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A neural mechanism of cognitive control for resolving conflict between abstract task rules

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Abstract

Conflict between multiple sensory stimuli or potential motor responses is thought to be resolved via bias signals from prefrontal cortex. However, population codes in the prefrontal cortex also represent abstract information, such as task rules. How is conflict between active abstract representations resolved? We used functional neuroimaging to investigate the mechanism responsible for resolving conflict between abstract representations of task rules. Participants performed two different tasks based on a cue. We manipulated the degree of conflict at the task-rule level by training participants to associate the color and shape dimensions of the cue with either the same task rule (congruent cues) or different ones (incongruent cues). Phonological and semantic tasks were used in which performance depended on learned, abstract representations of information, rather than sensory features of the target stimulus or on any habituated stimulus-response associations. In addition, these tasks activate distinct regions that allowed us to measure magnitude of conflict between tasks. We found that incongruent cues were associated with increased activity in several cognitive control areas, including the inferior frontal gyrus, inferior parietal lobule, insula, and subcortical regions. Conflict between abstract representations appears to be resolved by rule-specific activity in the inferior frontal gyrus that is correlated with enhanced activity related to the relevant information. Furthermore, multivoxel pattern analysis of the activity in the inferior frontal gyrus was shown to carry information about both the currently relevant rule (semantic/phonological) and the currently relevant cue context (color/shape). Similar to models of attentional selection of conflicting sensory or motor representations, the current findings indicate part of the frontal cortex provides a bias signal, representing task rules, that enhances task-relevant information. However, the frontal cortex can also be the target of these bias signals in order to enhance abstract representations that are independent of particular stimuli or motor responses.

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1. Introduction

Goal-directed behavior is thought to depend on the ability of the brain to represent and implement the task rules that would produce appropriate behavior for a given situation. Studies have shown that neurons in the prefrontal cortex (PFC) can encode abstract task rules that are not bounded by a specific set of stimuli or overlearned stimulus-response associations. Rather, these rule representations support generalization of task performance to familiar and novel situations alike (Asaad, Rainer, & Miller, 2000; Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Hoshi, Shima, & Tanji, 2000; Wallis, Anderson, & Miller, 2001). It has been proposed that this abstract representation of task rule within the PFC biases processing throughout the rest of the brain by selectively enhancing activity of brain areas that encode the task-relevant information (E. K. Miller & Cohen, 2001). This is supported by neuroimaging studies in humans demonstrating rule-dependent interaction between PFC and posterior sensorimotor regions responsible for task execution (e.g., Chiu, Esterman, Han, Rosen, & Yantis, 2011; Egner & Hirsch, 2005; B. T. Miller, Vytlačil, Fegen, Pradhan, & D'Esposito, 2011; Nelissen, Stokes, Nobre, & Rushworth, 2013; Sakai & Passingham, 2003, 2006; Stroop, 1935; Waskom, Kumaran, Gordon, Rissman, & Wagner, 2014), and transcranial magnetic stimulation studies in humans showing disruption of PFC causally modulates the neural activity in posterior sensory cortex (Higo, Mars, Boorman, Buch, & Rushworth, 2011; Lee & D'Esposito, 2012; Zanto, Rubens, Thangavel, & Gazzaley, 2011).

This mechanism in which feedback from the PFC exerts influence over posterior regions to bias competition in favor of task-relevant sensory and motor representations is well established (for reviews, see E. K. Miller, 2000; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004). It is not clear, however, whether the same mechanism can be applied to situations in which the competition is among abstract representations of task rules. When multiple task rules are simultaneously activated, analogous to when multiple sensory stimulus or motor response representations are activated, how is this competition resolved? Can the type of interaction that occurs between PFC and posterior regions also occur among different regions within the PFC itself, by biasing neural processing towards prefrontal neurons coding the relevant abstract information? It is an important issue because the mechanism responsible for resolving conflicts between abstract representations of non-sensory information might be different from those resolving conflicts between sensory representations of stimuli (for a review, see Kastner & Ungerleider, 2000) or between potential actions (for a review, see Cisek & Kalaska, 2010).

In the current study, we used functional magnetic resonance imaging (fMRI) to investigate the mechanism by which we can select relevant over irrelevant task rules. If the mechanism were similar to the mechanism that is thought to govern selection of sensory and motor representations (Desimone, 1998; E. K. Miller & Cohen, 2001), then we would expect to find two specific results. First, conflict between abstract rules would be expected to result in behavioral impairment and be accompanied by increased activity in a cognitive control network that helps to overcome the behavioral impairment. Second, conflict between abstract representations of task rules would be expected to be resolved by PFC interacting with brain regions processing the abstract information needed for the task, which is neither sensory nor motor related. We expected that this process would be achieved by enhancement

of relevant abstract information, and perhaps secondarily by inhibition of irrelevant abstract information.

Participants were extensively trained so that strong associations were formed between different cue dimensions and one of two abstract task rules. Conflict was manipulated by having different cue dimensions (color and shape) associated either with the same task rule (congruent) or different ones (incongruent). For the incongruent cues, one cue dimension is mapped onto one task rule and the other cue dimension is mapped onto the other task rule through extensive training. The appearance of an incongruent cue, therefore, can cause automatic activation of both task rule representations. These task rules defined what type of abstract information had to be retrieved for a target word, rather than specifying particular manual response mappings or sensory features, so the conflict occurred at the abstract task-rule level. Participants switched between two tasks according to the rule given by the currently relevant cue dimension (color or shape), which was instructed at the beginning of each block and alternated across blocks. Phonological and semantic tasks were used, as they were previously shown to preferentially activate distinct brain areas (Lau & Passingham, 2007; Sakai & Passingham, 2006), allowing us to measure the degree of conflict between relevant and irrelevant task rules, and the interactions among PFC regions that may enable conflict resolution. By using these abstract rules combined with trial-unique words to which the rules were applied, participants could not learn a specific stimulus-response association, but rather needed to resolve the conflict at a more abstract level of representation.

2. Material and methods

2.1. Participants

Sixteen (12 females, 4 males) right-handed, healthy young adults between 18 and 35 (mean age 20 ± 2.5 years) participated the study. All participants were native English speakers with normal or corrected-to-normal vision, no history of head injury, substance abuse, neurological or psychiatric disorders, and were not taking any medications at the time of the study. The protocol was approved by the Institutional Review Boards of the Johns Hopkins University and the Johns Hopkins Medical Institutions. All participants provided written informed consent.

2.2. Experimental procedure

Participants were asked to make either a phonological or a semantic judgment for a visually presented word, as quickly as possible, while maintaining accuracy. We chose these semantic and phonological tasks because previous studies have shown that they preferentially activate distinctive regions within the frontal cortex (McDermott, Petersen, Watson, & Ojemann, 2003; Sakai & Passingham, 2006). This enabled us to use the blood oxygenation level dependent (BOLD) activity in these task-selective areas as a proxy for measuring the degree to which the relevant versus the irrelevant rule representations were activated by the task cues. The phonological rule required the participants to indicate, by pressing one of two buttons, whether the presented word contained two syllables or not. The semantic rule required the participants to indicate whether the meaning of the word referred to a concrete object or not. Left/Right button response mappings were counterbalanced

across participants. To equate difficulty between the two task rules, the word stimuli were selected using criteria similar to that of Sakai and Passingham (2006). All the word stimuli were nouns with written frequency over 15, taken from the Medical Research Council Psycholinguistic Database (http://websites.psychology.uwa.edu.au/school/MRCDatabase/uwa_mrc.htm). Half of the words had two syllables and the other half had one or three syllables; half had abstract meaning with a concreteness rating below 300 and the other half had concrete meaning with a concreteness rating above 500, according to the database. Different word stimuli were used in the pre-task training, scanning session, and localizer scans. Furthermore, the word stimuli in the scanning session (320 words) and localizer scans (144 words) appeared only once without repetition. This approach ensured that participants could not learn a specific stimulus-response association, but rather had to maintain the relevant rule at a more abstract level.

2.3. Training sessions

An example trial is illustrated in Figure 1. The applicable rule was indicated by a task cue presented at the beginning of each trial. Importantly, participants trained on the two dimensions of the task cue (color and shape) on a computer prior to the scanning session. There were two separate training sessions, one for each cue dimension. In the color training session, participants responded according to the color dimension of the cue (e.g., green indicates the semantic task and blue indicates the phonological task), and in the shape training session, participants responded according to the shape dimension of the cue (e.g., circle indicates the semantic task and triangle indicates the phonological task). The task cue meaning and the response assignment for both training sessions, as well as the order of the training sessions were counterbalanced across participants. Task instruction and a brief practice consisting of 24 trials were given at the beginning of each training session to make sure the participants understood the stimuli and procedures. Participants were instructed to respond according to the relevant cue dimension (i.e., either shape or color), which remained constant over the entire course of the training sessions. To ensure both feature dimensions of the cue were strongly associated with their corresponding tasks, participants performed 320 trials over the course of 30 minutes on each dimension (an hour in total for both the color and shape training sessions) in a quiet laboratory room. A self-paced break was provided after every 64 trials. For each trial, the sequence began with a 300-ms task cue indicating the upcoming task, followed by a 300 ms delay. A target word then appeared and remained on screen until a response was made or the 2000 ms time limit was reached. After each response, feedback was presented for 300 ms to indicate whether the response was “Correct”, “Incorrect” or “Too slow”. The next trial began after a fixed interval of 3000 ms.

2.4. Functional magnetic resonance imaging (fMRI) session

After the training sessions, participants performed a brief practice of 64 trials outside of the scanner approximately 20 minutes before the scan began. Inside the scanner, participants performed 5 runs of 64 trials of the same semantic and phonological judgments. For each run, both in the practice and during scanning, trials were blocked into four “Color Blocks” (color was the relevant dimension), which alternated with four “Shape Blocks” (shape was the relevant dimension). Blocks were separated by a 11s rest period during which a fixation cross was presented. A 2-second instruction screen was presented at the beginning of each

block (“Attend Color” or “Attend Shape”) to inform the participants of the relevant cue dimension for that block. After the instruction screen, eight trials were presented using the identical trial sequence as previously described for the training phase, with the exception that the target word remained on the screen for the entire 2000 ms. Participants were told to focus on that cue dimension until the next instruction screen was presented. There were equal numbers of trials for the eight experimental conditions based on the relevant cue dimensions (color or shape), congruency of the cue (congruent or incongruent) and tasks (phonological or semantic), and the conditions were fully-crossed with left versus right response buttons, number of switch versus repeat trials, and whether the correct response for the target word for one task was the same or different as the correct response for that word according to the other task. The participants held one response button box in each hand, which sent the responses to a Cedrus RB-610 Response Box (Cedrus, San Pedro, CA) via fiber optic cables. Reaction time was measured from the onset of the target word until a response was made.

2.5. Functional localizer

The scanning session ended with functional localizer runs to independently identify brain regions preferentially activated during the use of phonological and semantic rules for every participant. During the localizer runs, participants performed phonological and semantic tasks in alternating blocks. Each localizer task sequence began with the presentation of a 2000ms instruction screen (“Syllable”, “Concrete”) indicating the upcoming task, which was followed by a 1000 ms preparation period and then by six trials of the corresponding task. Text instruction cues (“Syllable” for phonological task and “Concrete” for semantic task), rather than the colored shape cues, were used to avoid cue congruency effects. Within each block, word stimuli were presented for 1700 ms with a 300-ms inter-trial interval. Participants were instructed to respond while the word stimulus was on the screen. A brief 1000-ms feedback indicating the overall performance for that block was given at the end of each block. Participants completed two runs of the localizer task, each lasting 4.9 minutes. Each run consisted of 12 blocks (6 blocks of the semantic task alternated with 6 blocks of the phonological task), interleaved with 8 seconds of rest when participants passively viewed a fixation cross.

2.6. fMRI data acquisition and pre-processing

fMRI scanning was conducted at the F. M. Kirby Research Center for Functional Brain Imaging in Kennedy Krieger Institute (Baltimore, MD) on a 3.0T Philips Intera scanner equipped with 32-channel SENSE head coil. High-resolution T1-weighted anatomical images were collected using a MP-RAGE sequence (150 axial slices, TR = 7.9 ms, TE = 3.7 ms, flip angle = 8°, matrix = 212 × 172, voxel size of 1 × 1 × 1 mm). Whole brain T2*-weighted functional images were collected in an ascending sequential fashion, using an echo-planar imaging sequence (35 axial slices, TR = 2000 ms, TE = 3.7 ms, flip angle = 70°, in-plane resolution of 2.5 mm in 80 × 80 matrix, slice thickness = 2.5 mm, with a 0.5mm gap).

All preprocessing and statistical analyses were done using SPM8 (Wellcome Trust Centre for Neuroimaging). The first 6 volumes of each run were discarded to allow for scanner

equilibration. The remaining functional image volumes were corrected for differences in slice acquisition timing using *sinc* interpolation, realigned to the first image volume to correct for head motion. The anatomical image was first co-registered to the mean of the motion-corrected functional images, and then it was segmented and spatially normalized to the tissue probability maps included in the SPM8 toolbox using both linear and nonlinear transformations. The normalization parameters (i.e. deformation field) derived from the anatomical image were then applied to all the functional images. In this step, the functional images were re-sampled to the same dimension (1.5 mm cubic voxels) as the anatomical images. Finally, the functional images were smoothed with an 8 mm full-width at half-maximum (FWHM) Gaussian kernel. Temporal autocorrelation was corrected using a first-order autoregressive model, and low-frequency drifts were removed using a high pass filter with a cutoff of 256 seconds (a cutoff of 100 seconds was used for functional localizer runs).

2.7. Behavioral analyses

Paired *t*-tests were used to compare reaction time (RT) and accuracy between the incongruent trials and congruent trials. Additional *t*-tests were conducted to determine whether the behavioral congruency effect (RT difference between incongruent cues and congruent cues) changed as a function of task switching (switch trials versus repeat trials), block type (attend color versus attend shape), tasks (phonological versus semantic task) or response congruency with a target word (target word mapped to the same versus different response buttons for the two tasks). All RT analyses were limited to the correct trials. The statistical threshold was set at $p < 0.0167$ (alpha = 0.05, two-tailed, Bonferroni corrected for multiple comparisons) for all behavioral analyses.

2.8. Voxelwise general linear model (GLM)

Task-dependent changes in BOLD signal were modeled using separate regressors representing each possible combination of the block type (color, shape), cue congruency (congruent, incongruent) and task rule (phonological, semantic). Each regressor was time-locked to the onset of the task cue. In addition, error trials, the two instruction screens informing the upcoming relevant cue dimension, and six head-motion parameters were included in the model as regressors-of-no-interest. All regressors, except those for the head-motion, were modeled by stick functions and convolved with SPM's canonical hemodynamic response function. The GLM model was estimated for each participant separately using SPM's first-level, fixed-effect, analysis. The primary contrast of interest was created for each participant to identify voxels exhibiting greater BOLD responses on all incongruent cue trials compared with congruent cue trials. All contrasts created at the subject-level were entered into a group-level random-effect analysis using a one-sample *t*-test against a contrast value of zero at each voxel. The statistical maps were thresholded using a voxel-level threshold of $p < 0.005$, corrected for multiple comparisons at a cluster-level of $p < 0.05$ (family-wise error correction). The cluster-extent threshold was calculated based on Gaussian random field method implemented in SPM8 (Friston, Worsley, Frackowiak, Mazziotta, & Evans, 1994).

2.9. Region of interest analysis

Functional regions of interest (ROIs) were chosen to test for interactions between PFC and task-selective areas. Because there was a high degree of variation across participants, the task-selective ROIs were identified in each participant using an independent functional localizer task. For the functional localizer, the statistical analysis was performed on the smoothed and normalized data. Two regressors of interest indicating the type of task for that block (semantic task, phonological task) as well as six head-motion parameters as regressors-of-no-interest were included in a GLM. The blocks were modeled as epochs spanning across the entire duration of the 16-second block, which was then convolved with SPM's canonical hemodynamic response function. The GLM model was estimated for each participant separately using SPM's first-level fixed-effect analysis. Contrasts of interest were (1) phonological task > semantic task, and (2) semantic task > phonological task.

Additionally, the localization focused on the left premotor gyrus (PM) along the border of the inferior frontal gyrus (BA6/44) and the anterior portion of the left ventrolateral prefrontal cortex (aVLPFC) in BA47, because these areas have previously shown to be preferentially activated by the use of phonological rules versus semantic rules, respectively (Sakai & Passingham, 2006). To ensure each participant's task-selective ROIs were within these pre-specified areas (left PM and left aVLPFC), we used the group-level results to constrain the selection of subject-specific voxels. For the phonology-sensitive area, we selected voxels that (1) exceeded a threshold of $p < 0.05$ (uncorrected) in the phonological task greater than semantic task contrast in that participant, and (2) was within the left PM binary mask generated from the group-level random-effect analysis ($p < 0.05$, FWE-corrected) for the same contrast. Similarly, for the semantic-sensitive area, we selected voxels that (1) exceeded a threshold of $p < 0.05$ (uncorrected) in the semantic task greater than the phonological task contrast in the individual participant, and (2) was within the left aVLPFC binary mask generated from the group-level random-effects analysis ($p < 0.05$, FWE-corrected) for the same contrast. The peaks for PM ($-50, -8, 44$) and aVLPFC ($-46, 28, -10$) in our group analysis are consistent with what others have previously reported for these tasks (McDermott et al., 2003; Sakai & Passingham, 2006).

For each subject-specific ROI identified using the localizer scans, we extracted the beta values separately for each of the eight conditions from the first-level GLM of the main task in this $2 \times 2 \times 2$ design (Color/Shape, Phonological/Semantic, Incongruent/Congruent). Since there were no significant differences in behavior or fMRI activation for color versus shape blocks, and our primary interest was the congruency effect on task-selective areas, we pooled the beta values across block types, resulting in 4 beta values per participant for each condition (phonological task/incongruent cue; phonological task/congruent cue; semantic task/incongruent cue; semantic task/congruent cue). Beta values for these four conditions were averaged across voxels within each ROI using MarsBaR toolbox (Brett, 2002).

One main hypothesis to be tested in the current study was whether the type of interactions that occur between the PFC and sensory or motor regions during selection also occur within the PFC itself, by biasing neural processing towards the prefrontal neurons coding abstract information needed for the relevant task rule over the irrelevant one. Previous research in visual attention has shown the selection can be achieved in sensory and motor regions by

enhancing relevant information, suppressing irrelevant information, or a combination of both (Cohen, Dunbar, & McClelland, 1990). To delineate the precise mechanisms by which the PFC resolves conflicts among abstract task rules, we first identified the prefrontal region that showed significant activation using the incongruent > congruent contrast in the group-level analysis. This contrast identified a single cluster in the right inferior frontal gyrus (rIFG). Next, we calculated for each participant the extent to which activity in the task-relevant and in the task-irrelevant area was modulated during incongruent relative to the congruent trials using beta values ("modulation index" = incongruent - congruent). We then tested for a correlation between this index and the activity changes in rIFG (incongruent - congruent) across participants, separately for each task condition. A greater modulation value in the rIFG indicates greater recruitment of rIFG during incongruent trials compared to congruent trials. Therefore, if conflict resolution were to be mediated by the enhancement of task-relevant information, we would expect a significant positive correlation of modulation index between the rIFG and task-relevant areas. Conversely, if conflict resolution were to be mediated by the suppression of task-irrelevant information, we would expect a significant negative correlation of modulation index between the rIFG and task-irrelevant areas. Finally, if enhancement and suppression contributed to conflict resolution, then both of the above predictions would hold.

In addition to rIFG, previous studies have suggested that parietal cortex is part of the cognitive control network and its activity increases concurrently with PFC when participants actively maintain a relevant task rule in working memory (Brass & von Cramon, 2002; Bunge et al., 2003) and when participants switch rules from one task to another (Braver, Reynolds, & Donaldson, 2003; Sohn, Ursu, Anderson, Stenger, & Carter, 2000; Yeung, Nystrom, Aronson, & Cohen, 2006). Thus, we also performed the same across-participant correlation analysis in the right inferior parietal lobule (rIPL), a region of interest that was also identified by the incongruent > congruent contrast.

2.10. Multi-voxel Pattern Analysis (MVPA)

The across-participant correlational analyses tested whether rIFG helps to resolve conflict between abstract representations of task rules by interacting with areas that process the abstract task information, resulting in either enhancement of relevant information in the task-relevant areas or suppression of irrelevant information in the task-irrelevant areas. However, it is not known what is the representational content of rIFG that allows it to interact with task-selective areas so that conflict between abstract representations of task rules can be resolved. According to Miller and Cohen's (2001) prominent theory of cognitive control, prefrontal cortex exerts control over other parts of the brain by representing the goal or rule information in working memory. In our experiment, because the incongruent cue did not provide unequivocal task information, participants needed to actively maintain the current context (color or shape) in working memory in order to select the relevant task rule. Once the relevant rule was selected, they needed to maintain that rule information for the execution of the task. Thus, to further investigate the representational content of rIFG, we used MVPA to test whether the pattern of activity within rIFG contains rule information (phonological vs. semantic rule), context information (color or shape), neither, or both. This analysis was also performed in rIPL for comparison.

MVPA was performed using a linear support vector machine (LinearCSVMC) from LIBSVM library (Chang CC, 2011) implemented within the PyMVPA software package (Hanke et al., 2009). The preprocessing procedure included slice-timing and head movement correction. The resulting functional images were then smoothed with a 4 mm FWHM kernel. To reduce the problem related to BOLD signals overlapping across temporally adjacent events, a univariate GLM analysis was conducted to derive condition-specific beta estimates for each block. For each participant, beta values pertaining to either the semantic task or the phonological task were estimated in each of the 40 blocks, yielding two beta maps for each block. Trials were modeled as events time-locked to the onset of the cue using a stick function, which was then convolved with a canonical HRF. A constant of one for each of the 40 blocks was included in the model to remove the mean signal within each block. Error trials were excluded from analyses. In a separate GLM, a similar procedure was used to estimate beta values related to the color and shape contexts. Context here was functionally defined as the relevant cue dimension participants were cued to attend to within each block. Each of the eight trials within a block contributed to the estimation of beta value for that context, yielding one beta map for each block. Overall, these GLM analyses yielded 40 beta maps for each task condition (phonological, semantic), and 20 beta maps for each context condition (color, shape).

Classifications of task rules and contexts were performed separately within the rIFG and rIPL clusters derived from the incongruent > congruent contrast. Each ROI was transformed back to the participant's native space by applying the inverse of the normalization parameters. This allowed us to conduct pattern classifications without re-sampling the individual beta maps to standard space. For each participant, the pattern of beta values within each ROI was extracted from each of the relevant beta maps. A leave-one-run-out procedure was used for cross-validation. A classifier was trained using the beta maps from four of the five runs and then tested using the beta maps from the held-out run. Five iterations were performed so that each run was tested once. The mean classification accuracy for each individual was determined by averaging the results across five iterations. To assess whether the classification performance was significantly different from chance (50%) at the group level, we first performed the permutation testing for each individual. This was done by randomly shuffling the target feature labels in the training sets (test set was not included) 5000 times to simulate the null distribution for a single participant. From the single-subject null distribution, we then randomly selected one classification accuracy from each participant, averaged these across the participants, and repeated this step 5000 times to build the group-level null distribution. The group-level significance was determined by comparing the correct-label accuracy to the permuted-label accuracies at the level of $p < 0.05$ (two-tailed).

3. Results

3.1. Behavioral results

Overall, participants were significantly slower in the incongruent trials (Mean = 1145 ms, SD = 27 ms) relative to the congruent (Mean = 1108 ms, SD = 26 ms) trials ($t(15) = 3.341$, $p = 0.004$). Error rate was also significantly larger in the incongruent (Mean = 0.073, SD =

0.01) than the congruent (Mean = 0.053, SD = 0.008) trials ($t(15) = 2.991, p = 0.009$), indicating the congruency effect on RTs was not a result of speed-accuracy trade-offs. In addition, the observed congruency effect was not significantly different between phonological and semantic tasks ($t(15) = 0.948, p = 0.358$), between “Attend Color” and “Attend Shape” blocks ($t(15) = 0.052, p = 0.959$), between switch trials versus repeat trials ($t(15) = 0.183, p = 0.858$), or between congruent versus incongruent response trials based on the target word ($t(15) = 1.931, p = 0.073$). These behavioral results indicate that the congruency experimental manipulation resulted in rule conflict as intended, with no interaction from other potential factors such as relevant cue feature or the particular primary task to be performed.

3.2. Voxelwise GLM results

To identify the cognitive control networks involved in the resolution of conflicting abstract task representations, we performed a whole brain univariate analysis contrasting the incongruent trials to the congruent trials. Complementary to the behavioral congruency effects, a number of regions demonstrated greater activation in the incongruent condition compared to the congruent condition, including rIFG, right insula, rIPL, right putamen, right postcentral gyrus, right precuneus, and midbrain (Table 1 and Figure 2). The opposite contrast (congruent > incongruent) did not yield any significant activation differences. Of particular note, the rIFG cluster, which showed significantly greater activation for incongruent cue trials than congruent, located in the ventrolateral prefrontal cortex (MNI coordinates of peak: 48, 28, 15; BA 45/46) has been previously implicated in tasks that require inhibition of irrelevant task sets or overriding a pre-potent response (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Aron, Robbins, & Poldrack, 2004).

3.3. Congruency effects on task-selective areas

We first examined the congruency effect in areas preferentially active for the phonological or the semantic task using ROIs independently identified during the separate functional localizer scans. There were two alternative hypotheses for these task-relevant and task-irrelevant regions. Since we only analyzed correct trials where the conflict between task rules could have been mostly resolved by the time a motor response was made, and so we might have expected to see the activation for the incongruent cue condition as strong as for the congruent cue condition in task-relevant areas (i.e. left PM for the phonological task and left aVLPFC for the semantic task), and the activation for the incongruent cue condition as weak as for the congruent condition in task-irrelevant areas (i.e. left PM for the semantic task and left aVLPFC for the phonological task). That is, we could have seen strong activation in task-relevant areas and minimal activation in task-irrelevant area equally for both incongruent and congruent conditions. Alternatively, if the competition had not been completely resolved, then we would expect to see more activation in the task-irrelevant area and less activation in the task-relevant area during incongruent trials than during congruent trials. That is, we would expect to see an interaction between the cue congruency and task in these ROIs.

To test these predictions, the beta values for these two ROIs were extracted and plotted as a function of relevant tasks and cue congruency (Figure 3). Two repeated-measures ANOVAs

were conducted to test for an interaction between cue congruency (congruent, incongruent) and task (semantic, phonological) separately for each ROI. As expected because these ROIs were functionally defined using the localizer scans, there was a main effect of task, with activity in the left PM ROI was greater in the phonological task condition than the semantic task condition ($F(1,15) = 8.429, p = 0.011$), whereas the opposite pattern was observed in the left aVLPFC ROI ($F(1,15) = 21.963, p < 0.001$). There was no main effect of congruency in either ROIs (left PM, $F(1,15) = 0.003, p = 0.956$; left aVLPFC, $F(1,15) = 1.271, p = 0.277$). There was no significant interaction between congruency and task in either ROI (left PM, $F(1,15) = 0.231, p = 0.638$; left aVLPFC, $F(1,15) = 0.406, p = 0.142$). The absence of an interaction effect indicates that, at the group level, the conflict between task rules caused by the incongruent cue was likely mostly resolved by the time a motor response was made. However, it remains a possibility that the degree to which the conflict between task rules was resolved on incongruent trials could have varied across participants, and that this could be related to the degree to which an individual activated the rIFG. Hence, we tested this hypothesis by following with an across-participant correlation analysis.

3.4. Across participants correlation between rIFG and task-selective areas

An across-participants correlation analysis was performed to investigate whether the degree to which activity in the task-relevant and irrelevant areas during the incongruent relative to the congruent trials might be related to the degree to which an individual activated the rIFG to resolve the conflict. As shown in Figure 4, the degree to which rIFG activation was increased during the incongruent trials relative to the congruent trials predicted the size of the modulation effects in the task-relevant areas for the phonological task (left PM, $r = 0.79, p < 0.001$) and for the semantic task (left aVLPFC, $r = 0.546, p = 0.029$), but not the size of the modulation effects in the task-irrelevant areas for either the phonological task (left aVLPFC, $r = 0.333, p = 0.208$) or the semantic task (left PM, $r = 0.399, p = 0.126$). The same correlation analysis was also performed in rIPL. The size of the increase in rIPL during incongruent compared to congruent trials did not predict the size of the modulation effects in the task-relevant areas for the phonological task (left PM, $r = 0.237, p = 0.376$) or for the semantic task (left aVLPFC, $r = 0.426, p = 0.1$), nor did it predict the size of the modulation effects in the task-irrelevant areas for the phonological task (left aVLPFC, $r = 0.401, p = 0.124$) or for the semantic task (left PM, $r = -0.022, p = 0.936$). These results support the hypothesis that specific regions within PFC interact with other PFC regions processing abstract information needed for the task, which biases neural processing towards the PFC neurons coding the relevant abstract information over the irrelevant information. Furthermore, the data indicates that this resolution of conflict among abstract task rules is accomplished by the enhancement of activity in brain areas representing relevant abstract information, rather than by the suppression of activity in areas representing irrelevant abstract information.

3.5. MVPA Results

MVPA analysis was performed to investigate the nature of the neural population code in rIFG that enables it to influence task-relevant representations and resolve task conflict. The results were in line with the hypothesis that patterns of activity in rIFG contain both the relevant rule information (mean classification accuracy for semantic versus phonological

trials = 57.06%, $p < 0.001$) and contextual information (mean classification accuracy for color versus shape blocks = 54.22%, $p = 0.019$). For comparison, we also conducted another MVPA using patterns of activity from rIPL. The pattern of activity in rIPL yielded a significant classification result for the rule information (mean classification accuracy = 55.23%, $p < 0.001$), but not for the contextual information (mean classification = 52.27%, $p = 0.123$). To summarize, our results indicate that both rIPL and rIFG contain information about the current task rule, but only rIFG activation also contains information about the context and only the rIFG activation is correlated with the degree to which the task-relevant information is enhanced.

4. Discussion

We used functional neuroimaging techniques to examine the mechanism responsible for resolving conflict between abstract representations pertaining to task rules: selecting the relevant abstract task rule over the irrelevant one. In previous studies, the mechanism by which conflict between task sets was resolved was indirectly tested by measuring activity in task-relevant and task-irrelevant brain regions during task switching (Yeung et al., 2006) and during conflict adaptation (Egner & Hirsch, 2005). However, one unexplored avenue in previous work was that the conflict in the tasks used in those studies could have occurred at multiple levels of processing, ranging from stimulus representations, response representations, to rule representations. Thus, an important feature of the current study is that the rule conflict was manipulated independently of the sensory features of the task cues or any motor planning responses triggered by the targets, enabling us to manipulate the degree of conflict at the task-rule level. In the current study different features of the task cues were associated with either the same (congruent cues) or different task rules (incongruent cues). Both congruent and incongruent cue stimuli had both color and shape feature dimensions. The context instruction at the beginning of the block unambiguously indicated which feature dimension was relevant. The conflict arose on incongruent trials only because of the learned association between the irrelevant cue dimension and the irrelevant abstract task rule, not because of conflict at the sensory level itself. Furthermore, we used a unique target word for each trial to prevent learning of an association between the target word and a specific response. Thus, conflict at the response level was also minimized.

Behaviorally, we found task performance was slower and less accurate in the incongruent condition relative to the congruent condition, suggesting that additional control processes were required following incongruent cues. These behavioral results provide strong evidence that our congruency manipulation was successful. Using functional neuroimaging, we also demonstrated that the behavioral congruency effect was accompanied by greater BOLD activity in a network of regions commonly associated with cognitive control and conflict resolution, including lateral prefrontal cortex, parietal cortex, insula, and subcortical areas.

The primary goal of the current study was to test whether the mechanisms involved in resolving conflict among abstract representations within the PFC were similar to those involved in resolving conflict among as they do with sensory and motor representations. It is widely believed that the PFC serves as a source of top-down control over other brain areas to bias processing towards goal-relevant sensory and motor information (E. K. Miller & Cohen,

2001). Thus, we predicted that conflict between abstract representations of task rules would be resolved by prefrontal feedback to the brain areas processing the goal-relevant, abstract information. A previous study showed that when participants were subliminally primed to perform a different task than the one that was explicitly instructed, activity decreased in the brain area selective for the instructed (relevant) task and activity increased in the brain area selective for the primed (irrelevant) task (Lau & Passingham, 2007). The changes of activity during incongruent trials relative to congruent trials, in both that study and the current study, can be thought of as an index of the degree to which the participants engaged in the irrelevant task. In Lau and Passingham's (2007) study, the magnitude of irrelevant task activation was only apparent when the conflicting task cue was low visibility and participants were thus unaware of the conflict. In the current study, using highly visible task cues, we found the congruency of the task cues did not appear to change the overall strength of activation in either the task-relevant or task-irrelevant area, when activation differences were assessed in the group analysis, consistent with the previous result. However, when assessing individual differences in the responses during incongruent and congruent trials, a different interpretation emerged. The interesting question here was whether the difference in activity between the incongruent and congruent conditions for the task-relevant and task-irrelevant areas changes as a function of the degree to which different participants recruited PFC during incongruent trials. We tested this hypothesis by looking for correlations between the activation changes in task-selective areas and activation changes in (1) the rIFG, a functionally defined cognitive control locus within the ventrolateral PFC, and (2) in the rIPL, another functionally defined cognitive control region that is frequently concurrently activated with PFC during performance of cognitive control tasks (Bunge et al., 2003; Crone, Wendelken, Donohue, & Bunge, 2006; Yeung et al., 2006), and has been implicated in providing top-down modulation when the task requires spatial attention to particular location (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999).

Specifically, we found that, across participants, the degree to which the rIFG increased during the incongruent condition relative to the congruent condition predicted the magnitude of the modulation effect in the task-relevant area but not the modulation effect in the task-irrelevant area. This correlation between the rIFG and task-relevant area activations was significant regardless of which of the two task rules was currently relevant. On the other hand, we did not find a significant correlation between rIPL activation and task-selective areas for either task. These observed relationships provide important insights about how conflict between abstract rule representations is resolved and how it may be similar to or different from conflict resolution mechanisms in sensory and motor cortices. The classic model of "biased competition" for selective attention includes both enhancement of relevant information and mutually inhibitory interactions that result in a winner-take-all outcome (Desimone & Duncan, 1995). While the original models were developed primarily based on single cell electrophysiological data, fMRI studies have also found evidence for suppression of irrelevant sensory information by selective attention within visual areas (Kastner, De Weerd, Desimone, & Ungerleider, 1998). For the abstract representations within PFC in the current study, such suppression, if it exists, appears much smaller than the enhancement of relevant information. It is important to note, however, that the suppressive interaction among

multiple visual stimuli is a result of direct lateral inhibitory connections within a single functional area. Suppression of activity related to irrelevant visual stimuli occurs when those stimuli are within the receptive fields of the same neurons. The neural activity patterns related to the different types of abstract representations in the current study (i.e. left PM and left aVLPFC) reside in separate brain areas that likely do not share strong inhibitory connections with each other. Thus, the enhancement of neural activity in one area would not necessarily be expected to result in inhibition of the other. Overall, our data are in agreement with previous selective attention studies that showed competing sensory stimuli were resolved through enhancement of task-relevant target information, including selective attention between spatial locations (Heinze et al., 1994; Luck, Chelazzi, Hillyard, & Desimone, 1997), stimulus features (Chawla, Rees, & Friston, 1999; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991) and objects (O'Craven, Downing, & Kanwisher, 1999; Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004). These previous studies demonstrated resolution of sensory-based stimulus conflict through neural enhancement of brain areas coding the relevant sensory information. The current study extends these findings by showing that regions within prefrontal cortex representing the currently relevant context or task rules can enhance the relevant information needed to perform that task, even when that relevant information is neither sensory nor motor and is represented by neural populations that are also within the prefrontal cortex. Thus enhancement of task-relevant information within the areas that process that information may be a general mechanism for conflict resolution for both sensorimotor and abstract information. Furthermore, the lack of a significant correlation for rIPL also suggests that rIFG may be the primary loci of cognitive control that provides top-down modulation when it comes to resolution of conflict among abstract representations. The rIPL may provide feedback more specifically for the control of sensory representations.

To better understand the nature of the bias signal from rIFG, we conducted MVPA to investigate the representational content within this area. One possibility was that rIFG could have represented information about the currently relevant rule, which then would drive increases of activity in brain areas that code the abstract information pertaining to that relevant rule. Alternatively, rIFG could have represented the currently relevant contextual information (i.e., color or shape block). This contextual information, combined with particular cue-stimulus input, could have, in turn, driven changes of activity in brain areas representing the abstract information pertaining to the rule. Other alternatives were that rIFG could have represented both rule and contextual information, or neither. Successful MVPA classification indicates that the patterns of activity within this region spatially encode information about the representational content of interest. Our results indicate that rIFG represents both contextual and rule information. In contrast, the rIPL appears to represent rule information, but not context. The MVPA results are consistent with previous studies that showed IPL was involved in retrieving and maintaining rule information in working memory (Bunge et al., 2003; Crone et al., 2006). In relation to the across-participant correlation result, however, it appears that rIPL is not the source of the top-down signal that biases competition of abstract representations towards the relevant one. The results indicate that rIFG biases selection of the appropriate abstract task representations according to both the cue and the current, more temporally extended context. In contrast, the currently relevant

rule representations, or perhaps the bound sensory features of both color and shape that were presented to instruct the relevant rule for the current trial, may be represented in the rIPL, but it does not appear to play a direct causal role in the selection of the relevant over the irrelevant abstract information.

In conclusion, we have shown that when there is conflict between abstract rules, rIFG mediates that conflict by enhancing activity in brain areas representing relevant information, rather than by suppressing activity in brain areas representing irrelevant information. The rIFG has previously been implicated in multiple types of cognitive control processes, including motor inhibition (Aron et al., 2004) and reflexive attentional reorienting (Corbetta, Patel, & Shulman, 2008). Previous research has also suggested that different subregions of rIFG could have different roles in cognitive control (for review see Waskom et al., 2014). The current study suggests a general mechanism by which this region might exert these multiple types of control, namely by integrating recent (cue) and more temporally distant (context) information in order to represent information needed to selectively enhance other relevant information in the presence of conflicting irrelevant information, regardless of whether that information is sensory, motor, or abstract.

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Figure 1. Experimental protocol. (A) Example of trial events progression, and (B) schematic drawing of task cues and their associated task rules. Each task cue had two dimensions: color and shape. For a given cue, each dimension could either be associated with the same task rule (congruent cues) or with different task rules (incongruent cues). During the training phase, the participants only needed to respond according to one of the two cue dimensions for the entire training session (320 trials), and then to repeat the same procedure based on the other cue dimension (320 trials). During the scanning session, the relevant cue dimension was instructed at the beginning of each block (“Attend Color” or “Attend Shape”). The relevant dimension remained constant within a block (8 trials per block), but alternated across blocks.

Figure 2.
Areas that showed greater activation in the incongruent condition compared to the congruent condition.

Figure 3.

Neural congruency effects in brain areas preferentially activated by the phonological (left PM) or semantic task (left aVLPFC). Beta weights for each condition were extracted from subject-specific ROIs identified using the separate functional localizer scans. As expected, BOLD activity in the left PM was greater in the phonological condition compared to the semantic condition, whereas the opposite pattern was true in the left aVLPFC. However, the effect of the cue congruency did not appear to change the task activity in either ROI (both interaction effects have $p>0.05$). This suggests that the competition was at least partially resolved shortly after the cue presentation.

Figure 4.

Correlation of the neural congruency effect between the rIFG and the task-selective areas across participants. The top two graphs show data from the left PM, and the bottom two graphs show data from the left aVLPFC. The degrees of modulation effect in task-relevant areas (the left two graphs) and task-irrelevant areas (the right two graphs) were plotted as a function of the degree of which individual participant recruited rIFG during incongruent trials relative to congruent trials. Modulation index is calculated by the beta difference between incongruent versus congruent trials.

Table 1

MNI coordinates of activation maxima for the cue congruency contrast (incongruent > congruent) in the GLM analysis

Brain region	X	Y	Z	SPM{Z}
Right insula	38	-7	7	4.96
Right putamen	18	2	3	4.31
Right inferior frontal gyrus	48	28	15	3.41
Midbrain	3	-28	-5	4.85
Right inferior parietal lobule	45	-60	37	3.99
Right precuneus	15	-57	25	4.14