Implicitly Strengthened Task-Irrelevant Stimulus-Response Associations Modulate Cognitive Control: Evidence From an fMRI Study

Tiansheng Xia, Hui Li, and Ling Wang*

*Center for Studies of Psychological Application and School of Psychology,
Key Laboratory of Mental Health and Cognitive Science of Guangdong Province,
South China Normal University, Guangzhou, China*

Abstract: The dynamics of cognitive control have been investigated by the proportion congruency effect. However, the theory that this effect is due to attentional modulation has been challenged by contingency learning accounts. This raises the question of how the cognitive control system operates during and after increasing the strength of task-irrelevant stimulus-response (S-R) associations. We employed a novel paradigm that elicits positive and reversed Simon effects via task rule manipulations, and combined it with a between subjects proportion congruency manipulation. The pattern of enhancement and reversal of the positive and reversed Simon effects across conditions suggested that participants used strengthened task-irrelevant S-R associations to predict responses. Functional neuroimaging identified proportion congruency effects that interacted with task S-R associations, showing greater activity when strengthened task-irrelevant S-R associations conflicted with task-defined S-R associations in frontoparietal regions, including bilateral superior parietal lobule (SPL) and dorsal premotor cortex (dPMC), presupplementary motor area/anterior midcingulate cortex (Pre-SMA/aMCC), and left dorsolateral prefrontal cortex (DLPFC). These results suggest that the aMCC and DLPFC shifted to responding mainly to the conflict induced by the strengthened irrelevant S-R associations. The SPL and dPMC might represent the strengthened irrelevant S-R associations. *Hum Brain Mapp* 37:756–772, 2016. © 2015 Wiley Periodicals, Inc.

Key words: cognitive control; contingency learning; proportion congruency effect; stimulus-response associations; superior parietal lobule

INTRODUCTION

Additional Supporting Information may be found in the online version of this article.

Contract grant sponsor: Natural Science Foundation of China; Contract grant number: 31271085; Contract grant sponsor: South China Normal University Research Start-Up Grant

*Correspondence to: Ling Wang, PhD, Center for Studies of Psychological Application & School of Psychology, South China Normal University, Guangzhou, China. E-mail: lingwang@m.scnu.edu.cn

Received for publication 14 October 2015; Accepted 15 November 2015.

DOI: 10.1002/hbm.23064

Published online 23 November 2015 in Wiley Online Library (wileyonlinelibrary.com).

Cognitive control refers to the ability to coordinate cognitive processes to flexibly adapt behavior according to current goals [Miller and Cohen, 2001]. Previous research has suggested that the anterior midcingulate cortex (aMCC) is involved in monitoring for conflict, or initiating control whereas the dorsolateral prefrontal cortex (DLPFC) is involved in resolving conflict, or implementing control [Botvinick et al., 1999, 2001; Egner and Hirsch, 2005; Kerns et al., 2004; MacDonald et al., 2000]. The effect of conflict on cognitive control is often studied in interference tasks such as the Simon and Stroop tasks in which the desired response can be congruent or incongruent with a pre-existing prepotent response. Typically, reaction time (RT)

is slower and accuracy is lower on incongruent trials, which are referred to as the conflict effect. The proportion of congruent trials can be manipulated to affect cognitive control: typically the conflict effect rises or reduces as the proportion of congruent to incongruent trials increases or decreases [Jacoby et al., 2003; Lindsay and Jacoby, 1994; Logan and Zbrodoff, 1979], which is known as the proportion congruency effect. Neuroimaging studies examining the proportion congruency effect have reported similar effects on aMCC and DLPFC activity [Blais and Bunge, 2010; Carter et al., 2000; Grandjean et al., 2013]. The proportion congruency effect was originally explained by the adjustment of the top-down attentional control in terms of control demand (the attention modulation account) [Blais et al., 2007; Botvinick et al., 2001; Verguts and Notebaert, 2008].

However, some studies with the paradigm of the Simon effect showed that increasing the ratio of incongruent trials may even reverse the conflict (Simon) effect (i.e., slower RT in the congruent than in the incongruent condition) [Hommel, 1994; Marble and Proctor, 2000; Toth et al., 1995]. The Simon effect refers to the finding that participants respond faster when the location of stimulus corresponds to the location of response (congruent condition) than when it does not (incongruent condition), despite the fact that the location of stimulus is irrelevant to the task [Kornblum et al., 1990; Lu and Proctor, 1995; Simon, 1969]. This effect reflects the interference from the task-irrelevant spatially compatible stimulus-response (S-R) associations on the relevant S-R associations [e.g., De Jong et al., 1994], and has been employed as a standard paradigm to investigate cognitive control [Botvinick et al., 2004; Hommel, 2011]. The reversal of the Simon effect resulted from increasing the ratio of incongruent trials may not be explained solely by the adjustment of top-down control to stimuli representations [e.g., Botvinick et al., 2001]. Increasing the top-down control may reduce the interference of irrelevant S-R associations and hence the conflict effect decreases (maximally to zero if the interference of irrelevant S-R associations may be eliminated completely) but may not be reversed. The reversal of the Simon effect rather suggests that participants strengthen spatially incompatible S-R associations and use them to guide responses [Hommel, 1994], suggesting that S-R learning plays a critical role in the proportion congruency effect. This idea is also consistent with the contingency learning account proposed recently to interpret the item-specific proportion congruency effect [Schmidt, 2013b; Schmidt and Besner, 2008]. However, a remaining important theoretical question is how the cognitive control system responds to changes in the strength of irrelevant S-R associations. Specifically, the operation of the cognitive control system depends on the interaction between relevant and irrelevant S-R associations [Botvinick et al., 2001]. Therefore, one would expect changes in the cognitive control system if the irrelevant S-R associations altered. Note the

theoretical difference between this question and the questions investigated by many previous studies [e.g., Blais et al., 2007; Botvinick et al., 1999; MacDonald et al., 2000; Verguts and Notebaert, 2008], which rather focus on how cognitive control system responds to the need for control (e.g., variation in conflict effect). We investigated this question by combining the proportion congruency effect and a variant of the Simon effect, the Hedge, and Marsh task, using functional magnetic resonance imaging (fMRI).

Hedge and Marsh [1975] revealed that the Simon effect is dependent on task rules. In a typical Hedge and Marsh task, participants usually carry out a discrimination task on nonspatial features of stimuli (e.g., red-green color discrimination), which is similar to a typical Simon task. What differs is that the response keys are also color labeled (see Fig. 1). The task rule to follow is either same-color (SC) mapping, in which participants have to press the key that is labeled with the same color as the target, or alternate-color (AC) mapping, in which participants must press the key labeled with the color that is different to that of the target. The classic findings of the Hedge and Marsh task are that there is a standard Simon (incongruent slower than congruent) effect in the SC mapping but a reversed Simon effect (congruent slower than incongruent) in the AC mapping. These results have been replicated by many studies [De Jong et al., 1994; Lu and Proctor, 1994; Proctor and Pick, 2003; Simon and Vilapakkam, 1981; Wühr and Biebl, 2009]. According to the logical recoding and dual-process accounts [De Jong et al., 1994; Hedge and Marsh, 1975; Wühr and Biebl, 2009], the logical rule of the relevant S-R associations is generalized to the irrelevant S-R associations. Specifically, the logical character of the AC rule is “reversal”, which is applied to and therefore recodes the irrelevant spatially compatible S-R associations to activate the opposite (i.e., reversal) response. That is, in the AC rule the irrelevant spatially “incompatible” S-R associations are actually used to predict responses. In addition, a recent fMRI study [Li et al., 2015] investigated the neural substrates of the Hedge and Marsh task. The aMCC and DLPFC activity showed a similar pattern as the behavioral results: a positive Simon effect in the SC rule but a reversed Simon effect in the AC rule. These suggest that there is more conflict in the incongruent condition in the SC rule but in the congruent condition in the AC rule.

In this study, we tested the hypothesis that the cognitive control system responds to the conflict between the relevant S-R associations and the strengthened irrelevant S-R associations resulted from proportion congruency manipulation. The advantage of employing the Hedge and Marsh task is that the hypothesis may be tested twice: one based on the Simon effect in the SC rule and the other one based on the reversed Simon effect in the AC rule. At the behavioral level, we expect that the Simon effect in the SC rule may be reversed by increasing the ratio of incongruent trials because of the strengthened irrelevant spatially

Figure 1.

Experimental procedure. The S-R color mapping rules (same-color: SC; alternate-color: AC) were manipulated across blocks. At the beginning of each block, a display was presented indicating, which color mapping rule should be followed in the upcoming trials. The color labels for the response keys were varied across trials. Abbreviations, Con: congruent; Inc: incongruent. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

incompatible S-R associations. At the neural level, because the response predicted by the strengthened irrelevant incompatible S-R associations is different from the one defined by the relevant color S-R associations in the congruent condition (therefore more conflict) but the same in the incongruent condition, we predict that the aMCC and DLPFC show stronger activity in the congruent than in the incongruent condition (i.e., a reversal of the Simon effect) associated with the reversal of the Simon effect in the SC rule. In contrast, the reversed Simon effect in the AC rule may be reversed by increasing the ratio of congruent trials because of the strengthened irrelevant spatially compatible S-R associations. Similarly, we predict that there is stronger aMCC and DLPFC activity in the incongruent than in the congruent condition (i.e., a reversal of the reversed Simon effect) associated with the reversal of the reversed Simon effect in the AC rule, because the responses activated by the relevant and the strengthened irrelevant spatially compatible S-R associations are different in the incongruent condition (therefore more conflict) but the same in the congruent condition. Note that previous cognitive control theory (e.g., conflict monitoring) [Botvinick et al., 2001] may not predict the reversals of conflict effects at both the behavioral and neural levels via manipulating proportion congruency. The results confirmed our hypothesis.

MATERIALS AND METHODS

Participants

Fifty-four healthy volunteers (mean age $\pm$ SD: 22.4 ± 2.6 years; 25 females) participated in the experiment. The

participants were randomly divided into three groups, 18 participants in each group. They were all right-handed according to Edinburgh Handedness Inventory [Oldfield, 1971], and had normal or corrected to normal vision. All participants provided written informed consent and were paid for their participation. This study was approved by the local Ethics Committee of School of Psychology, South China Normal University.

Apparatus and Stimuli

Presentation software (version 16.3, Neurobehavioral Systems) was used to program the task, present stimuli and record behavioral responses in the experiment. Stimuli were displayed to the subjects on a back-projection screen, which could be viewed via a mirror attached to the MRI headcoil. The background of the visual display was black. A white cross hair presented ($2.8^\circ \times 2.8^\circ$) in the screen center served as a fixation point. The target stimulus was a square ($3^\circ \times 3^\circ$) in red (RGB values: 255, 0, 0) or green (RGB: 0, 255, 0). The red and green squares were displayed above the fixation cross and on the left or right side of the screen (visual angle between the fixation cross and the stimulus: 7.1° vertical $\times$ 8.5° horizontal). Two rectangles (1.4° vertical $\times$ 2.8° horizontal; in red and green, respectively) with a white line (0.4° vertical $\times$ 4.2° horizontal) below each of them were displayed at the bottom of the display and served as response labels. One was presented on the left and the other on the right side of the screen (visual angle between the fixation and the rectangle: 7.1° vertical $\times$ 8.5° horizontal) randomly from trial to trial. Two MRI-compatible response pads with fiber optic cables

were placed beside the left and right thigh of participants, respectively. Participants held the response pads with their hands and pressed the key on the left pad (hereafter the left key) or the key on the right pad (hereafter the right key) with their left or right thumb to respond to target stimuli.

Procedure

Participants were assigned randomly to one of the three conditions based on the proportion of congruent to incongruent trials: 75/25, 50/50, and 25/75. We manipulated the proportion congruency as a between-subject factor, as there could be an asymmetrical shifting effect between mostly congruent and mostly incongruent sessions [Abrahamse et al., 2013]. Each participant performed a red-green color discrimination task. The S-R color mapping rules (SC and AC) alternated across blocks. At the beginning of each block, a 5-s instruction showed subjects, which color mapping rule should be employed in the upcoming block. After the instruction, eight trials were presented successively in each block (see Fig. 1). There were a total of 64 blocks (32 for each color mapping rule), resulting in a total of 384 experimental and 128 null trials. The null trials were used to jitter interstimulus-interval to increase design efficiency [Dale, 1999]. Of the experimental trials, there were 288 congruent and 96 incongruent trials in the 75/25 group, 192 congruent, and 192 incongruent trials in the 50/50 group, and 96 congruent and 288 incongruent trials in the 25/75 group. On each experimental trial, the fixation cross appeared alone for 400 ms, followed by the response labels for 600 ms. Subsequently, the target stimulus (a red or green square) was displayed and remained visible for 1,500 ms or until a response was made. In the latter case, the response was followed by a blank screen in black up to the end of the trial. Subjects had to respond to the stimulus as quickly and accurately as possible according to the current S-R color mapping rule. The total duration of a trial was 2,500 ms. The response labels indicated the color assignment of the response keys, which was varied pseudorandomly from trial to trial. For example, when the red response label was presented in the left side and the green label in the right side, in the SC rule participants had to press the “red” (i.e., left) key in response to the red stimulus but the “green” (i.e., right) key to the green stimulus. However, participants had to press the “green” key to the red stimulus and the “red” key to the green stimulus in the AC rule. In the null trials, only the central fixation cross was presented for 1,600 ms followed by a blank screen in black for 900 ms.

Data Acquisition

All MRI images were acquired with a Siemens Magnetom Trio Tim 3-T scanner (Siemens, Germany). We used a gradient echo planar imaging (EPI) sequence to acquire

fMRI data with the following parameters: repetition time (TR) = 2,000 ms, echo time (TE) = 30 ms, field of view (FOV) = 192 mm, 32 axial slices, slice thickness = 3.0 mm, slice gap = 0.75 mm, in-plane resolution = $3.0 \times 3.0 \text{ mm}^2$, and flip angle = 90° . The comfortable external head restraint was used to minimize head movement during scanning. Eight hundred and ten whole-brain images were obtained over 22 min. The first 4 volumes were discarded to allow for T1 equilibration effects. Additional high-resolution anatomical images (voxel size = $1 \times 1 \times 1 \text{ mm}^3$) were acquired using a standard T1-weighted 3-D Magnetization-Prepared Rapid Gradient-Echo (MP-RAGE) sequence.

Data Analysis

Images were analyzed using the Statistical Parametric Mapping (SPM) software (SPM8; Wellcome Trust Centre for Neuroimaging, University College London, UK). EPI volumes were first corrected for head movements by affine registration. After realignment, the high-resolution T1-weighted image of the respective subject was coregistered to the mean realigned image. The coregistered T1-weighted image was spatially normalized to the Montreal Neurological Institute (MNI) template using the unified segmentation approach [Ashburner and Friston, 2005]. The resulting deformation parameters were then applied to the individual EPI volumes. All images were thereby transformed into standard stereotaxic space and resampled at $2 \times 2 \times 2 \text{ mm}^3$ voxel size. The normalized images were smoothed using an 8 mm full-width at half-maximum isotropic Gaussian kernel to compensate for residual variability after spatial normalization across subjects.

For the first-level individual statistical analysis, the fMRI blood-oxygen-level dependent (BOLD) data were analyzed in the framework of a general linear model. Each experimental condition was time-locked to the onset of the target color stimulus and was modeled using delta functions convolved with a canonical hemodynamic response function and its temporal and dispersion derivatives [Friston et al., 1998]. Low-frequency signal drifts were high-pass filtered using a cut-off period of 128 s. Temporal autocorrelation of fMRI volumes was modeled using an AR(1) process. The head movement estimates from the realignment procedure were entered as covariates to remove movement-related variance from the EPI time series. There were in total four experimental conditions modeled in the design matrix: (1) congruent and (2) incongruent conditions in the SC rule, (3) congruent and (4) incongruent conditions in the AC rule. In addition, error responses were modeled (if there were) as effects of no interest. For each participant, a contrast image was created for each of the four experimental conditions (each condition versus baseline) and entered into the subsequent group analysis.

For the second-level random-effects analysis, the parameter estimates of the BOLD response derived from the first-level analysis were entered into a full factorial

Figure 2.

RT and PE of behavioral results. **A:** RT. **B:** PE. **C:** Simon effect (in RT): incongruent minus congruent condition. **D:** Simon effect (in PE): incongruent minus congruent condition. The proportion congruency of each group is indicated in terms of con/inc (e.g., 75/25 means that 75% trials were congruent and 25% trials

were incongruent). Error bars denote standard error. Abbreviations, AC: alternate-color rule; Con: congruent; Inc: incongruent; SC: same-color rule. ***: $P < 0.001$. **: $P < 0.01$, *: $P < 0.05$. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

ANOVA with the factors “group” (3 levels of proportions of congruent to incongruent trials [between-subjects]: 75/25, 50/50, 25/75), “S-R color mapping” (2 levels [within-subjects]: SC rule, AC rule), and “spatial congruency” (2 levels [within-subjects]: congruent [Con], incongruent [Inc]). The statistical threshold was set at $P < 0.05$ (family wise error [FWE] corrected at the cluster level; $P < 0.001$ uncorrected at the voxel level).

RESULTS

Behavioral Results

We first excluded outliers from the correct response data, which were out of the range of 3 standard deviations from the mean of each condition. Then, we performed a mixed-design $3 \times 2 \times 2$ analysis of variance (ANOVA) with the between subjects factor of group (3 levels of

proportions of congruent to incongruent trials: 75/25, 50/50, 25/75), and within subjects factors of S-R color mapping (2 levels: SC rule, AC rule), and spatial congruency (2 levels: Con, Inc) for both mean RT and percentage error (PE). As illustrated in Figure 2A, the ANOVA for RT revealed a significant main effect of S-R color mapping, $F(1, 51) = 449.97$, $P < 0.001$, $\eta_p^2 = 0.898$ showing faster RTs in the SC rule (512 ms) than in the AC rule (607 ms). The main effect of spatial congruency was also significant, $F(1, 51) = 5.80$, $P = 0.020$, $\eta_p^2 = 0.102$. The main effect of group was not significant, $F(2, 51) = 0.34$, $P = 0.710$, $\eta_p^2 = 0.013$. There was a marginally significant three-way interaction of group $\times$ S-R color mapping $\times$ spatial congruency, $F(2, 51) = 2.48$, $P = 0.094$, $\eta_p^2 = 0.089$, indicating that the Simon effect varied according to both group and S-R color mapping. There was a significant interaction between mapping and congruency, $F(1, 51) = 91.17$, $P < 0.001$, $\eta_p^2 = 0.653$, indicating that RTs were faster in the congruent condition

(500 ms) than in the incongruent condition (522 ms) in the SC rule, but slower (633 vs. 588 ms) in the AC rule. The interaction between group and congruency was also significant, $F(2, 51) = 48.62$, $P < 0.001$, $\eta_p^2 = 0.656$, showing that RTs were faster in the congruent condition (539 ms) than in the incongruent condition (576 ms) in the 75/25 group, but slower (577 vs. 526 ms) in the 25/75 group. To examine the Simon effect in more detail we compared the RT difference measure (incongruent – congruent) between the AC and SC rules within each group. As shown in Figure 2C, we found a standard Simon effect for the SC rule (25 ms) but a reversed Simon effect for the AC rule (–65 ms) in the 50/50 group, which was similar to the classic findings in the Hedge and Marsh task [e.g., De Jong et al., 1994]. When the proportion of congruent trials was higher, in the 75/25 group, the standard Simon effect for the SC rule increased (78 ms) but the reversed Simon effect for the AC rule disappeared and instead showed a small positive Simon effect (5 ms). However, the Simon effect in the 75/25 group was significantly smaller for AC than for SC, $t(17) = 5.52$, $P < 0.001$, $d = 1.685$, indicating that the S-R color mapping still interacted with spatial congruence to influence performance. In contrast when the proportion of congruent trials was lower than 50/50, in the 25/75 group, the standard Simon effect for the SC rule reversed direction (incongruent was faster than congruent by 24 ms), and the reversed Simon effect for the AC rule increased (–74 ms). The difference in the reversed Simon effect between the AC and SC rules was significant, $t(17) = 4.08$, $P = 0.001$, $d = 1.357$. This again indicated that an interaction between S-R color mapping and spatial congruency still affected performance. In addition, we compared the spatial congruency effect between groups for each color mapping rule. For the SC rule, the Simon effect in the 75/25 group was significantly bigger than in the 50/50 group, $t(34) = 4.49$, $P < 0.001$, $d = 1.540$, and the Simon effect in the 25/75 group was significantly smaller than in the 50/50 group, $t(34) = 4.76$, $P < 0.001$, $d = 1.632$. For the AC rule, the reversed Simon effect in the 75/25 group was significantly smaller than in the 50/50 group, $t(34) = 4.77$, $P < 0.001$, $d = 1.636$, but difference in the reversed Simon effect between the 25/75 and 50/50 groups did not reach significance, $t(34) = 0.76$, $P = 0.456$, $d = 0.261$. Interaction between group and S-R color mapping was not significant, $F(2, 51) = 0.80$, $P = 0.457$, $\eta_p^2 = 0.030$, showing that the difference between the SC and AC rules were similar across groups.

For PEs, as illustrated in Figure 2B, there was a marginally significant main effect of group, $F(2, 51) = 2.52$, $P = 0.090$, $\eta_p^2 = 0.090$, indicating that the error rate in the 25/75 group (8.2%) was larger than in the 50/50 (6.3%) and 75/25 (5.1%) groups, and a significant main effect of S-R color mapping, $F(1, 51) = 20.33$, $P < 0.001$, $\eta_p^2 = 0.285$, with errors being less likely in the SC (4.8%) than in the AC rule (8.2%). The three-way interaction of group $\times$ S-R color mapping $\times$ spatial congruency was not significant,

$F(2, 51) = 1.58$, $P = 0.216$, $\eta_p^2 = 0.058$, but there was a significant two-way interaction of group $\times$ spatial congruency, $F(2, 51) = 12.62$, $P < 0.001$, $\eta_p^2 = 0.331$, showing that there were more errors in the incongruent (6.5%) compared to the congruent (3.7%) condition in the 75/25 group but fewer errors in the incongruent condition (5.8%) than in the congruent (10.6%) condition in the 25/75 group. The interaction between color mapping and spatial congruency was also significant, $F(1, 51) = 19.22$, $P < 0.001$, $\eta_p^2 = 0.274$, indicating that more errors were found in the incongruent (5.0%) than in the congruent (4.6%) condition in the SC rule, but less errors (6.3 vs. 10.1%) in the AC rule. Interaction between group and S-R color mapping was not significant, $F(2, 51) = 0.74$, $P = 0.481$, $\eta_p^2 = 0.028$, indicating that the difference between the SC and AC rules did not differ across groups. We also computed the Simon effects in PE in detail. These results showed a similar pattern as in RT with the manipulation of proportion congruency (see Fig. 2D).

Learning effects

The reversals of the Simon effect in the 25/75 group or of the reversed Simon effect in the 75/25 group suggested that participants strengthened task-irrelevant spatially incompatible or compatible S-R associations. Previous studies have found that S-R associations may be learned gradually with practice [Boettiger and D'Esposito, 2005; Grol et al., 2006; Ruge and Wolfensteller, 2010]. As the strength of task-irrelevant S-R associations may be increased gradually over practice, we here tested the idea that the modulated Simon effects were correlated with the time of practice. For each participant, we divided the RTs of all trials in each condition into quartiles according to the time of the entire experiment. We calculated mean RT based on the trials with correct responses for each quartile in each condition. The Simon effects (Inc – Con difference) in the SC and AC rules in each quartile were then computed; these are plotted in Figure 7E. We then calculated correlation coefficients between the Simon effects and temporal quartile number (1–4). In the 50/50 group, neither the positive Simon effect in the SC condition ($r = 0.11$, $P = 0.361$) nor the reversed Simon effect in the AC condition ($r = -0.08$, $P = 0.526$) was correlated with temporal quartile, indicating no learning effect for this condition. In the 75/25 group, the Simon effect under both the SC ($r = 0.36$, $P = 0.002$) and the AC ($r = 0.24$, $P = 0.040$) rules were significantly correlated with temporal quartile, indicating that both increased with practice. In contrast, in the 25/75 group the Simon effect under both the SC ($r = -0.32$, $P = 0.006$) and the AC ($r = -0.26$, $P = 0.031$) rules were negatively correlated with temporal quartile, indicating that both increased with practice.

Manipulating proportion congruency results in an imbalance in the total number of trials in each trial type, and therefore results in an increase in likelihood of stimulus or response repetition for the more likely trial types.

Figure 3.

Results of fMRI analysis for the effect of S-R color mapping. The coordinates of the local maxima of the brain regions are in MNI space (x, y, z). Abbreviations, AC: alternate-color rule; Con: congruent; dPMC: dorsal premotor cortex; IFG: inferior frontal gyrus; Inc: incongruent; L: left; pre-SMA: presupplementary

motor area; R: right; SC: same-color rule; SFG: superior frontal gyrus; SPL: superior parietal lobule; TPJ: temporoparietal junction. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

We analyzed the data excluding trials with the repetition of stimulus or response. Stimulus repetition was defined as the repetition of the whole visual display including both target and response labels. The results were in accord with the previous results. Thus, it was unlikely that the modulated conflict effects resulted from the repetition effect.

fMRI Results

Main effects

We first compared the BOLD activity between the SC rule and AC rule. The contrast showed significantly increased BOLD activity in the bilateral superior parietal

lobule (SPL) and areas around intraparietal sulcus (IPS), bilateral dorsal premotor cortex (dPMC), presupplementary motor area (pre-SMA)/anterior cingulate cortex (aMCC), bilateral cerebellum, and the right insula (FWE corrected $P < 0.05$) in the AC rule compared to the SC rule (Fig. 3, see Table I). The reverse contrast revealed significantly stronger BOLD activity in the temporoparietal junction (TPJ), middle temporal gyrus, superior frontal gyrus (SFG), and inferior frontal gyrus (IFG) in both hemispheres (FWE corrected $P < 0.05$) in the SC rule compared with the AC rule (Fig. 3, see Table I). We then compared the BOLD activity between the groups and found significantly increased BOLD activity in the bilateral cerebellum and left cuneus in the 75/25 group compared to 50/50 group (FWE corrected $P < 0.05$, Table I), as well as significantly

TABLE I. Local maxima of significantly activated regions of main effects

Anatomical region	Hemisphere	x	y	z	z-score	Voxels
(a) Alternate-color rule > SC rule						
SPL	R	24	-64	50	Inf	5796
Inferior Parietal Lobule	R	40	-40	46	6.87	
Cerebellar Vermis		4	-60	-18	7.24	4325
Cerebellum	L	-20	-60	-28	6.33	
Cerebellum	R	26	-56	-28	5.29	
Inferior Parietal Lobule	L	-42	-42	44	6.41	5007
SPL	L	-18	-66	50	6.36	
Middle Frontal Gyrus	L	-26	-2	54	6.04	697
Insula	R	30	32	4	4.43	633
SFG	R	26	2	54	5.72	1311
Presupplemental motor Area/aMCC	R	8	14	48	4.62	
IFG (Pars Opercularis)	R	52	10	24	5.07	478
(b) SC rule > alternate-color rule						
Angular Gyrus	R	50	-68	42	6.97	1497
Middle Temporal Gyrus	R	64	-56	10	3.59	
Middle Occipital Gyrus	L	-38	-84	32	6.43	2024
Inferior Parietal Lobule	L	-48	-56	40	4.88	
Rectal Gyrus	L	0	54	-16	5.76	9975
Middle Frontal Gyrus	L	-20	26	50	5.70	
IFG	L	-24	26	-14	5.64	
SFG	R	24	28	48	5.11	
IFG	R	26	28	-14	4.16	
Middle Cingulate Cortex	L	0	-40	40	5.31	2943
Precuneus	R	4	-60	36	4.52	
Cuneus	L	-8	-64	28	4.41	
Middle Temporal Gyrus	R	46	4	-30	4.96	849
Medial Temporal Pole	R	42	12	-34	4.76	
Middle Temporal Gyrus	R	62	-10	-12	4.27	
Middle Frontal Gyrus	L	-40	16	42	4.49	240
Postcentral Gyrus	R	60	-6	22	4.16	262
Rolandic Operculum	R	62	0	6	3.78	
Middle Temporal Gyrus	L	-60	4	-20	3.94	458
Inferior Temporal Gyrus	L	-46	-10	-26	3.88	
(c) 75/25 group > 50/50 group						
Cerebellum	R	16	-74	-16	7.40	1168
Cerebellum	L	-24	-84	-22	4.63	
Cuneus	L	-8	-82	28	4.73	435
(d) 25/75 group > 50/50 group						
Lingual Gyrus	R	18	-74	-14	6.80	2721
Cerebellum	L	-10	-72	-12	4.80	
Superior Occipital Gyrus	L	-10	-98	6	4.76	
Superior Occipital Gyrus	R	20	-78	18	4.52	762
Cuneus	R	16	-76	32	4.29	
Postcentral Gyrus	L	-44	-10	40	4.51	233
SPL	L	-16	-42	50	4.48	530

These analyses were conducted with a P value < 0.05 FWE corrected at the cluster level. The SPM Anatomy toolbox was used to locate anatomical regions (Eickhoff, et al., 2005). L = left; R = right; x, y, z: coordinates (mm) in the stereotactic space defined by the MNI.

increased BOLD activity in the bilateral superior occipital gyrus, right lingual gyrus, left cerebellum, right cuneus and left postcentral gyrus and SPL in the 25/75 group compared to 50/50 group (see Table I). The comparison between the incongruent and congruent condition did not reveal any significant results.

Interaction effects

The three-way interaction of group $\times$ S-R color mapping $\times$ spatial congruency did not reveal any significant brain activation. However, there was a significant interaction between group and spatial congruency. The contrast of [75/25_(Inc > Con) > 25/75_(Inc > Con)] revealed significant

Figure 4.

Results of fMRI analysis for the interaction between proportion congruency and spatial congruency. The figure shows the results of the contrast of $[75/25_{\text{Inc}} - \text{Con}] > 25/75_{\text{Inc}} - \text{Con}]$. Abbreviations, AC: alternate-color rule; aMCC: anterior midcingulate cortex; Con: congruent; DLPFC: dorsolateral prefrontal

cortex; dPMC: dorsal premotor cortex; IFJ: inferior frontal junction; Inc: incongruent; L: left; pre-SMA: presupplementary motor area; R: right; SC: same-color rule; SPL: superior parietal lobule. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

interaction in bilateral SPL along IPS and dPMC, pre-SMA/aMCC, the left DLPFC, the bilateral inferior temporal gyrus and thalamus (FWE corrected $P < 0.05$; Fig. 4 and Table II). Specifically, independent of S-R color mapping there was stronger activity in the incongruent than in

the congruent condition in the 75/25 group but weaker activity in the incongruent than in the congruent condition in the 25/75 group in these areas. Note that most of these areas overlap the regions showing increased activity in the AC mapping compared with the SC mapping. The

TABLE II. Local maxima of significantly activated regions of interaction effects

Anatomical region	Hemisphere	x	y	z	z-Score	Voxels
(a) Proportion congruency effect: 75/25_(Inc > Con) > 25/75_(Inc > Con)						
Inferior Parietal Lobule	L	-40	-42	46	7.65	11,065
SPL	L	-12	-68	56	7.51	
SupraMarginal Gyrus	R	40	-36	44	6.97	
SPL	R	18	-60	58	4.98	
Inferior Temporal Gyrus	L	-54	-58	-8	4.86	3142
Inferior Temporal Gyrus	R	58	-54	-10	4.64	
Middle Frontal Gyrus	L	-26	-2	54	7.28	
SFG	R	24	-4	52	6.15	
Presupplemental Motor Area/aMCC	L	-4	12	52	5.09	308
Thalamus	R	20	-24	16	5.91	
Precentral Gyrus	L	-48	6	34	5.76	655
Thalamus	L	-16	-28	14	5.45	337
DLPFC	L	-38	28	28	4.28	363
(b) Conjunction of proportion congruency effect and S-R mapping effect (AC > SC)						
SPL	R	20	-68	50	6.91	4256
SupraMarginal Gyrus	R	40	-38	44	6.72	
SPL	R	32	-50	60	5.16	3512
Inferior Parietal Lobule	L	-42	-42	44	6.41	
SPL	L	-18	-66	50	6.36	
Middle Frontal Gyrus	L	-26	-2	54	6.04	
SFG	R	26	-2	52	5.61	899
Cerebellum	R	24	-60	-28	4.57	878
Cerebellar Vermis	R	4	-74	-22	4.38	263
Thalamus	L	-18	-26	14	4.28	
(c) Proportion congruency effect: 75/25_(Inc > Con) > 50/50_(Inc > Con)						
SPL	R	20	-70	48	6.57	34,604
Middle Occipital Gyrus	L	-46	-78	6	6.52	
Superior Occipital Gyrus	L	-22	-66	32	6.43	
Precentral Gyrus	L	-42	4	32	5.36	
Postcentral Gyrus	L	-60	-2	14	3.81	908
Th-Visual	L	-22	-30	-2	4.69	
Putamen	L	-26	-16	6	4.59	
(d) Proportion congruency effect: 50/50_(Inc > Con) > 25/75_(Inc > Con)						
Precuneus	L	-10	-64	64	5.15	1891
Inferior Parietal Lobule	L	-40	-50	44	4.43	

These analyses were conducted with a P value < 0.05 FWE corrected at the cluster level.

conjunction analysis of the above interaction contrast and the contrast of (AC > SC) confirmed this overlap, revealing brain areas including bilateral SPL along IPS and dPMC (FWE corrected P < 0.05; Table II), right cerebellum and left thalamus, as well as a marginally significant activation in the pre-SMA/aMCC ($x = 4$, $y = 14$, $z = 50$; FWE corrected $P = 0.056$). In addition, we carried out similar interaction analyses between the 75/25 and 50/50 group and between the 25/75 and 50/50 group. The results were similar to those of the comparison between the 75/25 and 25/75 group. The contrast of [75/25_(Inc > Con) > 50/50_(Inc > Con)] showed significant activation in bilateral SPL/IPS and dPMC, pre-SMA/aMCC, left inferior frontal junction, left postcentral gyrus, left putamen (FWE corrected P < 0.05; Table II). The contrast of [50/50_(Inc > Con) > 25/75_(Inc > Con)] showed significant activation in left precuneus and left inferior parietal lobule

(FWE corrected P < 0.05; Table II), and with more liberal threshold (uncorrected P < 0.01) in bilateral SPL/IPS and dPMC and pre-SMA/aMCC. Furthermore, to dissociate contingency learning from adjustment of cognitive control, we carried out a conjunction analysis with contrasts (75/25 > 50/50) and (25/75 > 50/50) to identify the common areas shown in both groups representing the learned contingency of irrelevant S-R associations. The 75/25 and 25/75 groups should both represent the learned contingency of irrelevant S-R associations, although one with compatible and the other with incompatible spatial S-R associations. Therefore, the activated regions in Figure 4 that represented the learned contingency of irrelevant S-R associations should also show the main effect of Group. The results of the conjunction analysis masked by the fMRI results of Figure 4 in dorsal revealed frontoparietal regions, including IPS and dPMC (P < 0.05, voxel = 100; Fig. 5).

Figure 5.

Results of fMRI conjunction analysis for the group effect. The figure shows the results of conjunction analysis of the contrast of (75/25 > 50/50) and (25/75 > 50/50). Abbreviations, dPMC: dorsal premotor cortex; IPS: intraparietal sulcus. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Behavioral results showed significant interaction between color mapping and spatial congruency in each group. We here tested the hypothesis that this interaction was also present in each group in the frontoparietal regions as revealed in Figure 4. We masked these regions by the interaction between color mapping and spatial congruency ($P < 0.05$) separately in each group. These analyses showed activation in the bilateral SPL, pre-SMA/aMCC, and the left DLPFC in the 75/25 group, activation in the pre-SMA/aMCC in the 50/50 group, and activation in the bilateral SPL and dPMC in the 25/75 group ($P < 0.001$, voxel = 30; Fig. 6). To illustrate the results, we plotted the data in the pre-SMA and the left SPL. Similar to the behavioral results, in these regions the difference between the incongruent and congruent conditions was greater for the SC rule than for the AC rule in the 75/25 group. In contrast, the difference was smaller for the SC rule than for the AC rule in the 25/75 group. Neural activity was stronger in the incongruent condition than in the congruent condition in the SC rule but weaker in the AC rule in the 50/50 group.

Learning effects

Behavioral results showed that the modulated Simon effects were correlated with practice. We here tested whether these correlations were present in the frontoparietal regions, where there were interactions between group and spatial congruency (Fig. 4). We divided the stimulus onsets of all trials in each condition into quartiles for each participant as in the behavioral analyses. The stimulus onsets of the trials with correct responses were then modeled for each quartile of each condition in the individual subject analysis. Therefore, there were four conditions in each quartile: SC_Con, SC_Inc, AC_Con, and AC_Inc (a total of 16 conditions in the design matrix). All other analysis procedures were the same as those reported in Methods for fMRI analysis. We then computed the contrasts, (SC_Inc - SC_Con) and (AC_Inc - AC_Con) for each quartile. In the group analysis, we correlated these contrast

images with temporal quartile number for each group. The results were masked by the contrast of [75/25_(Inc > Con) > 25/75_(Inc > Con)] ($P < .001$). The results showed significant correlation in the bilateral SPL and areas around IPS, bilateral dPMC, pre-SMA/aMCC and the left DLPFC ($P < 0.05$, voxel = 30) in the SC rule of the 75/25 group (Fig. 7). Significant correlations were present in similar regions in the AC rule of the 75/25 group. In contrast, significantly negative correlations were found in the bilateral SPL/IPS and dPMC in the SC rule of the 25/75 group. However, only the pre-SMA/aMCC and left dPMC showed negative correlation in the AC rule of the 25/75 group. No significant correlation was found in both the SC and AC rules in the 50/50 group ($P > 0.05$). In addition, we performed brain-behavior correlation analyses between both learning effects by correlating these contrast images with the Simon effect of each quartile. The results showed a similar brain activation pattern as the results of the fMRI learning effect (Supporting Information Fig. S1).

DISCUSSION

In the Hedge and Marsh task, the positive Simon effect under the SC mapping and the reversed Simon effect under the AC were both reversed with increasing the ratio of incongruent and congruent trials, respectively. These results suggest that participants strengthened task-irrelevant spatial S-R associations and used them to guide responses. fMRI results revealed a similar pattern in the activity of the aMCC, DLPFC, SPL, and dPMC as in the behavioral results. Increasing the ratio of incongruent or congruent trials reversed the positive Simon effect under the SC mapping or the reversed Simon effect under the AC mapping in the aMCC and the left DLPFC activity. These results suggest that the aMCC and DLPFC shifted to responding to the conflict between the strengthened irrelevant spatial S-R associations and the relevant S-R associations. The reversals of the conflict effects due to manipulating proportion congruency were also present in

Figure 6.

Results of fMRI analysis for the interaction between color mapping and spatial congruency in each group. **A:** the 75/25 group. **B:** the 50/50 group. **C:** the 25/75 group. Abbreviations, AC: alternate-color rule; aMCC: anterior midcingulate cortex; Con:

congruent; dPMC: dorsal premotor cortex; Inc: incongruent; L: left; pre-SMA: presupplementary motor area; SC: same-color rule; SPL: superior parietal lobule. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

the activity of the bilateral SPL and dPMC, suggesting that these areas might represent the strengthened irrelevant spatial S-R associations. In addition, the learning effects across temporal quartiles of the task found in both behavioral and fMRI data suggest that the strengthened task-irrelevant S-R associations were enhanced gradually with practice.

Strengthened Irrelevant S-R Associations and the Proportion Congruency Effect

The classic Simon effect under the SC mapping was reversed in the 25/75 group compared with the 50/50 group, which replicated previous findings [Hommel, 1994; Marble and Proctor, 2000; Toth et al., 1995]. These results

Figure 7.

Results of learning effect. **A**: the results of correlation between the difference (Inc - Con) in BOLD activity and temporal quartile number in SC and AC in the 75/25 and 25/75 groups. To illustrate the results, we plotted the data in the aMCC/pre-SMA (**B**), right SPL (**C**), and left dPMC (**D**). The x axis denotes temporal quartile number. The MNI coordinates in the figure were the local maximum of activation, where the data were extracted. As there was no significant correlation in the 50/50 group, we used the coordinates in the 25/75 group. **E**: the correlation

between the Simon effects in RT and temporal quartile number. Abbreviations, AC: alternate-color rule; aMCC: anterior midcingulate cortex; Con: congruent; DLpFC: dorsolateral prefrontal cortex; dPMC: dorsal premotor cortex; Inc: incongruent; L: left; pre-SMA: presupplementary motor area; R: right; SC: same-color rule; SPL: superior parietal lobule. Asterisks denote significant correlation. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

suggest that the 25/75 group increased the strength of task-irrelevant spatially incompatible S-R associations and used them to predict responses, as these pairs of stimulus and response (left location-right response and right location-left response) were present frequently during the task. The “logical recoding” account for the Hedge and Marsh task suggests that the rule of the relevant S-R associations (e.g., the AC mapping is “opposite”) is generalized to the irrelevant S-R associations, and therefore the location of a stimulus activates its noncorresponding (i.e., “opposite”) response [De Jong et al., 1994; Hedge and Marsh, 1975; Wühr and Biebl, 2009]. In other words, there were spatially incompatible S-R associations under the AC mapping predicting responses. The reversed Simon effect under the AC mapping was slightly reversed in the 75/25 group. This suggests that the 75/25 group increased the strength of task-irrelevant spatially compatible S-R associations and used them to predict responses. Note that participants in the 75/25 and 25/75 groups could also learn to associate a given location to the SC response in the SC rule but to the alternate-color response in the AC rule, in addition to learning the spatially compatible or incompatible S-R associations. If this is the case, however, these irrelevant location-color S-R associations might have fewer influences on task performance. Because different stimulus locations (i.e., left and right) are associated to the same response in a given task rule (i.e., the SC in the SC rule but the alternate-color in the AC rule), the irrelevant location-color S-R associations are less likely to affect the execution of the relevant S-R associations.

From a computational modeling perspective, the reversals of the conflict effects due to manipulating proportion congruency may not be explained by only adjusting the activity level of the task representation unit or/and the connection strength of the task representation-to-input links (i.e., top-down modulation of stimulus representation). Therefore, these results do not support a “pure” attention modulation account [e.g., Botvinick et al., 2001], but rather suggest changed weight of the input-to-output links (i.e., S-R associations), partially supporting the contingency learning account [Schmidt and Besner, 2008]. The data suggest that the proportion congruency effect results critically from increasing the strength of task-irrelevant S-R associations and apply these strengthened task-irrelevant S-R associations to predict responses. In addition, our fMRI results suggest that changes not only in S-R associations but also in the cognitive control system underlie the proportion congruency effect (see discussion below), which is different from the contingency learning account strongly claiming that the proportion congruency effect is not related to cognitive control at all [Schmidt and Besner, 2008]. One possible reason for the increased strength of S-R associations is the contingency learning as detailed by the Parallel Episodic Processing model [Schmidt, 2013b]. Another possible reason is attention

modulation. According to the models of cognitive control [Blais and Verguts, 2012; Blais et al., 2007; Verguts and Notebaert, 2008], it is theoretically possible to use conflict (i.e., attention) to modulate the strength of all connections between units, including not only top-down task demand-stimulus units but also S-R units. This question is worth investigating in future research.

aMCC, DLPFC, and Conflict Monitoring

The dynamics of aMCC and DLPFC activity induced by varying proportion congruency are consistent with previous findings [Blais and Bunge, 2010; Carter et al., 2000; Grandjean et al., 2013; Kerns et al., 2004]. The aMCC and DLPFC have been suggested to act as the devices that detect the need for control [Blais et al., 2007; Botvinick et al., 2001; Verguts and Notebaert, 2008] and implement control [Kerns et al., 2004; MacDonald et al., 2000], respectively, for example, monitoring for and resolving response conflict [Botvinick et al., 2001]. Note that in the 50/50 group, there was stronger activity in the congruent than in the incongruent condition in the AC rule but weaker in the SC rule in aMCC (Fig. 6). This suggests that there was response conflict in the congruent condition in the AC rule. Similar results were observed in another study from our lab (Li, et al., 2015). Similar to the behavioral results, the aMCC and DLPFC activity showed a reversed Simon effect under the SC mapping in the 25/75 group and a reversed-reversed (i.e., positive) Simon effect under the AC mapping in the 75/25 group compared with the 50/50 group. Similar explanation may also apply to the results of the aMCC and DLPFC. The 25/75 and 75/25 groups employed the strengthened irrelevant spatially incompatible and compatible S-R associations, respectively, to predict correct responses. There was higher level of conflict and therefore stronger aMCC and DLPFC activity when the task-defined response was different from the response predicted by the strengthened irrelevant S-R associations. Thus, these results provided clear evidence supporting that the cognitive control system responds to the conflict between the relevant S-R associations and the strengthened irrelevant S-R associations. In addition, the learning effect showed that the difference between the incongruent and congruent conditions in frontoparietal regions was positively correlated with temporal quartile in the 75/25 and negatively correlated with quartile in the 25/75 group. These results suggest that the strength of the task-irrelevant compatible or incompatible S-R associations increased with practice, and subsequently the cognitive control processes in aMCC and DLPFC shifted gradually to detect and resolve the conflict induced by the strengthened task-irrelevant S-R associations.

In addition, one may argue that aMCC is not related to conflict monitoring, but is correlated with time-on-task [Grinband et al., 2011; Weissman and Carp, 2013]. The aMCC even shows stronger activity in the congruent trials

with longer RT than in the incongruent trials with shorter RT in the Stroop task [Grinband et al., 2011]. This suggests that stronger aMCC activity might result from increased RT but not congruency effect. This idea also suggests an alternative explanation for the present aMCC and DLPFC results. Consistent with the temporal learning account [Schmidt, 2013a], aMCC might learn about the distribution of response times and DLPFC might learn to rhythmically respond based on the distribution [Schmidt, 2014; Schmidt et al., 2014].

SPL, dPMC, and S-R Associations

We suggest that the SPL and dPMC might represent the strengthened irrelevant spatial S-R associations. These regions are involved not only in top-down control of isolated selection of a stimulus or a response, but also in the coordination of S-R associations [Corbetta and Shulman, 2002]. For example, electrophysiological studies in monkeys show that subregions of IPS may encode movement plans based on both spatial information and nonspatial feature of stimuli [Fitzgerald et al., 2011; Zhang and Barash, 2000], suggesting the representations of spatial and nonspatial S-R mappings. Consistent with the findings in monkeys, human neuroimaging studies have suggested that SPL/IPS represents all possible S-R associations within a task and updates task-appropriate S-R mappings [Brass and von Cramon, 2002; Thoenissen et al., 2002]. For example, SPL activity increased with increasing the number of S-R associations and with practicing arbitrary S-R associations [Brass and Von Cramon, 2004; Bunge et al., 2002; Crone et al., 2006; Grol et al., 2006]. The dPMC is important for the preparation and selection of movements based on sensory information [Picard and Strick, 2001]. Human neuroimaging studies also found practice-dependent increase in dPMC activity after overlearning S-R associations [Grol et al., 2006; Ruge and Wolfensteller, 2010]. This could reflect more steady preparation for the movements associated with given stimuli. In addition, transcranial magnetic stimulation over dPMC interfered with the performance of a choice RT task, suggesting disturbance to response selection processes [Schluter et al., 1998].

In this study, the SPL and dPMC activity also showed a similar pattern as in the behavioral results. This could be also due to the conflict between the relevant nonspatial S-R associations and the strengthened irrelevant spatial S-R associations, which both might be represented in the SPL and dPMC. We have proposed above that the SPL and dPMC might represent the learned contingency of irrelevant S-R associations. This idea is supported by the conjunction analysis showing stronger activity in IPS and dPMC in the 75/25 and 25/75 groups compared with the 50/50 (baseline) group (Fig. 5). The 75/25 and 25/75 groups should both represent the learned contingency of irrelevant S-R associations, though one with compatible and the other with incompatible spatial S-R associations.

Therefore, the activated regions in Figure 4 that represented the learned contingency of irrelevant S-R associations should also show the main effect of Group. However, additional studies are needed to directly test this hypothesis, for example, using event-related potential to examine if lateralized readiness potential [De Jong et al., 1994] varies according to the strengthened spatial S-R associations.

CONCLUSION

The proportion congruency effect in the Hedge and Marsh task, especially the reversals of the classic and reversed Simon effects, suggests that participants strengthened task-irrelevant spatial S-R associations and used them to guide responses. The aMCC, left DLPFC and bilateral SPL and dPMC showed increased activity when there was conflict between the strengthened task-irrelevant and task-relevant S-R associations, suggesting that the cognitive control system shifted to responding mainly to the conflict induced by the strengthened task-irrelevant S-R associations.

ACKNOWLEDGMENTS

The authors are grateful to Dr. Carol Seger for help with editing the manuscript. They also thank Dr. Glyn Humphreys for helpful comments on the study. Conflict of Interest: No.

REFERENCES

- Abrahamse EL, Duthoo W, Notebaert W, Risko EF (2013): Attention modulation by proportion congruency: The asymmetrical list shifting effect. *J Exp Psychol Learn* 39:1552–1562.
- Ashburner J, Friston KJ (2005): Unified segmentation. *Neuroimage* 26:839–851.
- Blais C, Bunge S (2010): Behavioral and neural evidence for item-specific performance monitoring. *J Cogn Neurosci* 22:2758–2767.
- Blais C, Verguts T (2012): Increasing set size breaks down sequential congruency: Evidence for an associative locus of cognitive control. *Acta Psychol (Amst)* 141:133–139.
- Blais C, Robidoux S, Risko EF, Besner D (2007): Item-specific adaptation and the conflict-monitoring hypothesis: A computational model. *Psychol Rev* 114:1076–1086.
- Boettiger CA, D'Esposito M (2005): Frontal networks for learning and executing arbitrary stimulus-response associations. *J Neurosci* 25:2723–2732.
- Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD. (2001): Conflict monitoring and cognitive control. *Psychol Rev* 108: 624–652.
- Botvinick MM, Cohen JD, Carter CS (2004): Conflict monitoring and anterior cingulate cortex: An update. *Trends Cogn Sci* 8: 539–546.
- Botvinick Nystrom LE, Fissell K, Carter CS, Cohen JD (1999): Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature* 402:179–181.

- Brass M, von Cramon DY (2002): The role of the frontal cortex in task preparation. *Cereb Cortex* 12:908–914.
- Brass M, Von Cramon DY (2004): Selection for cognitive control: A functional magnetic resonance imaging study on the selection of task-relevant information. *J Neurosci* 24:8847–8852.
- Bunge SA, Dudukovic NM, Thomason ME, Vaidya CJ, Gabrieli JD (2002): Immature frontal lobe contributions to cognitive control in children: evidence from fMRI. *Neuron* 33:301–311.
- Carter CS, Macdonald AM, Botvinick M, Ross LL, Stenger VA, Noll D, Cohen JD (2000): Parsing executive processes: Strategic vs. evaluative functions of the anterior cingulate cortex. *Proc Natl Acad Sci USA* 97:1944–1948.
- Corbetta M, Shulman GL (2002): Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3: 201–215.
- Crone EA, Wendelken C, Donohue SE, Bunge SA (2006): Neural evidence for dissociable components of task-switching. *Cereb Cortex* 16:475–486.
- Dale AM (1999): Optimal experimental design for event-related fMRI. *Hum Brain Mapp* 8:109–114.
- De Jong R, Liang CC, Lauber E (1994): Conditional and unconditional automaticity: a dual-process model of effects of spatial stimulus-response correspondence. *J Exp Psychol Hum Percept Perform* 20:731–750.
- Egner T, Hirsch J (2005): Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nat Neurosci* 8:1784–1790.
- Eickhoff SB, Stephan KE, Mohlberg H, Grefkes C, Fink GR, Amunts K, Zilles K (2005): A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage* 25:1325–1335.
- Fitzgerald JK, Freedman DJ, Assad JA (2011): Generalized associative representations in parietal cortex. *Nat Neurosci* 14:1075–1079.
- Friston KJ, Fletcher P, Josephs O, Holmes A, Rugg MD, Turner R (1998): Event-related fMRI: characterizing differential responses. *Neuroimage* 7:30–40.
- Grandjean J, D'Ostilio K, Fias W, Phillips C, Baletu E, Degueldre C, Luxen A, Maquet P, Salmon E, Collette F (2013): Exploration of the mechanisms underlying the ISPC effect: Evidence from behavioral and neuroimaging data. *Neuropsychologia* 51: 1040–1049.
- Grinband J, Savitskaya J, Wager TD, Teichert T, Ferrera VP, Hirsch J (2011): The dorsal medial frontal cortex is sensitive to time on task, not response conflict or error likelihood. *NeuroImage* 57:303–311.
- Grol MJ, de Lange FP, Verstraten FA, Passingham RE, Toni I (2006): Cerebral changes during performance of overlearned arbitrary visuomotor associations. *J Neurosci* 26:117–125.
- Hedge A, Marsh N (1975): The effect of irrelevant spatial correspondences on two-choice response-time. *Acta Psychol* 39:427–439.
- Hommel B (1994): Spontaneous decay of response-code activation. *Psychol Res* 56:261–268.
- Hommel B (2011): The Simon effect as tool and heuristic. *Acta Psychol* 136:189–202.
- Jacoby LL, Lindsay DS, Hessels S (2003): Item-specific control of automatic processes: Stroop process dissociations. *Psychon Bull Rev* 10:638–644.
- Kerns JG, Cohen JD, MacDonald AW, Cho RY, Stenger VA, Carter CS (2004): Anterior cingulate conflict monitoring and adjustments in control. *Science* 303:1023–1026.
- Kornblum S, Hasbroucq T, Osman A (1990): Dimensional overlap: Cognitive basis for stimulus-response compatibility—a model and taxonomy. *Psychol Rev* 97:253–270.
- Li H, Xia T, Wang L (2015): Neural correlates of the reverse Simon effect in the hedge and marsh task. *Neuropsychologia* 75:119–131.
- Lindsay DS, Jacoby LL (1994): Stroop process dissociations: The relationship between facilitation and interference. *J Exp Psychol Human* 20:219–234.
- Logan GD, Zbrodoff NJ (1979): When it helps to be misled: Facilitative effects of increasing the frequency of conflicting stimuli in a Stroop-like task. *Mem Cogn* 7:166–174.
- Lu CH, Proctor RW (1994): Processing of an irrelevant location dimension as a function of the relevant stimulus dimension. *J Exp Psychol Hum Percept Perform* 20:286–298.
- Lu CH, Proctor RW (1995): The influence of irrelevant location information on performance: A review of the Simon and spatial Stroop effects. *Psychon Bull Rev* 2:174–207.
- MacDonald AW, Cohen JD, Stenger VA, Carter CS (2000): Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science* 288: 1835–1838.
- Marble JG, Proctor RW (2000): Mixing location-relevant and location-irrelevant choice-reaction tasks: Influences of location mapping on the Simon effect. *J Exp Psychol Hum Percept Perform* 26:1515–1533.
- Miller EK, Cohen JD (2001): An integrative theory of prefrontal cortex function. *Annu Rev Neurosci* 24:167–202.
- Oldfield RC (1971): The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9:97–113.
- Picard N, Strick PL (2001): Imaging the premotor areas. *Curr Opin Neurobiol* 11:663–672.
- Proctor RW, Pick DF (2003): Display-control arrangement correspondence and logical recoding in the Hedge and Marsh reversal of the Simon effect. *Acta Psychol* 112:259–278.
- Ruge H, Wolfensteller U (2010): Rapid formation of pragmatic rule representations in the human brain during instruction-based learning. *Cereb Cortex* 20:1656–1667.
- Schluter N, Rushworth M, Passingham R, Mills K (1998): Temporary interference in human lateral premotor cortex suggests dominance for the selection of movements. A study using transcranial magnetic stimulation. *Brain* 121:785–799.
- Schmidt (2013a): Questioning conflict adaptation: Proportion congruent and Gratton effects reconsidered. *Psychon Bull Rev* 20: 615–630.
- Schmidt JR (2013b): The Parallel Episodic Processing (PEP) model: Dissociating contingency and conflict adaptation in the item-specific proportion congruent paradigm. *Acta Psychol* 142: 119–126.
- Schmidt JR (2014): List-level transfer effects in temporal learning: Further complications for the list-level proportion congruent effect. *J Cogn Psychol* 26:373–385.
- Schmidt JR, Besner D (2008): The Stroop effect: Why proportion congruent has nothing to do with congruency and everything to do with contingency. *J Exp Psychol Learn* 34: 514–523.
- Schmidt JR, Lemerrier C, De Houwer J (2014): Context-specific temporal learning with non-conflict stimuli: proof-of-principle for a learning account of context-specific proportion congruent effects. *Front Psychol* 5:1241.
- Simon JR (1969): Reactions toward the source of stimulation. *J Exp Psychol* 81:174–176.

- Simon, Sly PE, Vilapakkam S (1981): Effect of compatibility of SR mapping on reactions toward the stimulus source. *Acta Psychol* 47:63–81.
- Thoenissen D, Zilles K, Toni I (2002): Differential involvement of parietal and precentral regions in movement preparation and motor intention. *J Neurosci* 22:9024–9034.
- Toth JP, Levine B, Stuss DT, Oh A, Winocur G, Meiran N (1995): Dissociation of processes underlying spatial S-R compatibility: Evidence for the independent influence of what and where. *Conscious Cogn* 4:483–501.
- Verguts T, Notebaert W (2008): Hebbian learning of cognitive control: Dealing with specific and nonspecific adaptation. *Psychol Rev* 115:518–525.
- Weissman DH, Carp J (2013): The congruency effect in the posterior medial frontal cortex is more consistent with time on task than with response conflict. *PLoS One* 8:e62405.
- Wühr P, Biebl R (2009): Logical recoding of S-R rules can reverse the effects of spatial S-R correspondence. *Atten Percept Psychophys* 71:248–257.
- Zhang M, Barash S (2000): Neuronal switching of sensorimotor transformations for antisaccades. *Nature* 408:971–975.