panel B, CAE: 2.96) and the red background (Panel C, CAE: 20.90) in Experiment 2 and under the gray background (Panel D, CAE: 20.77), the blue background (Panel E, CAE: −1.40) and the red background (Panel F, CAE: 15.74) in Experiment 3. Error bars donate the SEM across subjects.

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Table 1
The statistics for the accuracy rates from behavioral performance data by trial types and background color types.

ACC, SD	cC	cI	iC	iI
Gray	96.04%, 4.23%	96.26%, 3.92%	96.70%, 4.76%	95.70%, 4.24%
Blue	96.52%, 3.92%	94.04%, 7.23%	96.00%, 6.35%	94.04%, 5.00%
Red	96.96%, 2.48%	96.22%, 3.77%	98.09%, 2.13%	96.26%, 3.83%

Note. The ACC is the accuracy rate and SD refers to their corresponding standard deviation.

compare the different thalamus–rIFG couplings across the three backgrounds during conflict adaptation, the post hoc t-tests were performed with the PPI values extracted from the rIFG in gray, blue and red backgrounds. Results showed that there was significant difference between the blue and red backgrounds on the thalamus–rIFG coupling value, mean difference (MD) = 0.31, $P < 0.01$ (Fig. 4B).

To further examine that the role of the thalamus–rIFG coupling in conflict adaptation, we separately correlated the PPI value of thalamus–rIFG coupling during iI vs. cI contrast with the behaviorally reduced interference as measured by cI minus iI trials reaction time differences across three backgrounds. As a result, those individuals who displayed stronger functional connectivity between the thalamus and the rIFG showed significantly greater reduced interference within gray and red backgrounds ($r = 0.43$, $P < 0.05$, Fig. 4C; $r = 0.47$, $P < 0.05$, Fig. 4E). However, there was no significant correlation between the strength value of the thalamus–rIFG coupling and reduced interference within blue background ($r = -0.22$, $P > 0.05$, Fig. 4D).

To further confirm the modulation of the background color in the prediction of the thalamus–rIFG coupling on reduced interference, we conducted the moderating effect analysis. Specifically, the independent and the predictor variables were respectively the PPI value of the thalamus–rIFG coupling and the behaviorally reduced conflict, and the background color type was the moderator variable. The results showed that the regression equations were significant in the gray and red backgrounds ($R^2 = 0.19$, $P < 0.05$; $R^2 = 0.22$, $P < 0.05$), but not in the blue background ($R^2 = 0.05$, $P > 0.05$), indicating a significant moderating effect of the background color on the prediction of the thalamus–rIFG coupling on reduced interference.

4. Discussion

4.1. Discussion for Experiment 1

To examine the influence of color on alertness level, we asked participants to perform the ANT in the three background colors in Experiment 1. As illustrated in Fig. 1A, compared with the gray background, the blue background affected the scores of the three attentional functions, but the red background did not. Specifically, relative to the other two colors, the blue decreased the scores of alerting and executive control, but increased the score of orienting. Therefore, the results of Experiment 1 clarified the possibility raised in the introduction by showing that the blue color indeed decreased the participants' alertness level, but the red color did not change it. However, in addition to alerting, executive control and orienting functions were also affected by the blue color in Experiment 1. Interestingly, compared with alerting and executive control scores, blue increased the orienting score, showing an opposite tendency, which brings a meaningful direction to the future research.

4.2. Discussion for Experiment 2

Unsurprisingly, conflict adaptation effect was significantly present in the gray background, because gray was one of monochrome colors frequently used in previous related studies (Gratton et al., 1992; Kerns et al., 2004) where conflict adaptation effect was typically observed. However, as can be seen in Fig. 2C, the red background did not enhance the conflict adaptation effect, which may be due to the ceiling effect of red modulation, or that red color does not increase alertness level. Interestingly, we found that the conflict adaptation effect was not significantly present in the blue background.

Taken the results from Experiments 1 and 2 together, we proposed that the blue color may impair conflict adaptation effect through decreasing the alertness level. More importantly, the behavioral results from Experiments 1 and 2 could not provide direct evidence for the involvement of alertness in the modulation of color on conflict adaptation. Accordingly, the fMRI data during the modulation of color on conflict adaptation could be used to address which functions should be responsible for this modulation from imaging level.

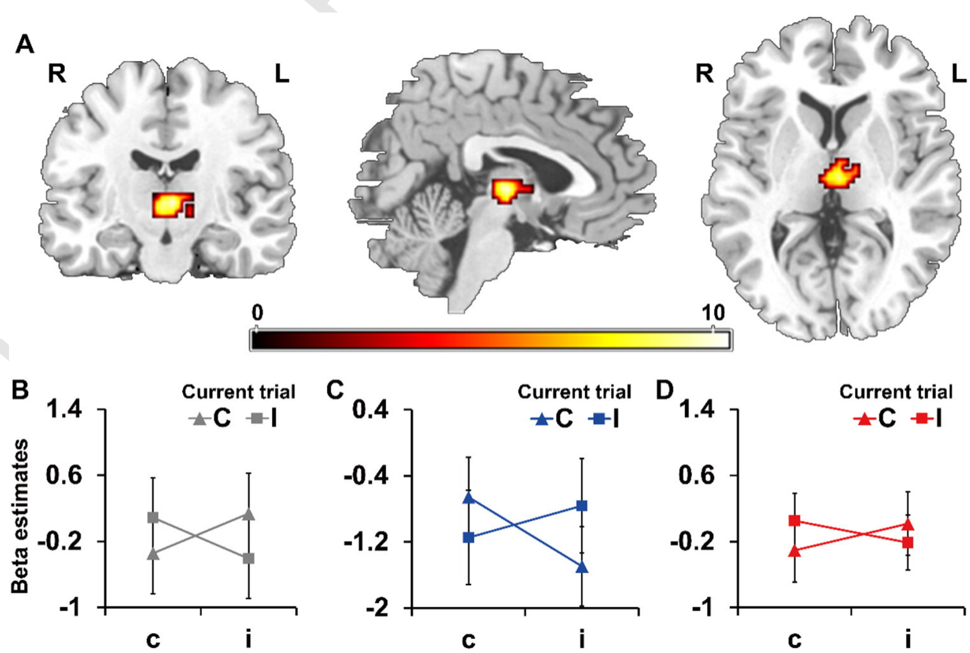

Fig. 3. Color effect on regional activation patterns in Thalamus. The background color type × previous trial × current trial type interaction effect on BOLD response of thalamus (Panel A) and its activation patterns (Panels B, C, and D for the gray, blue and red backgrounds, respectively). Error bars donate the SEM across subjects.

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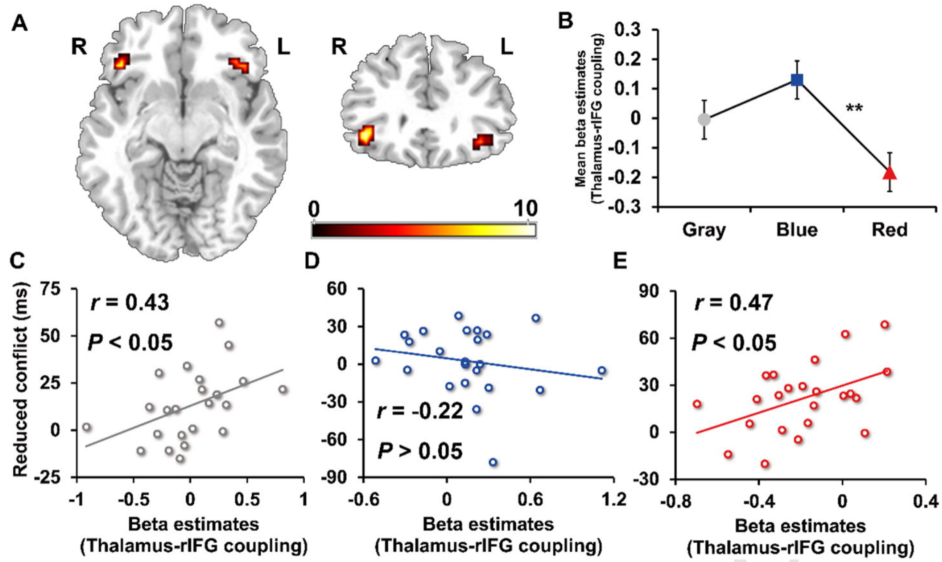

Fig. 4. The color modulated thalamus-seeded connectivity in conflict adaptation. (A) The inferior prefrontal gyrus (IFG) showing significant stronger connectivity with the thalamus in high versus low conflict resolution trials in blue background relative to the gray and red backgrounds ($P < 0.005$ uncorrected, cluster size > 10). (B) The beta estimates of the thalamus–rIFG coupling during conflict adaptation across three backgrounds showed a significant one-way ANOVA result, $F_{(2,\,44)} = 4.85$, $P < 0.05$, $\eta^2 = 0.18$. The lower panel show the beta estimate of the thalamus–IFG coupling as a function of the reduced interference in gray ($r = 0.43$, $P < 0.05$) (C), blue ($r = -0.22$, P > 0.05) (D) and red (r = 0.47, P < 0.05) (E) backgrounds. ** refers to a significant level of $P < 0.01$.

4.3. Discussion for Experiment 3

Consistently with Experiment 2, the conflict adaptation effect in Experiment 3 was significantly present in the gray and red backgrounds but absent in the blue background, which confirms that this critical finding in this study is rather stable. As illustrated in Fig. 3A, the fMRI results showed that the thalamus displayed a significant three-factor (background color, previous trial congruency, and current trial congruency) interaction effect, implying that the thalamus was responsible for the modulation of the background color on conflict adaptation. The follow-up two-factor (previous trial congruency and current trial congruency) ANOVA based on the beta estimates of the thalamus indicated that the activated patterns in the gray and red backgrounds (Fig. 3B and D) were similar, but different from that in the blue background (Fig. 3C). Obviously, the activated patterns in the gray and red backgrounds conform to the typical conflict adaptation pattern on behavioral level (Egner, 2007). Thus, the activated patterns of the thalamus in the gray and red backgrounds index conflict adaptation effect. However, the activated pattern of the thalamus in the blue background did not reflect conflict adaptation. Therefore, the blue background affected the engagement of the thalamus in conflict adaptation.

Previous imaging researches have suggested that the thalamus is part of alerting network (Paus et al., 1997; Fan et al., 2005; Raz and Buhle, 2006). Fan et al. (2005) examined the neural structures of the three functions (alertness, orienting, and executive control) of attentional network and found that the thalamus activation was associated with the alertness function. And in a positron emission tomography (PET) study, Paus et al. (1997) examined the thalamic blood-flow responses to an auditory alertness task. During the auditory alertness study, the blood-flow responses in the thalamus and mesencephalic reticular formation decreased at similar rates over a 50-min testing period. This finding of Paus et al. (1997) is well supporting the critical roles of thalamus and mesencephalic reticular formation, as this kind of neuronal adaptation technique is widely and validly used to reveal neural substrates of certain cognitive functions (Desimone, 1996; Henson and Rugg, 2003). Additionally, Posner and Petersen (1990) proposed that alertness system relied on the norepinephrine (NE) pathways that result from the locus coeruleus (i.e., LC), which implying the LC may play a key role in alertness. Thus, combining previous research with our results, it seems to support the hypothesis that the thalamus was involved in modulating the alertness level.

By exploring those regions in the whole brain coupled with the thalamus, we found that the thalamus–rIFG functional coupling was engaged in the modulation of color on conflict adaptation. The results of the further correlation analysis demonstrated that the thalamus–rIFG functional coupling could predict the conflict adaptation effect under the gray and red backgrounds (Fig. 4C and E); however, this relationship could not be established in the blue background (Fig. 4D). Furthermore, the modulation of background color on the prediction of thalamus–rIFG coupling on conflict adaptation was confirmed by the modulating effect analysis. These results suggested that, in the gray and red backgrounds, the thalamus exerts its normal function including the functional coupling with the rIFG; accordingly, the conflict adaptation effect significantly presented in the two conditions. However, in the blue background, the thalamus may dysfunction in conflict adaptation, and thalamic functional coupling with the rIFG may also be damped, both of which together lead the conflict adaptation effect to be eliminated.

4.4. General discussion

Intriguingly, the conflict adaptation effect was absent in the blue background, which was repeatedly demonstrated in Experiments 2 and 3 and therefore is a stable and reliable finding. Moreover, the behavioral results of Experiment 1 and the results of Experiment 3 can be used to address how the blue color eliminated the conflict adaptation effect. In Experiment 1, the blue color affected the scores of the three attentional functions; in contrast, the modulation of the background color on conflict adaptation only activated the thalamus in Experiment 3. Considering that the thalamus has been associated with alertness (Fan et al., 2005; Raz and Buhle, 2006), and the peaceful and tranquil mood induced by the blue color means that this color could decrease alertness (NAz and Epps, 2004; Mehta and Zhu, 2009), we proposed that the blue color influences conflict adaptation through decreasing individual's alertness level. Moreover, the significant conflict adaptation effects in the gray and red backgrounds could be interpreted using the same mechanism. One, the red color can make people more vigilant (higher alerting) (Elliot et al., 2007; Mehta and Zhu, 2009); two, participants usually cooperate well in psychological experiments (with gray backgrounds) and therefore are in a high arousal state (i.e., high alerting) to achieve optimal performances. Accordingly, the significant conflict adaptation effects in the two backgrounds are driven by the high alertness. Thus, alertness is determinant in the generation of conflict adaptation effect, which straightforward supports the Hebbian learning model of conflict adaptation (Verguts and Notebaert, 2008).

Our fMRI results suggested that, when the thalamus is in a high alerting state (in the gray and red backgrounds), it can effectively execute its functions and subserve conflict adaptation. Interestingly, the conflict is believed to be high in cI trials but low in iI trials (Botvinick et al., 1999; Egner and Hirsch, 2005a). Therefore, in the gray and red backgrounds, the result that the activation of the thalamus is higher in cI trials than in iI trials suggested that the thalamus indeed responds to conflict occurrence. However, in the low alertness state induced by the blue background, the functions of the thalamus may be damped: the activation of the thalamus in cI trials was lower than that in iI trials, suggesting that the thalamus in the blue background became insensitive to conflict occurrence. Notably, the three-factor interaction did not activate the brain areas monitoring conflict (e.g., the ACC), suggesting that the monitoring system was not affected by the color background. Although at a more liberal threshold ($P < 0.05$), the conflict monitoring system (e.g., ACC) was not activated in the three-factor interaction analysis. In this case, the thalamus would receive conflict signal in the three color backgrounds. Furthermore, the non-conflict adaptation activation pattern of the thalamus in the blue background would be due to the decreased alertness rather than no input conflict signal.

Here, it is necessary to elucidate whether the alertness function of the thalamus is involved in the modulation of background color on conflict adaptation effect. Notably, the accumulated data from fMRI studies have associated the three attentional functions with some specific brain areas, respectively. In details, right/left frontal and parietal areas, thalamic areas were typically engaged in alertness function (Posner and Petersen, 1990; Thomas et al., 2003). The orienting system has been associated with areas of the parietal and frontal lobes (Fan et al., 2005; Corbetta and Shulman, 2002). And the executive control usually recruited the dorsal anterior cingulate and the lateral prefrontal cortex (Bush et al., 2000; MacDonald et al., 2000). Generally, the frontal and parietal cortexes are shared by the three functions, but the thalamus seems to be one of the neural substrates of alertrness rather than orienting and executive control. On the other hand, the alertness may be a common component shared by the orienting and executive control processing. Posner and Petersen (1990) suggested that alertness exerted the influence on the posterior attention subsystems to support orienting processing and possibly also impacts other attentional subsystems. Specifically, individuals need to keep optimal alertness during the performance of orienting and executive control. This may be the reason that the thalamus was also activated during executive control (Fan et al., 2005). Furthermore, one study had demonstrated that the alerting function, but rather the orienting and executive control, of the attentional network is positively correlated with the conflict adaptation effect (Liu et al., 2013), indicating the alertness may engage more during conflict adaptation.

One-way ANOVA on PPI values across three backgrounds implied that the thalamus-IFG functional integration was modulated by the background color (Fig. 4B). Although several studies reported the inhition related activation of the left IFG (Konishi et al., 1999; Swick et al., 2008), the engagement of this region in inhition control is not generally accepted (Aron, 2003; Verbruggen and Logan, 2008). In fact, it has been reported that the left IFG was mainly associated with the semantic processing (Rosen et al., 2000; Thompson-Schill et al., 1997; Xiao et al., 2005). Therefore, the coupling between the thalamus and the left IFG may serve to process the sematic information of the stimuli. However, the rIFG was mainly engaged in the inhibition as a central mechanism of executive control (Aron et al., 2003, 2004; Hampshire et al., 2010; Swann et al., 2012). Addionally, Egner (2011) suggested that the IFG was involved in the processing of conflict adaptation. Therefore, the rIFG may mainly engage more in congtive control processes relative to the lIFG. However, it remains to be examined whether the left IFG interacts with the right IFG in support of conflict control.

Specifically, the thalamus–rIFG coupling value was significantly opposite in the blue and red backgrounds. Behaviorally, red (versus blue) associated with higher alertness level facilitates conflict adaptation, however, blue (versus red) associated with lower alertness level impairs conflict adaptation. The alertness may function as concentration on current trial. Specifically, the alertness may be influenced more by previous trial and thus show less response to current trial in the blue background, which is associated with longer RT under conflict adaptation. From the neural level perspective, the function of the thalamus may be to dynamically regulate the alertness level. As the alertness level was reduced under the blue background (versus red), the thalamus may need to keep positive correlation with the rIFG in order to hold enough arousal to resolve current conflict. However, under the higher alertness level induced by the red background (versus blue), the thalamus may need to keep negative correlation with the rIFG in order to control excessive arousal to resolve current conflict. Because the previous research suggested that excessive arousal went against conflict resolution(Padmala et al., 2011).

Response to the different arousal levels across the blue and red backgrounds, the thalamus may be turned on/off to modulate the activation of the rIFG to facilitate conflict resolution, which is represented on the thalamus–rIFG coupling. Specifically, the connectivity would be strengthened under the blue background (i.e., low alertness level), while inhibited under the red background (i.e., high alertness level). Notably, even the strengthened thalamus–rIFG functional integration, modulation from the thalamus on the rIFG is better late than never in conflict adaptation under the blue background. According to the correlation results (Fig. 4C, D, and E), it can be known that when the conflict adaptation effect was lowest under the red background, the inhibition on the thalamus–rIFG connectivity would be strongest (i.e., the most negative correlation). On the contrary, the conflict adaptation effect was lowest under the blue background, the thalamus–rIFG connectivity would be strongest, albeit not to statistically significance.

In conclusion, our behavioral results consistently demonstrated that conflict adaptation effect was eliminated at the low alertness condition induced by the blue background, but significantly presented at the high alertness conditions induced by the gray and red backgrounds. Moreover, the results of brain activation and functional coupling showed that the modulation of alertness on conflict adaptation relies on the thalamus. Thus, we propose that the alertness is determinant for the occurrence of conflict adaptation, and the thalamus is one key region of the brain network subserving the modulations of alertness on conflict adaptation.

This research thus facilitates our understanding of the neural mechanism underlying the modulation of alertness on cognition function. Future research could examine the effect of brain arousal level on cognition from cellular level to reveal how the hormone system related with arousal (e.g., norepinephrine, NA) exert the influence on cognition processes. Clinically, when medical drugs and equipment for the improvement of cognition function were developed, the effect of arousal level should be fully considered. Additionally, it advances current research on the effect of color on cognition and behavior. What wall color of classroom do we choose for an educational facility? What color enhances pilot in an aircraft cabin? Depending on the background color, individual performance, under the tasks needed to optimize the alertness level, may be different. If the task requires individual's vigilant attention (e.g., simulating operation of the pilot in plane cabin), then red might be particularly appropriate. However, blue would be less beneficial.

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