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Task-dependent response conflict monitoring and cognitive control in anterior cingulate and dorsolateral prefrontal cortices

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ABSTRACT

Previous experience affects our behavior in terms of adjustments. It has been suggested that the conflict monitor-controller system implemented in the prefrontal cortex plays a critical role in such adjustments. Previous studies suggested that there exists multiple conflict monitor-controller systems associated with the level of information (i.e., stimulus and response levels). In this study, we sought to test whether different types of conflicts occur at the same information processing level (i.e., response level) are independently processed. For this purpose, we designed a task paradigm to measure two different types of response conflicts using color-based and location-based conflict stimuli and measured the conflict adaptation effects associated with the two types of conflicts either independently (i.e., single conflict conditions) or simultaneously (i.e., a double-conflict condition). The behavioral results demonstrated that performance on current incongruent trials was faster only when the preceding trial was the same type of response conflict regardless of whether they included a single- or double-conflict. Imaging data also showed that anterior cingulate and dorsolateral prefrontal cortices operate in a task-specific manner. These findings suggest that there may be multiple monitor-controller loops for color-based and location-based conflicts even at the same response level. Importantly, our results suggest that double-conflict processing is qualitatively different from single-conflict processing although double-conflict shares the same sources of conflict with two single-conflict conditions.

1. Introduction

Goal-directed behavior requires an adaptive cognitive control system in order to adjust our performance based on previous experience (Miller and Cohen, 2001). According to conflict monitoring theory which is the predominant account of cognitive control, adjustment in behavior is accomplished through the conflict monitor-controller system implemented in the prefrontal cortex (Botvinick et al., 2001, 2004). This theory suggests that the dorsal anterior cingulate cortex

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(dACC) plays an important role in detecting response conflict (i.e., monitor) and the dorsolateral prefrontal cortex (DLPFC) plays a critical role in regulating the conflict (i.e., controller) by attentional biasing.

The conflict monitoring theory explains how the monitor-controller system dynamically operates in conflicting situations. For example, in the Stroop color-naming task (Stroop, 1935), which is a prototypical conflict task, conflict is greater in incongruent trials (e.g., "RED" printed in green ink) than in congruent trials (e.g., "RED" printed in red ink). Importantly, performance in incongruent trials is faster in trials following incongruent trials (iI) compared to those following congruent trials (cI), referred to as the conflict adaptation effect (Gratton et al., 1992; Mayr et al., 2003). According to the conflict monitoring theory, decreased reaction times in iI trials compared to cI trials are interpreted such that the level of cognitive control is higher in iI trials than in cI trials due to temporary up-regulation of control through the monitor-controller system. Consistently, neuroimaging studies found a decrease in dACC activity and an increase in DLPFC activity in iI trials compared to cI trials (Botvinick et al., 1999; Kerns et al., 2004).

Although early conflict monitoring studies assumed a domain-general cognitive control system, recent findings suggest that different types of conflicts at different information processing levels (e.g., perceptual and response levels) involve independent cognitive control systems (Kim et al., 2010, 2011, 2012). Specifically, in a series of studies, we found that response conflict recruited the anterior portion of dACC and DLPFC whereas perceptual conflict engaged the posterior portion of dACC and the anterior portion of the dorsal premotor cortex (pre-PMd). More importantly, the conflict adaptation effects were absent when the response-incongruent trials were preceded by perceptual-incongruent trials and vice versa. In contrast, significant adaptation effects were found when response-incongruent trials were preceded by response-incongruent trials and when perceptual-incongruent trials were preceded by perceptual-incongruent trials. These findings suggest that there exists multiple sets of domain-specific conflict monitor-controller loops according to the level of information processing (Egner, 2008).

However, it is unknown whether different types of conflicts at the same information processing level (e.g., response conflict) recruit the same monitor-controller loop (e.g., dACC and DLPFC). If the monitor-controller loop operates in a task-general manner for response conflict regardless of the source of conflict, it would show conflict adaptation even when there is preceding response conflict from another source (e.g., color-based response conflict trials preceded by location-based response conflict trials, or vice versa). In contrast, if the monitor-controller loop operates in a task-specific manner for response conflict, conflict adaptation would be absent when there is preceding response conflict from another source. In order to address this question, we tested whether one type of response conflict yields conflict adaptation in another type of response conflict. We also tested whether one type of single-conflict yields conflict adaptation in the following double-conflict trials which included both types of response conflicts and whether double-conflict trials yielded adaptation in the following trials which included only one of conflict types.

It is also important to note that there could be three possible expectations with regard to double-conflict processing: if the conflict adaptation effect exists in the double-conflict trials following the single-conflict trials for both types (e.g., color-based and location-based), this would be interpreted such that the sum of the two types of conflicts is likely to be equivalent to the double-conflict; if the adaptation effect exists in the double-conflict trials following the single-conflict trials only for one type (e.g., color-based), this would be interpreted such that this type of single-conflict is dominant in double-conflict processing; and if the adaptation effect is absent in the double-conflict trials following any type of single-conflict, this would be interpreted such that double-conflict processing is qualitatively different from single-conflict.

In order to address the above questions, we designed a double-conflict task using color-based and location-based conflict stimuli (Fig. 1). This task was to evoke two types of conflict at the response level either simultaneously or separately in order to test the neural activity in dACC and DLPFC in the context of the conflict adaptation paradigm.

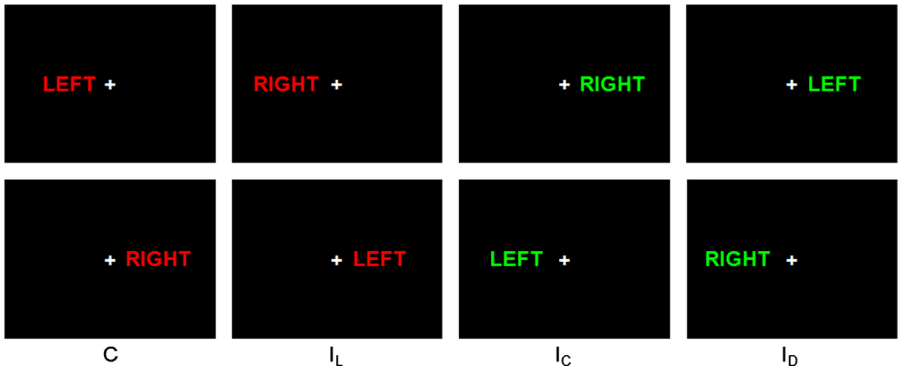

Fig. 1 – Task paradigm used in the current study. The task required subjects to respond to the left or right based on the task rules. In one half of the trials, the location was same as the meaning of the word and they were opposite to each other in the other half (location-based conflict). When the color of the word was red, subjects were required to respond to the meaning of the word. When the color of the word was green, they were required to respond in the opposite direction of the word (color-based conflict). Accordingly, there were four types of stimuli: congruent (C), location-based incongruent (I_L), color-based incongruent (I_C), and double incongruent (I_D) stimuli.

2. Results

2.1. Behavioral data

Planned comparisons using one-way repeated measures ANOVAs were employed in order to test whether performance on each current trial type (i.e., current C, I_L, I_C, and I_D trials) was affected by different types of the preceding trials. Mean error rates and reaction times (RTs) are presented in Fig. 2. Accuracy was generally high across task conditions (all conditions ≥ 94.1%). In the analyses of accuracy for all current trials, the effects of the preceding trial type were not significant (*ps* ≥ 0.169).

For the analyses of RT data, error trials and post-error trials were excluded in calculating the RTs for each condition (see Section 4). The analysis of the current C trials showed that the effect of the preceding trial type was significant ($F(3,45)=17.29$, $p<0.001$). Post-hoc comparisons using Bonferroni correction indicated that this difference was due to the fact that performance was faster in the CC trials ($M=607$ ms, $SD=61$) than in the I_LC ($M=638$ ms, $SD=69$), I_CC ($M=646$ ms, $SD=68$), and I_DC ($M=644$ ms, $SD=60$) trials (ps < 0.001). For the analysis of the current I_L trials, the effect of the preceding trial type was significant ($F(3,45)=24.97$, $p<0.001$), due to faster RTs in the I_LI_L trials ($M=621$ ms, $SD=65$) than in the CI_L ($M=660$ ms, $SD=74$), I_CI_L ($M=677$ ms, $SD=81$), and I_DI_L ($M=681$ ms, $SD=82$) trials (ps < 0.001). However, no difference was found in pair-wise comparisons among CI_L, I_CI_L, and I_DI_L trials (ps ≥ 0.080). In the same manner, the analysis of the current I_C trials showed that the effect of the preceding trial type was significant ($F(3,45)=24.60$, $p<0.001$), due to faster RTs in the I_CI_C trials ($M=653$ ms, $SD=84$) than in the CI_C ($M=698$ ms, $SD=85$), I_LI_C ($M=708$ ms, $SD=77$), and I_DI_C ($M=688$ ms, $SD=94$) trials (ps < 0.001). However, pair-wise comparisons among the CI_C, I_LI_C, and I_DI_C trials were not significant (ps ≥ 0.092). Finally, for the analysis of the current I_D trials, the effect of the preceding trial type was also significant ($F(3,45)=10.94$, $p<0.001$). Specifically, RTs were faster in the I_DI_D trials ($M=713$ ms, $SD=66$) than in the CI_D ($M=765$ ms, $SD=99$), I_LI_D ($M=763$ ms, $SD=98$), and I_CI_D ($M=753$ ms, $SD=94$) trials (ps < 0.001). However, RTs were not different among the CI_D, I_LI_D, and I_CI_D trials (ps ≥ 0.674). These results show that response conflicts from the same sources were modulated by the previous incongruent trials but that those from two different sources were not modulated by each other. The same patterns were observed in the double-conflict trials.

Additionally, we tested whether performance in the I_D trials were more difficult than in the single-conflict trials (i.e., I_C and I_L trials). For this purpose, the means of all I_D trials were compared to the means of all I_C trials and those of all I_L trials, respectively. The results showed that the accuracy of the I_D trials was lower than those of the I_C and I_L trials (ps < 0.005) and the RTs of the I_D trials were slower than those of the I_C and I_L trials (ps < 0.001).

2.2. Imaging data

Functional imaging data were analyzed to test whether the same frontal regions (i.e., dACC and DLPFC) associated with response conflict show different activation patterns according to the source of conflict in the context of conflict adaptation. In order to identify the dACC and DLPFC regions associated with response conflict unbiased by the source of conflict, all incongruent trials (I_L, I_C and I_D trials) were first contrasted with congruent trials. The results showed that both dACC (*x*, *y*, *z* = 10, 27, 23; BA 32) and left DLPFC (*x*, *y*, *z* = −30, 25, 32; BA 9) were activated by incongruent trials compared to congruent trials (Fig. 3).

BOLD signal changes associated with each condition (see Section 4) were extracted from the ROIs found in the above analysis, for the following detailed analyses. First, signal changes of dACC were analyzed (Fig. 3). The effect of the preceding trial type for the current I_L trials was significant ($F(3,45)=12.88$, $p<0.001$), due to the fact that the signal changes of I_LI_L trials ($M=0.11$, $SD=0.07$) were lower than those of CI_L ($M=0.16$, $SD=0.11$), I_CI_L ($M=0.16$, $SD=0.10$), and I_DI_L ($M=0.18$, $SD=0.09$) trials (ps < 0.002). Similar results as in the current I_L trials were found in the analysis of the current I_C trials. Specifically, the effect of the preceding trial type for the current I_C trials was significant ($F(3,45)=4.54$, $p=0.007$), attributable to lower signal changes of I_CI_C trials ($M=0.15$, $SD=0.08$) than those of CI_C ($M=0.21$, $SD=0.11$), I_LI_C ($M=0.20$, $SD=0.08$), and I_DI_C ($M=0.20$, $SD=0.10$) trials (ps < 0.043). For the analysis of the current I_D trials, the effect of the preceding trial type was also significant ($F(3,45)=3.119$, $p<0.001$) due to the lower signal changes of I_DI_D trials ($M=0.18$, $SD=0.10$) than those of CI_D ($M=0.26$, $SD=0.12$), I_LI_D ($M=0.25$, $SD=0.11$), and I_CI_D ($M=0.27$, $SD=0.10$) trials (ps ≤ 0.033). In contrast, for the

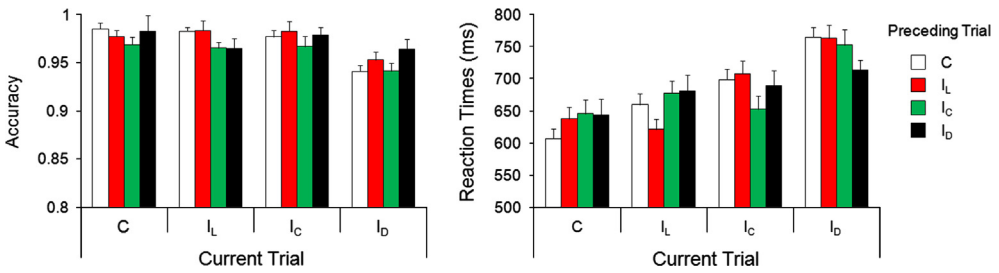

Fig. 2 – Behavioral results. Mean accuracy and reaction times are presented for each condition. Error bars indicate the standard errors of the means. Note: C, congruent; I_L, location-based incongruent; I_C, color-based incongruent; I_D, double incongruent.

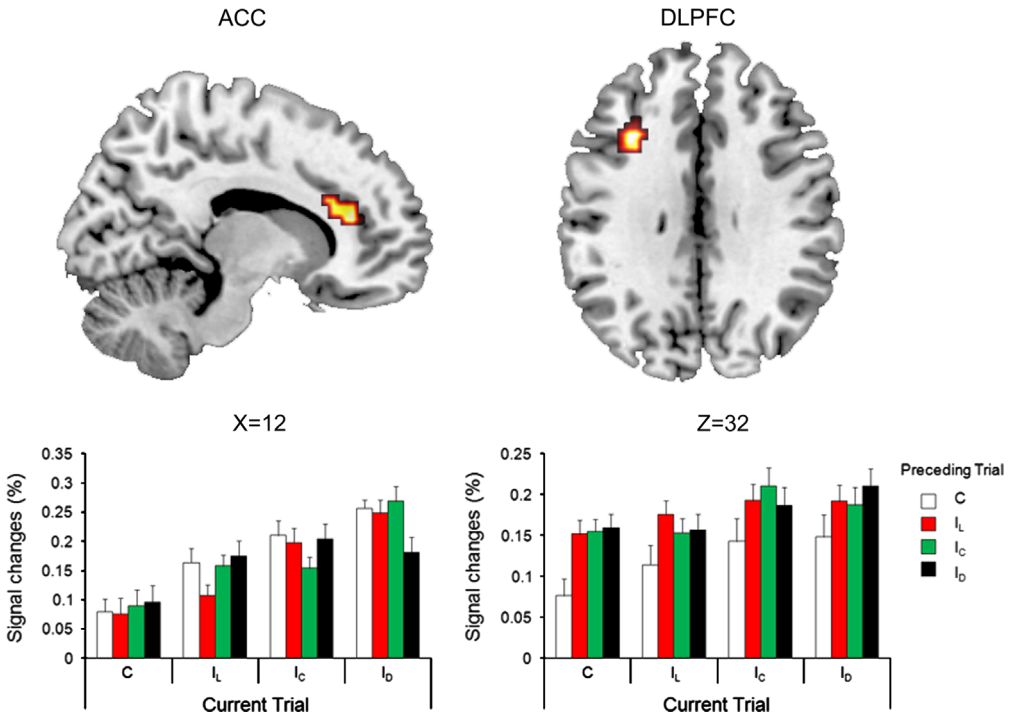

Fig. 3 – dACC and DLPFC activation (top) and BOLD signal changes for each condition (bottom). Note: C, congruent; I_L, location-based incongruent; I_C, color-based incongruent; I_D, double incongruent.

current C trials, the effect of the preceding trial type was not significant ($F(3,45)=0.573$, $p=0.636$).

Additionally, we tested whether the signal changes of I_D trials were different from those of I_C and I_L trials. As conducted in the behavioral analyses, in addition, the mean signal changes of all I_D trials were compared to the means of all I_C trials and those of all I_L trials, respectively. The results showed that the signal changes of dACC were higher during the I_D trials than during the I_C and I_L trials (ps <0.005).

The next analyses focused on the left DLPFC ROI. For the current C trials, the effect of the preceding trial type was significant ($F(3,45)=17.241$, $p<0.001$). Specifically, Post-hoc comparisons using Bonferroni correction indicated that I_LC ($M=0.15$, $SD=0.09$), I_CC ($M=0.16$, $SD=0.11$), and I_DC ($M=0.16$, $SD=0.11$) trials showed higher signal changes than that of CC ($M=0.77$, $SD=0.08$) trials (ps <0.001). The analysis of the current I_L trials showed a trend towards significance ($F(3,45)=2.685$, $p=0.058$), which was attributable to the higher signal changes for I_LI_L ($M=0.18$, $SD=0.07$) than for CI_L ($M=0.11$, $SD=0.68$) trials ($p<0.001$). A similar trend was found in the analysis of the current I_C trials ($F(3,45)=2.629$, $p=0.062$). Specifically, I_CI_C trials ($M=0.21$, $SD=0.09$) showed higher signal changes than that of C I_C ($M=0.14$, $SD=0.06$) trials ($p<0.020$). The analysis of the current I_D trials showed that the effect of the preceding trial type was significant ($F(3,45)=3.966$, $p=0.014$), due to the higher signal changes of I_DI_D trials ($M=0.21$, $SD=0.08$) than that of CI_D trials ($M=0.15$, $SD=0.07$). In contrast, no difference between I_DI_D and I_LI_D trials ($M=0.19$, $SD=0.08$) and between I_DI_D and I_CI_D trials ($M=0.19$, $SD=0.09$) was observed (ps ≥ 0.197). As performed in the dACC analyses, we tested whether the signal changes of DLPFC during I_D trials were different from those during the I_C and I_L trials. The results show that the signal changes of DLPFC were higher during the I_D trials than during the I_L trials ($p<0.005$) whereas there was no difference between the I_D and I_L trials ($p>0.86$).

The next analysis was to test whether the dACC activity on the preceding incongruent trials predicts the DLPFC activity on the current incongruent trials (Fig. 4). In doing so, the signal changes of dACC on the preceding I_L, I_C, and I_D trials were correlated with those of DLPFC on the current I_L, I_C, and I_D trials. For the I_LI_L condition, a significant positive correlation was observed between the preceding dACC activity and the current DLPFC activity ($r=0.752$, $p<0.001$) whereas the correlations were not significant in I_CI_L ($r=0.219$, $p>0.05$) and I_DI_L ($r=0.380$, $p>0.05$). For the I_CI_C condition, the correlation between the preceding dACC activity and current DLPFC activity was significant ($r=0.637$, $p<0.01$) whereas the correlations were not significant in I_LI_C ($r=0.414$, $p>0.05$) and I_DI_C ($r=0.001$, $p>0.05$). The analysis of the I_DI_D condition showed that the correlation between the preceding dACC activity and current DLPFC activity was significant ($r=0.689$, $p<0.01$) whereas the correlations were not significant in I_LI_D ($r=0.374$, $p>0.05$) and I_CI_D ($r=0.410$, $p>0.05$).

Finally, we tested whether the dACC activity on the preceding incongruent trials predicts behavioral conflict adaptation effects on the current incongruent trials (Fig. 5). These analyses were restricted only to the I_LI_L, I_CI_C, and I_DI_D conditions which showed significant adaptation effects in the behavioral results. The results showed that the correlation between the dACC activity on the preceding I_L trials and the adaptation effect was significant ($r=0.508$, $p<0.05$). Similarly, the correlations were significant in the I_CI_C and I_DI_D conditions ($r=0.664$, $p<0.005$; $r=0.660$, $p<0.005$, respectively).

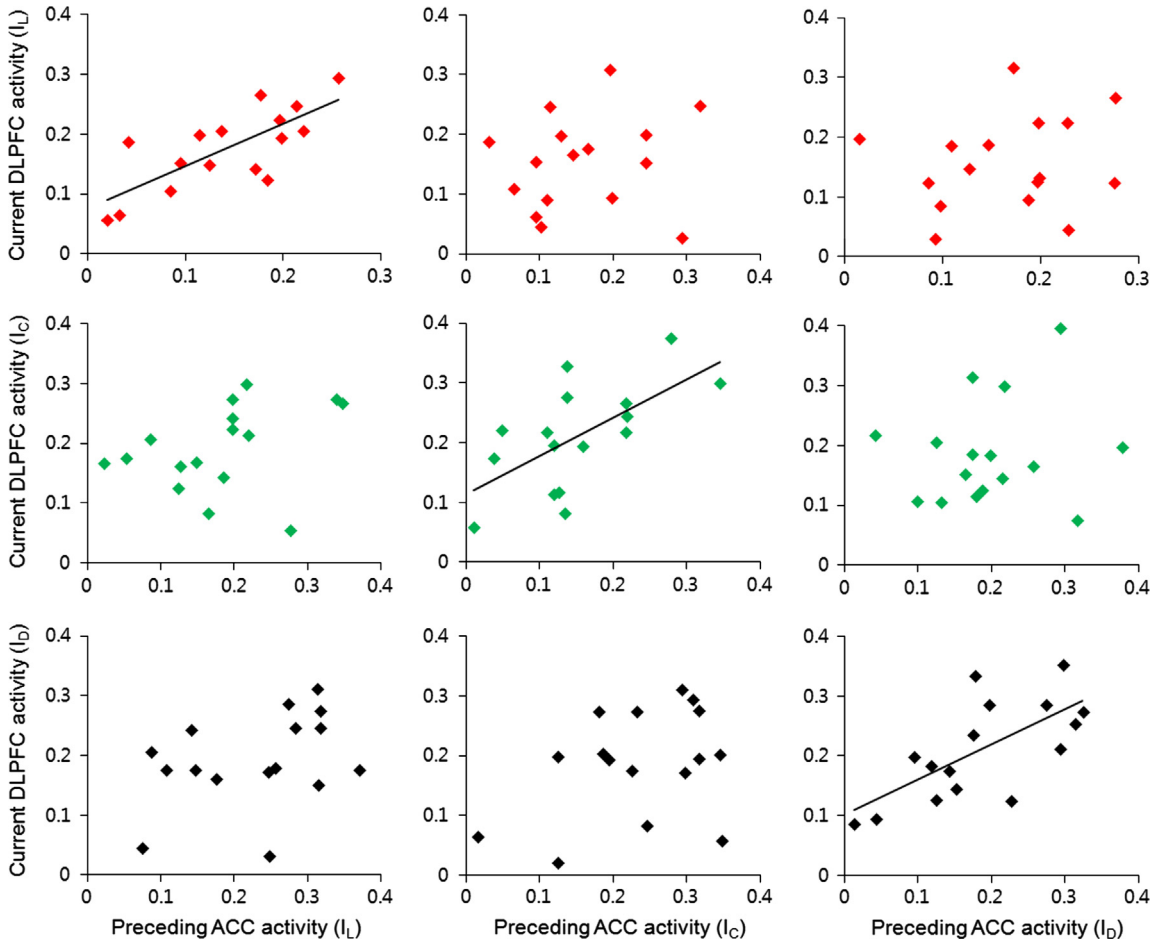

Fig. 4 – Correlations between the preceding dACC activity and current DLPFC activity. Note: I_L, location-based incongruent; I_C, color-based incongruent; I_D, double incongruent.

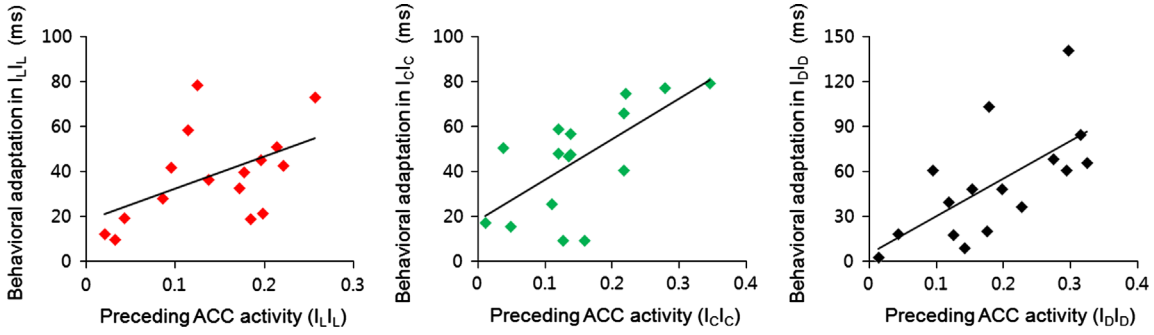

Fig. 5 – Correlations between the preceding dACC activity and behavioral adaptation effects. Note: I_L, location-based incongruent; I_C, color-based incongruent; I_D, double incongruent.

3. Discussion

In the current study, we found that performance on the current incongruent trials was faster only when the same type of response conflict was presented in the preceding trial regardless of whether they included single-conflict or double-conflict. The absence of conflict adaptation effects across conflict types suggests that each type of response conflict would be qualitatively different from the others. Specifically, color-based and location-based conflicts seemed to be processed independently although these two types of conflicts were evoked at the same response level. Consistent with the current findings, previous studies have demonstrated that a specific type of conflict was modulated only by the same type of conflict (Egner et al., 2007; Kim et al., 2012; Verbruggen et al., 2005; Wendt et al., 2006). For example, the conflict adaptation effect for the incongruent Simon-type trial was observed not when the preceding trial was the flanker-type trial but when it was the same type trial (Wendt et al., 2006). Furthermore, the absence of adaptation both in the double-conflict trial following any single-conflict

and in the single-conflict trial following a double-conflict trial suggests that the double-conflict is unequal to the sum of the two single-conflict types. There could be two potential interpretations for this finding. First, this could be due to interference from the other source of response conflict while performing double-conflict trials. If this were the case, there should be increased RTs on the single-conflict trials following the other type of conflict (e.g., when color-based conflict preceded by location-based conflict) due to interference from the preceding trials. However, our results did not support this interpretation. Another interpretation is that it could be because double-conflict processing is qualitatively different from single-conflict processing despite the fact that the sources of double-conflict were overlapped with two single-conflict conditions.

The imaging data demonstrated that the monitor-controller loop operates in a task-specific manner for response conflict. In detail, dACC showed lower neural activity during conflict processing when the same type of conflict preceded it than when another conflict type preceded it. In the same manner, DLPFC showed increased neural activity during the current response conflict processing when the same type of conflict preceded it. The current findings support previous studies which proposed that the monitor-controller loop operates in a task-specific manner (Egner et al., 2007; Egner, 2008; Kim et al., 2012). These studies suggested that there exist multiple monitor-controller loops according to the information processing levels (i.e., stimulus-selection level vs. response-selection level). This enabled us to expect that two types of conflicts at the same information processing level would recruit the same monitor-controller loop. However, our results demonstrated that there exist task-specific monitor-controller loops even at the same processing level (i.e., response conflict). Thus, it is reasonable to consider why conflict adaptation was not observed in the current results. One possible answer could be because the sources of the response conflicts were different. The task in the current study was manipulated to evoke two types of response conflicts using incompatibility between the stimulus features (color or location) and response features. It has been proposed that this type of response conflict is resolved through biasing response processes including inhibition of task-irrelevant stimulus features (Egner et al., 2007; Sturmer et al., 2002; Sturmer and Leuthold, 2003). This suggests that there may exist multiple monitor-controller loops for color-based and location-based conflicts even at the same response level and thus the same dACC and DLPFC regions may be able to tune to both types of response conflicts in order to regulate the same type of upcoming conflict. However, future research will be required to directly test whether the same dACC and DLPFC regions interact with distinct posterior regions representing either color or location in order to resolve each type of response conflict.

In our task design, the double-conflict trials included both color-based and location-based conflicts such that each source of incompatibility was exactly same as the color-based or location-based single-conflict. For this reason, the above interpretation enables us to predict that there would be conflict adaptation effects in the double-conflict trials preceded by any single-conflict trials and/or in the single-conflict trials preceded by double-conflict trials. However, we found no evidence of conflict adaptation effects in the double-conflict trials following single-conflict trials or in single-conflict trials following double-conflict trials. Consistent with behavioral results, this suggests that double-conflict processing is qualitatively different from single-conflict processing.

According to the conflict monitoring theory, dACC activity reflects the detection of response conflict (Botvinick et al., 2001, 2004). Accordingly, there would be two expectations for the dACC activation patterns when double-conflict is detected. First, if dACC operates in an all-or-none manner, the activation levels during single-conflict and double-conflict would be equivalent. In contrast, if dACC operates in a linear manner, neural activity would be higher in the double-conflict trials than in the single-conflict trials. Consistent with the behavioral results, dACC appears to support the latter expectation. This suggests that dACC activity increases as a function of the amount of conflict. A previous study supports our findings (Durston et al., 2003). Specifically, Durston et al. demonstrated that the dACC activity increased in incongruent trials as the magnitude of conflict increased. In their study, the number of preceding congruent trials was manipulated in order to test whether neural activity associated with conflict processing increases as a function of the number of preceding congruent trials. They assumed that the magnitude of conflict in the current incongruent trials increases as the number of preceding congruent trials increased, based on the conflict monitoring theory (Botvinick et al., 2001, 2004). As expected, they found linear increases in dACC, DLPFC, and posterior parietal cortex as the magnitude of conflict increased.

Since dACC showed increased activation in the double-conflict trials compared to the single-conflict trials, it would be reasonable to expect that DLPFC shows a similar activation pattern. However, DLPFC exhibited somewhat different activations. Specifically, the results demonstrated that DLPFC showed an increase during the double-conflict trials compared to the location-based conflict trials. In contrast, we found no difference in DLPFC activations between the double-conflict trials and the color-based conflict trials. We speculate that this result could be because of the fact that DLPFC is capable of interacting with parietal and temporal cortices simultaneously and efficiently. This is supported by the fact that DLPFC is connected to a variety of brain regions including the parietal and temporal cortices (Petrides, 2000). However, it is still possible that DLPFC could process two types of conflicts in a serial manner. For instance, when color-based and location-based conflict stimuli were presented (i.e., double-conflict stimuli), subjects were required to inhibit its location first, and then to flip the response buttons in order to answer correctly. This might be able to explain why DLPFC showed no increase in activation during the double-conflict trials compared to the color-based conflict trials. Thus, further research will be required to test whether the same DLPFC region is capable of interacting with distinct posterior regions simultaneously.

Taken together, our data suggest that dACC and DLPFC play critical roles in detecting and resolving response conflict in a task-specific manner. Although the two types of conflicts were evoked at the response level, each of the conflicts was modulated only when the same type of response conflict preceded it. Importantly, we provide evidence that double-conflict processing appears to be qualitatively different from

single-conflict processing although double-conflict shares the same sources of conflict with two single-conflict conditions.

4. Experimental procedure

4.1. Participants

Sixteen healthy volunteers between the ages of 19 and 32 years (7 females, mean age=23.4 years, SD=3.96) participated in this study. All subjects were right-handed and native Korean speakers with normal or corrected-to-normal vision without color blindness, who reported no psychiatric or neurological problems. Subjects provided written informed consent approved by the Brain Science Research Center at KAIST, Daejeon, South Korea

4.2. Materials and procedure

A task paradigm was designed that allowed two different types of response conflicts to be measured either independently or simultaneously, using color-based and location-based conflict stimuli (Fig. 1). The task stimuli consisted of the word, "LEFT" or "RIGHT" presented on either the left or right side, which was printed in either a red or green color. Two types of response conflicts were manipulated by the location of the word and its color. The first type of response conflict was evoked by the incongruency between the meaning of the word (i.e., correct response) and its location. For example, when the word "LEFT" printed in red was presented on the right side of the screen, the meaning of the word and its location was incongruent (i.e., location-based conflict trials, I_L trials). The second type of response conflict was manipulated by the color of the word (i.e., color-based conflict trials, I_C trials). Specifically, subjects were asked to respond to the meaning of the word when its color was red (e.g., when "LEFT" printed in red color was displayed, subjects were required to respond to the left), and in the opposite direction of the word when its color was green (e.g., when "LEFT" printed in green color was displayed, subjects were required to respond to the right). When the word printed in green and its meaning was incongruent with its location (e.g., "LEFT" printed in green color displayed on the right side of the screen), subjects were required to consider two independent types of response conflicts simultaneously, resulting in double-conflict trials (i.e., double conflict trials, I_D trials). Finally, when the word printed in red and its meaning was congruent with its location, no response conflict was included (i.e., congruent trials, C trials).

Four trial types were pseudo-randomly intermixed in order to measure neural activity specific to post-conflict adjustment associated with each single conflict and a double-conflict condition. This manipulation resulted in four current trial types (i.e., C, I_L, I_C, and I_D trials) with four preceding trial types. Accordingly, 16 trial-to-trial transitions were included in the experimental conditions: CC, I_LC, I_CC, I_DC, CI_L, I_LI_L, I_CI_L, I_DI_L, CI_C, I_LI_C, I_CI_C, I_DI_C, CI_D, I_LI_D, I_CI_D, and I_DI_D. To avoid any effects associated with potential confounds such as the repetition priming effect (Mayr et al., 2003), no repetition of identical stimuli was included in the task.

Subjects were instructed to press either a left or right button corresponding to the correct answer, using their index or middle fingers. Stimuli were displayed for 1 s with a jittered inter-stimulus-interval (ISI), distributed from 1.5 s to 4.7 s (mean ISI=2.5 s). A total of 40 trials were included in each condition. The words for the task were presented in native language (i.e., Korean). The experiment was programmed using E-Prime v1.2

4.3. Imaging acquisition

Functional and anatomical images were acquired on a 3-T MRI system (Oxford magnet, Varian console magnet built by ISOL) at the Brain Science Research Center (KAIST, Daejeon, South Korea). T2*-weighted functional images using a gradient echo (EPI) sequence (25 inter-leaved slices, repetition time (TR)=2 s, echo time (TE)=35 ms, flip angle (FA)=85°, field of view (FOV)=220 mm^2, matrix=64 × 64, slice thickness=4.5 mm). Five runs were scanned for the fMRI experiment. Each run consisted of 242 volumes and 16 conditions were included in each run. T1-weighted high-resolution anatomical images using the magnetization-prepared rapid gradient-echo (MPRAGE) sequence (256 × 256 × 128 mm^3, sagittal partitions) were collected for all subjects.

4.4. Data analyses

Statistical Parametric Mapping (SPM 5; Wellcome Department of Cognitive Neurology, UCL, London, UK) was used in the preprocessing and statistical analyses of the fMRI data. The first five volumes of each run were discarded prior to preprocessing. First, the differences in timing between slices were adjusted via sinc interpolation (Henson et al., 1999). These images were spatially realigned to the first volume of the first run using a six-parameter rigid body transformation. Images were then co-registered with the MPRAGE image and were spatially normalized into 2 mm isotropic voxels using the Montreal Neurological institute (MNI) template. Finally, the normalized images were smoothed with an 8 mm full-width at half-maximum Gaussian kernel, and high-pass filtering (128 s cutoff) was applied to the images in order to remove cardio-respiratory factors.

For the first-level single-subject analysis, all experimental conditions were included in constructing a general linear model using a canonical hemodynamic response function (HRF) with temporal and dispersion derivatives. Error trials, post-error trials and the first trial of each run were constructed for a separate regressor of non-interest. Head movement parameters in six dimensions were also modeled as covariates of non-interest. Accordingly, only correct trials for 16 event types were included in the fMRI analyses. This resulted in 16 regressors of interest for each subject. The purpose of the current study was to explore and compare neural activity of brain regions known to be typically involved in response conflict adjustment, namely, dACC and DLPFC. For second-level group analyses, all the conflict conditions (i.e., I_L, I_C, and I_D trials) were compared with the congruent condition (i.e., C trials) in order to identify regions of interest (ROIs) involved in response conflict unbiased by any specific source. These ROIs were defined by supra-threshold clusters

of voxels, using an uncorrected threshold of $p<0.001$ and a minimum cluster size of 10 contiguous voxels, in the left and right middle frontal gyri (DLPFC) and the left and right anterior cingulum regions (dACC) using the automated anatomical labeling (AAL) map (Tzourio-Mazoyer et al., 2002).

For the first ROI analyses, the signal changes of these ROIs for all 16 conditions were extracted and analyzed in the context of the analyses of variance (ANOVA) for each current trial type (i.e., current C, I_L, I_C, and I_D trials) to test whether the current signal changes of these ROIs were different according to the preceding trial types. In other words, this was to test whether the same region contributes to different conflict adaptation effects according to the source of response conflict. For the next ROI analyses, signal changes of dACC ROI on the preceding incongruent trials (i.e., I_L, I_C, and I_D trials) were extracted and were correlated with the signal changes of the current DLPFC ROI. For these analyses, a separate model was applied to individual data in order to extract the dACC activity on the preceding incongruent trials. These data were then correlated with the current DLPFC activity in order to test whether the dACC activity on the different types of preceding incongruent trials predicts increases in the DLPFC activity on the current DLPFC activity according to the source of response conflict. Finally, signal changes of dACC on the preceding incongruent trials were correlated with behavioral adaptation effect to test whether the dACC activity on the preceding incongruent trials predicts behavioral conflict adaptation effects. These were restricted only to the incongruent conditions showing significant behavioral adaptation effects. Marsbar (http://marsbar.sourceforge.net) was used to extract the ROI data.

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REFERENCES

Botvinick, M.M., Nystrom, L.E., Fissell, K., Carter, C.S., Cohen, J.D., 1999. Conflict monitoring versus selection-for-action in anterior cingulate cortex. Nature 402, 179–181.

Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. Psychol. Rev. 108, 624–652.

Botvinick, M.M., Cohen, J.D., Carter, C.S., 2004. Conflict monitoring and anterior cingulate cortex: an update. Trends Cogn. Sci. 8, 539–546.

Durston, S., Davidson, M.C., Thomas, K.M., Worden, M.S., Tottenham, N., Martinez, A., Watts, R., Ulug, A.M., Casey, B.J., 2003. Parametric manipulation of conflict and response competition using rapid mixed-trial event-related fMRI. NeuroImage 20, 2135–2141.

Egner, T., Delano, M., Hirsch, J., 2007. Separate conflict-specific cognitive control mechanisms in the human brain. NeuroImage 35, 940–948.

Egner, T., 2008. Multiple conflict-driven control mechanisms in the human brain. Trends Cogn. Sci. 12, 374–380.

Gratton, G., Coles, M.G., Donchin, E., 1992. Optimizing the use of information: strategic control of activation of responses. J. Exp. Psychol. Gen. 121, 480–506.

Henson, R.N., Buchel, C., Josephs, O., Friston, K.J., 1999. The slice-timing problem in event-related fMRI. NeuroImage 9, 125.

Kerns, J.G., Cohen, J.D., MacDonald III, A.W., Cho, R.Y., Stenger, V.A., Carter, C.S., 2004. Anterior cingulate conflict monitoring and adjustments in control. Science 303, 1023–1026.

Kim, C., Chung, C., Kim, J., 2010. Multiple cognitive control mechanisms associated with the nature of conflict. Neurosci. Lett. 496, 156–160.

Kim, C., Kroger, J.K., Kim, J., 2011. A functional dissociation of conflict processing within anterior cingulate cortex. Hum. Brain Mapp. 32, 304–312.

Kim, C., Chung, C., Kim, J., 2012. Conflict adjustment through domain-specific multiple cognitive control mechanisms. Brain Res. 1444, 55–64.

Mayr, U., Awh, E., Laurey, P., 2003. Conflict adaptation effects in the absence of executive control. Nat. Neurosci. 6, 450–452.

Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. 24, 167–202.

Petrides, M., 2000. The role of the mid-dorsolateral prefrontal cortex in working memory. Exp. Brain Res. 133, 44–54.

Stroop, J.R., 1935. Studies of interference in serial verbal reactions. J. Exp. Psychol. 28, 643–662.

Sturmer, B., Leuthold, H., Soetens, E., Schroter, H., Sommer, W., 2002. Control over location-based response activation in the Simon task: behavioral and electrophysiological evidence. J. Exp. Psychol. Hum. Percept. Perform. 28, 1345–1363.

Sturmer, B., Leuthold, H., 2003. Control over response priming in visuomotor processing: a lateralized event-related potential study. Exp. Brain Res. 153, 35–44.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. NeuroImage 15, 273–289.

Verbruggen, F., Liefooghe, B., Notebaert, W., Vandierendonck, A., 2005. Effects of stimulus–stimulus compatibility and stimulus-response compatibility on response inhibition. Acta Psychol. 120, 307–326.

Wendt, M., Kluwe, R.H., Peters, A., 2006. Sequential modulations of interference evoked by processing task-irrelevant stimulus features. J. Exp. Psychol. Hum. Percept Perform. 32, 644–667.