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Coactivation of Cognitive Control Networks During Task Switching

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Objective: The ability to flexibly switch between tasks is considered an important component of cognitive control that involves frontal and parietal cortical areas. The present study was designed to characterize network dynamics across multiple brain regions during task switching. **Method:** Functional magnetic resonance images (fMRI) were captured during a standard rule-switching task to identify switching-related brain regions. Multiregional psychophysiological interaction (PPI) analysis was used to examine effective connectivity between these regions. **Results:** During switching trials, behavioral performance declined and activation of a generic cognitive control network increased. Concurrently, task-related connectivity increased within and between cingulo-opercular and fronto-parietal cognitive control networks. Notably, the left inferior frontal junction (IFJ) was most consistently coactivated with the 2 cognitive control networks. Furthermore, switching-dependent effective connectivity was negatively correlated with behavioral switch costs. The strength of effective connectivity between left IFJ and other regions in the networks predicted individual differences in switch costs. **Conclusions:** Task switching was supported by coactivated connections within cognitive control networks, with left IFJ potentially acting as a key hub between the fronto-parietal and cingulo-opercular networks.

General Scientific Summary

This study suggests that changing between 2 demanding tasks is supported by the coactivation of 2 widely distributed networks of brain regions known to serve cognitive control. The results suggest that during task switching 1 cortical region in the networks, the left inferior frontal junction, serves as a key hub. These results provide new information about how these networks serve controlled cognitive activity, and contribute to understanding the functions of the left inferior frontal junction.

Keywords: connectivity, fMRI, inferior frontal junction, switch cost, task switching

To adapt to the changing conditions in the environment, humans can flexibly modify goal-related task set and goal-directed behaviors. This capacity for flexibility is commonly investigated using a task switching paradigm, wherein participants are periodically cued to switch between two tasks that entail conflicting stimulus-response contingencies (e.g., Kiesel et al., 2010; Monsell, 2003; Vandierendonck, Liefoghe, & Verbruggen, 2010). In every trial,

participants should adopt the current task contingencies or “task-set,” by activating a specific, relevant configuration of perceptual, attentional, mnemonic and motor processes (Meiran, 1996; Sakai, 2008). In task switching paradigms, a cue to change from one task to another typically initiates ‘task-set updating’ processes. These processes have been shown to elicit different cortical network activity patterns than the processes associated with responding repeatedly to only one of the tasks (Karayanidis et al., 2010; Ruge, Jamadar, Zimmermann, & Karayanidis, 2013).

In the past two decades, neuroimaging studies have shown that task switching entails greater activation of a network of fronto-parietal control-related regions (for a review see Ruge et al., 2013). These regions have been found to consistently associate with various control processes involved in task switching. They include: posterior intraparietal sulcus (IPS) and superior parietal lobule (SPL), which are associated with attention shifting (Bode & Haynes, 2009; Chiu & Yantis, 2009); anterior lateral prefrontal cortex (aLPFC), associated with maintaining task goal information (Braver, Reynolds, & Donaldson, 2003; Crone, Wendelken, Donohue, & Bunge, 2006); anterior cingulate (ACC) cortex, associated with adjustments in control over action selection (Hyafil, Summerfield, & Koehlin, 2009; Liston, Matalon, Hare, Davidson, &

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Casey, 2006; Woodward, Metzack, Meier, & Holroyd, 2008); and presupplementary motor area (pre-SMA) and dorsal premotor cortex (dPMC), associated with specific response selection and initiation (Crone et al., 2006; Jamadar, Hughes, Fulham, Michie, & Karayanidis, 2010; Kim, Johnson, Cilles, & Gold, 2011; Rushworth, Hadland, Paus, & Sipila, 2002). Because task switching entails multiple control processes extended across cues and responses, it should also depend on interactions between these regions. However, little is known about the dynamic interactions between these control-related regions during task switching. Because the regions and related processes support not just task switching but also controlled action selection and planning more broadly, many investigators believe that they constitute a *general* cognitive control network (e.g., Cole & Schneider, 2007; Power & Petersen, 2013). Recent studies have indicated that control functions rely on the interaction between large-scale brain networks (Bressler & Menon, 2010; Cocchi, Zalesky, Fornito, & Mattingley, 2013; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Power & Petersen, 2013). Furthermore, Dosenbach et al. (2007) proposed two anatomically and functionally segregated brain networks that are central to cognitive control: a fronto-parietal network (FPN) and a cingulo-opercular network (CON). However, a direct investigation of task-switch-related interactions between large-scale brain networks has not yet been undertaken. Thus, in the present study, we sought to characterize dynamic brain network activity during task switching, and in particular to determine whether task switching activity is related to the interactivity between the FPN and CON.

An ancillary goal was to test a hypothesis that the left inferior frontal junction (IFJ) is a crucial region for task switching (e.g., Brass, Derrfuss, Forstmann, & von Cramon, 2005; De Baene, Albers, & Brass, 2012; Kim, Cilles, Johnson, & Gold, 2012; Kim, Johnson, Cilles, & Gold, 2011; Stelzel, Basten, & Fiebach, 2011). The left IFJ is activated by updating task-set, as when processing a switch cue (Brass & von Cramon, 2002; Derrfuss, Brass, Neumann, & von Cramon, 2005; Kim et al., 2011). Researchers have found that the left IFJ is involved in both task goal and stimulus-response (S-R) mapping (De Baene et al., 2012), and shows domain-general activation during three kinds of switching (stimulus, response, and cognitive-set switches; Kim et al., 2011). Further, Stelzel et al. (2011) reported increased activation of left IFJ in both hand switching and abstract rule switching. Notably, they also found increased connectivity between left IFJ and motor regions during hand switching, and between left IFJ and rule-related regions during abstract rule switching. This finding suggests that the left IFJ is involved in a wide range of task or response switching task, and other regions are coactivated according to task content or response demands. Consistent with these results, Brass et al. (2005) summarized early fMRI studies of task switching and proposed that the left IFJ plays a pivotal role in integrating many kinds of task-related information during task-set updating.

Although the left IFJ is activated during a variety of switching tasks, previous results do not clarify the nature of its role. For example, the left IFJ might be involved in modulating other switching-related regions to effectively update task-set during switch trials. Alternately, its activation might be a byproduct of ancillary demands that are common in task switching (and perhaps other cognitive control-demanding) paradigms. In the current

study, we predicted that left IFJ will be coactivated within the fronto-parietal and cingulo-opercular cognitive control networks (FPN and CON) during task switching. By examining patterns of coactivation between left IFJ and the FPN and CON, we can constrain hypotheses about the functional role of left IFJ in cognitive control network dynamics.

We used multiregional psychophysiological interaction (multi-PPI) analysis to examine interactions between switch-related regions. Typically, trials and intervals between trials in task switching paradigm are brief, and switching can result in extensive activation across many widely distributed brain regions. Multi-PPI analysis is a newer method for quantifying context-dependent effective connectivity among multiple brain regions (see Friston, 2011). It permits researchers to explore how high-order cognitive functions are modulated by large-scale networks. It has an advantage in examining connectivity among multiple regions in rapidly event-related fMRI data (see Cocchi et al., 2014; Hearne, Cocchi, Zalesky, & Mattingley, 2015). Here we identified switch-related regions by examining differences between task-switch-related and task-repetition-related activation in a general-linear model (GLM) analysis. We then modeled switch-induced effective connectivity among the regions through multi-PPI analysis.

Method

Participants

Twenty-nine right-handed college students from Southwest University in China were recruited for the study. All participants had normal or corrected-to-normal vision. No participant reported a history of substance dependence, significant head injury, or current use of psychotropic medications. Three participants were excluded from the analyses due to excessive head motion (>2 mm) during image acquisition. Thus, data from 26 participants (12 females), aged 21 to 25 years ($M = 21.3$), were retained. All participants provided informed written consent to participate in the study. All procedures were approved by the University Human Ethics Committee.

Behavioral Paradigm

All stimuli were created in Photoshop by superimposing a yellow (RGB 255 255 153) name on a monochrome face picture. Six common female names and six common male names were adopted based on He and Chen (2010), who asked 50 undergraduate students to choose the six most common female names and six most common male names from larger lists of 20 common names each. Each name consisted of two Chinese characters. In addition, six female faces and six male faces were selected from a database of neutral faces in the Chinese affective picture system (Bai, Ma, & Huang, 2005). These were standardized by the same procedure above. Faces were presented with names written across them. To make a face and a name match in terms of gender, one face was matched with 12 names including six male names and six female names, so that there were 144 combinations. All stimuli (size: 4.5° visual arc) were stored as 260 × 300 pixel image sequences and were presented with a black background on a screen positioned 100 cm from the participants.

Each trial (see Figure 1) began with the presentation of a fixation cross for 800 ms. Then a task cue (red rectangle or blue rectangle; size = 1° arc) was presented for 200 ms to indicate which task (face or name) the participant should perform in that trial. Then the stimulus was presented for 1,000 ms. Participants had 2,000 ms to respond after the onset of a stimulus. They had been instructed to respond as quickly as possible, without sacrificing accuracy. The interval between trials was variable (pseudorandom: $M = 3,100$ ms; range = 2,000 to 4,200 ms). The tasks were to judge the gender of either the face or of the name, and to indicate the gender with left button or right button (gender positions were counterbalanced between participants). Each trial after the first was defined as a *switch trial* if the task changed from face-judgment in the previous trial to name-judgment in the current trial, or vice versa. The trial was a *repetition trial* if the task remained the same as the previous trial. The genders of the faces and names, the types of judgment (face and name) and the response buttons were counterbalanced between switching and repetition trials. Before scanning, all participants completed a practice session (64 trials) like the formal task, to ensure that the cues and the stimulus-response assignments were clearly understood. In the scanner, participants completed three blocks (121 trials per block) in which the two trial types (switching and repetition) were equally distributed and randomly intermixed.

Visual stimuli were generated using the E-Prime software (Psychology Software Tools, Inc. Pittsburgh, PA) and projected onto a screen at the rear of the scanner, which the participants could comfortably see on a mirror mounted on the head-coil. Participants' responses were recorded using an MRI-compatible response box connected to the response computer via a fiber optic cable.

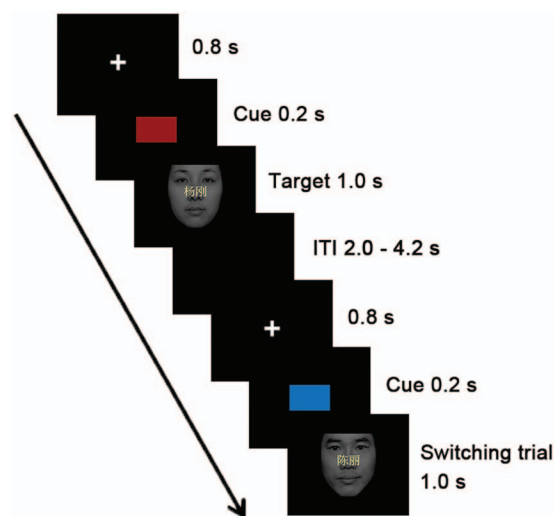


Figure 1. Design of the experiment. A trial started with the presentation of a fixation cross for 800 ms. Then one of two cues (a red rectangle or a blue rectangle) was presented for 200 ms to indicate which of the two tasks (face or name) to perform. A stimulus then was presented for 1,000 ms. Participants had up to 2,000 ms to respond after stimulus onset. The intertrial interval was variable (pseudorandom: $M = 3,100$ ms; range = 2,000 to 4,200 ms). Participants judged, on every trial, the gender of either the face or of the name by pressing one of two (left or right) buttons. See the online article for the color version of this figure.

Scanning Procedure

Participants were positioned head first and supine in the magnetic bore. Images were acquired with a Siemens 3T scanner (Siemens Magnetom Trio TIM, Erlangen, Germany), using a standard eight-channel radio-frequency head coil. Participants were instructed not to move their heads to minimize motion artifacts. An ascending scanning sequence was used. An echo-planar imaging (EPI) sequence was used for data collection, and 367 T2*-weighted images were recorded per run (TR = 1,500 ms, TE = 29 ms, flip angle = 90°, FoV = 192 × 192 mm², matrix size = 64 × 64, 25 ascending 5 mm-thick slices, in-plane resolution = 3 × 3 mm², slice skip = 0.5 mm). A structural scan was acquired at the end of the test session (T1-weighted 3D MP-RAGE sequence, 176 slices, TR = 1,900 ms, TE = 2.52 ms, flip angle = 9°, FoV = 250 × 250 mm², voxel size = 1 mm³).

Data Analysis

Behavioral data, including accuracy and response time (RT), were analyzed using paired sample *t* tests (2-tailed) in SPSS18 (Chicago, IL, U.S.A.). Image preprocessing and analyses were performed in SPM8 (Wellcome Department of Cognitive Neurology, London, U.K.). The first 10 images were discarded to achieve magnet-steady images. After discarding the first five functional volumes of each run, differences in timing between slices were adjusted and images realigned toward the 13th slice. Then, the data were realigned to estimate and modify the six parameters of head movement. To normalize functional images, each participant's structural brain image was coregistered to the mean functional image and was subsequently segmented into gray matter, white matter, and cerebrospinal fluid. The parameters obtained in segmentation were used to normalize each participant's functional image onto the Montreal Neurological Institute space (resampling voxel size = 3 mm³). A filter of 8 mm FWHM (full-width at half maximum) was used to spatially smooth the normalized data.

For the first-level individual analysis, a GLM approach (Friston et al., 1994) was used to estimate parameter values for event-related responses. For the short interscan interval we used here, the microtime onset was set to the default value in SPM. After slice timing, stimulus (not cue) onsets diverge slightly from real onsets, but this variance is widely considered acceptable in fMRI data analysis. Thus, for each participant, stimulus onsets were extracted for two conditions and the time series data were modeled for two different vectors, corresponding to switch and stay target epochs, respectively. The first trial of each run was excluded from analyses, and all erroneous trials and trials following errors were pooled together and modeled separately, excluded from the main analyses. Head movement parameters in six dimensions, estimated during motion correction, were included in the model as nuisance covariates. All of these vectors were convolved with the canonical hemodynamic response function (HRF). A high-pass filter was implemented with a cut-off of 128 seconds to remove low-frequency drift from the time-series. Contrast on task-switch-trials and on task-repetition trials was calculated separately, resulting in two contrast images for each participant. Using the random effects procedure, these contrasts were submitted to group analysis. Group SPMs were generated using paired sample *t* test, and the statistical threshold was set to $p < .005$ (voxel level) to correct for false discovery rate (Genovese, Lazar, & Nichols, 2002). Only areas of

significantly activated clusters with a minimum size of 30 voxels are reported.

Functional interactions between switch-related regions were investigated by PPI analysis (Friston et al., 1997), an established method to quantify changes in connectivity between regions during a given context or task. Typically, PPI analysis is implemented to assess which voxel in the brain shows an increase in context-specific connectivity with a single predefined seed region. Here, we defined multiple regions and assessed connectivity between each pair of regions, rather than assessing the connectivity between a single seed region and all other voxels. This approach is suited for exploring the dynamics of functional brain networks in a specific context (e.g., Cocchi et al., 2014; Hearne et al., 2015). We considered 10 regions defined by positive activation during the switching epochs minus repetition epochs in the GLM analysis. For each participant and region, brain activity was extracted from a spherical seed region with a diameter of 6 mm around the peak activation voxel.

PPI terms were generated using SPM8 for each region, condition and participant. The PPI signal for switching epochs was defined as the region's activity only during times associated with switching; conversely, the PPI signal for repetition epochs was defined as the region's activity during repetition trial intervals. This yielded a switch-related PPI term and a repetition-related PPI term. Then, as with the standard PPI analysis, the HRF was deconvolved from the region's activity before multiplication, and the final PPI term was convolved with the HRF. For every pair of regions, the PPI regressor (switching or repetition), and the signals of the region used to determine the PPI term (i.e., the main effects of psychological and physiological factors), were included as nuisance covariates. This procedure reduced correlations due to shared task input, and resulted in a 10×10 connectivity matrix for each participant and condition. For each element (i, j) of the connectivity matrix, the parameter estimate (β) for the corresponding PPI term quantified the influence of region i on region j in a specific condition (i.e., effective connectivity; see Friston, 2011, for details). Within-subject analyses of variance (ANOVAs) were used to test whether switching and repetition significantly differed in a given region. Then 90 connections (from each of the 10 regions to every other region) were tested. The network-based statistic (NBS; Zalesky, Fornito, & Bullmore, 2010) was used to correct for multiple comparisons. The ANOVAs and NBS were performed with the codes from Cocchi et al. (2014). A total of $K = 5000$ permutations were computed for each threshold, and an exploratory F -statistic threshold of 4.0 was used for the NBS. The NBS generated a corrected p value for each pair of regions that showed an interaction between (switching - repetition) differences.

To test whether network dynamics predicted behavioral effects, we calculated correlations between behavioral switch costs and connectivity. In task switching paradigms, *switch costs* are higher RTs, and sometimes lower accuracy, in switch trials than in repetition trials. We defined switch costs for each participant as the increase in the grand mean RT on repetition trials over the grand mean RT on switch trials. Differences of connectivity for each participant were defined as differences in the beta regressor value (switching - repetition) for a given connection.

Results

Behavioral Data

The first trial of each run, error trials, and posterror trials were excluded from the analyses. As depicted in Figure 2, participants showed slower response, $t(25) = 10.05$, $p < .001$ and lower accuracy, $t(25) = 4.02$, $p < .001$ in switching trials than repetition trials. These results confirm the predicted switch costs.

To examine whether switch costs were attenuated by practice, we conducted a 2 (block: first vs. third) \times 2 (trial type: switch vs. repeat) within-subjects ANOVA on RTs. Results showed that both main effects were significant: RTs were longer in the first block than the third block, $F(1, 25) = 4.59$, $p < .05$, and were longer on switching trials than repetition trials, $F(1, 25) = 74.50$, $p < .001$. Importantly, however, there was no significant interaction of block and trial type, $F(1, 25) = 0.09$, $p > .77$, indicating that switch costs were not eliminated by practice. To examine whether switch costs were affected by stimulus congruence, we conducted a 2 (congruence: incongruence vs. congruence) \times 2 (trial type: switch vs. repeat) within-subjects ANOVA on RTs. There were significant main effects of congruence, $F(1, 25) = 24.99$, $p < .001$, with slower RTs to incongruent stimuli, and of trial-type, $F(1, 25) = 71.35$, $p < .001$. However, the interaction of block sequence and trial type was not significant, $F(1, 25) = 2.31$, $p > .14$, indicating that switch costs and incongruence costs were additive. To determine whether participant gender interacted with stimulus gender, male and female participants' data were examined separately. Female participants did not show any difference in responding to female faces or names, $t(11) = 0.23$, $p > .82$. Similarly, male participants did not show any difference in responding to male faces or names, $t(13) = 0.71$, $p > .48$.

fMRI Data

The comparison between switch trials and repetition trials positively activated a set of brain regions encompassing left dorsolateral prefrontal cortex (DLPFC), bilateral anterior insula (AI), ACC, bilateral dPMC, left IFJ, bilateral inferior parietal lobule (IPL), bilateral IPS, bilateral SPL, and bilateral occipital cortex (see Figure 3 and Table 1). These are the same regions as those reported to be activated in a majority of task switching studies, and include the major nodes of the proposed CON and FPN networks

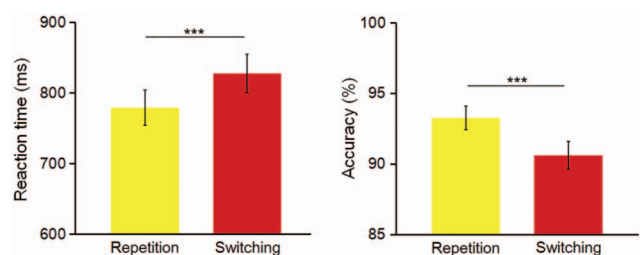


Figure 2. Behavioral data obtained during scanning. Mean response times (left) and percent accuracy (right) are shown for switch and repeat trial types (error bars: within-participants standard error of the mean). *** $p < .001$. See the online article for the color version of this figure.

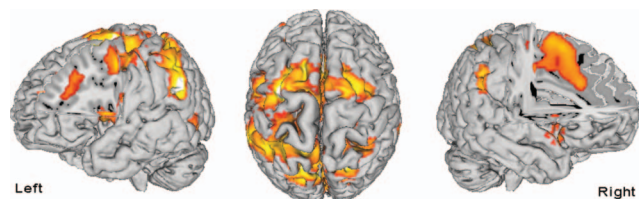


Figure 3. Brain activity during switching. The comparison between switching trials and repetition trials resulted in significant activity in a diffuse set of regions encompassing lateral prefrontal cortex, anterior insula, anterior cingulate cortex, superior frontal cortex, parietal cortex and occipital cortex ($p < .005$, FDR corrected). See the online article for the color version of this figure.

(Dosenbach et al., 2007; Power et al., 2011; Power & Petersen, 2013).

Changes in effective connectivity during switching were assessed in the cortical clusters (see Table 2 for details) identified by the GLM analysis described above. Among these 10 regions, multi-PPI analysis identified 28 connections that significantly increased in relation to switching trials (Figure 4A). Thus, increased connectivity was observed across the functional architecture of both FPN and CON (Figure 4C). To test whether the switching-related network activity was related to switch costs, we examined correlations between mean connectivity changes (switching - repetition) among these 28 connections, and behavioral switch costs. Results showed that the mean connectivity change was negatively correlated to the individual's mean switch costs, $r = -0.45$, $p < .05$ (Figure 4B). This suggests that task switching was related to network connectivity changes between and within CON and FPN: specifically, increasing connectivity was related to lower relative slowing on switch trials.

Closer examination reveals that the left IFJ and the left AI were involved in most of the connections in the network, implying that those regions might play important roles in mediating the FPN and CON control networks (Figure 4B). Previous studies indicate that left IFJ is a core region task-set updating (Kim et al., 2011, 2012), and left AI is a core region in the salience network (Menon & Uddin, 2010). Thus, the two regions might be the key hubs in the present switching-dependent brain network. Although we cannot test the independent contribution of each connection because col-

Table 2
Brain Regions Included in Connectivity Analysis

Regions	Hemisphere	MNI coordinates		
		x	y	z
Dorsolateral prefrontal cortex (DLPFC)	L	-30	42	18
Left anterior insula (LAI)	L	-51	9	6
Right anterior insula (RAI)	R	48	15	0
Anterior cingulate cortex (ACC)	L	-6	18	45
Left dorsal pre-motor cortex (LdPMC)	L	-27	-6	57
Right dorsal pre-motor cortex (RdPMC)	R	21	-3	63
Inferior frontal junction (IFJ)	L	-51	3	39
Intraparietal sulcus (IPS)	L	-39	-39	45
Left superior parietal lobule (LSPL)	L	-15	-63	51
Right superior parietal lobule (RSPL)	R	18	-57	57

Note. MNI = Montreal Neurological Institute.

linearity of the connections is very strong, we employed principal component analysis (PCA) as an exploratory analysis of which connections were functionally similar. This analysis revealed that the largest contributors to the first component (accounting for 30% of the total variance) were six connections between left AI and other regions. The largest contributors to the second component (13% of the total variance) were five connections between left IFJ and other regions. Although this analysis did not reveal a solution that partitioned all 28 connections into several components, the results imply that connections involving left IFJ, and other connections involving left AI, might play disproportionately consistent roles in mediating activity of FPN and CON during task-switching.

Specifically, the left IFJ appears to be a target region for CON inputs, as well as bilateral SPL, dPMC, and left DLPFC inputs, outputs, or both. By contrast, the left AI might exert influence on other regions including FPN nodes and motor regions. The correlation results further underscore the functional relevance of this connectivity pattern. To test whether the univariate activation of left IFJ and left AI contribute to the behavioral switch cost, we extracted the percent signal change of left IFJ and left AI, respectively, and calculated the correlations between behavioral switch costs and neural activation changes (i.e., each subject's percentage signal change in repetition vs. switching trials). The correlation

Table 1
Brain Activity During Switching

Regions	Left hemisphere		Right hemisphere	
	MNI coordinates	t-value	MNI coordinates	t-value
Dorsolateral prefrontal cortex (BA9/10)	-30, 42, 18	5.24		
Anterior insula/inferior frontal gyrus (BA44)	-51, 9, 6	5.37	48, 15, 0	3.68
Anterior cingulate cortex (BA32)	-6, 18, 45	7.01		
Dorsal pre-motor cortex (BA6)	-27, -6, 57	7.78	21, -3, 63	6.25
Inferior frontal junction (BA6/9)	-51, 3, 39	5.42		
Inferior parietal lobule (BA40)	-60, -45, 24	7.67	66, -36, 30	4.74
Intraparietal sulcus (BA40)	-39, -39, 45	6.40	33, -36, 45	5.71
Superior parietal lobule (BA7)	-15, -63, 51	7.26	18, -57, 57	7.22
Occipital cortex (BA17/18/19)	-18, -75, 6	6.09	9, -75, 12	5.29

Note. MNI = Montreal Neurological Institute.

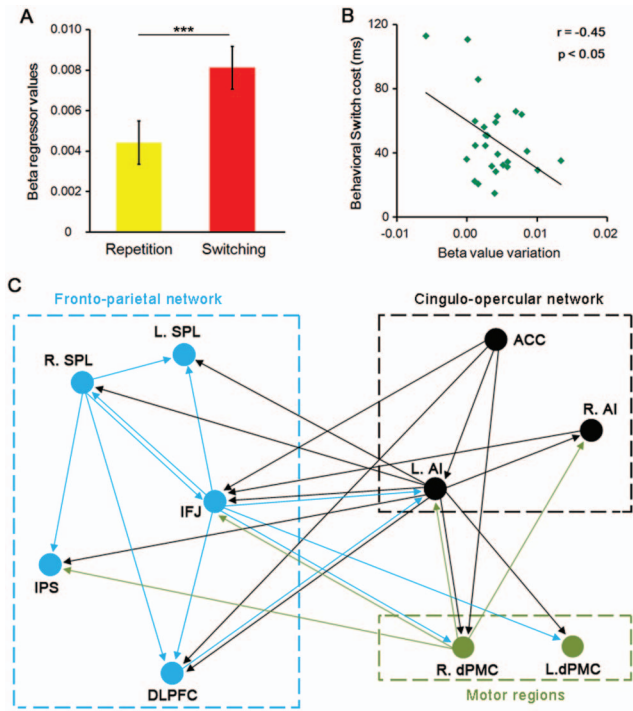


Figure 4. The coactivation of large-scale brain network during task switching (A). Large-scale brain network showing global changes in connectivity for switching and repetition. The *x*-axis in the bar chart depicts switching and repetition condition, and the *y*-axis indicates the mean value of all the connections during switching ($*** p < .001$). (B) Switch cost correlation relationships of effective connectivity of large-scale brain network. The *x*-axis indicates the mean value of all connections during switching, and the *y*-axis indicates the behavioral switch cost. Each dot represents data for a single subject (C). Schematic representation of the connectivity of large-scale brain networks during switching: fronto-parietal network (light blue), cingulo-opercular network (black), and motor regions (green). The network was isolated by conducting a psychophysiological interaction analysis (PPI) for every pair of regions of interest (see Materials and Methods for details). The 10 regions represent the main clusters involved in switching isolated using the general linear model framework (see Table 2 for details). The edges indicate the effective connectivity between switching-related regions. L = left; R = right; AI = anterior insula; ACC = anterior cingulate cortex; IFJ = inferior frontal junction; DLPFC = dorsolateral prefrontal cortex; SPL = superior parietal lobule; IPS = intraparietal sulcus; dPMC = dorsal premotor cortex. See the online article for the color version of this figure.

was not significant for left IFJ, $r = .28$, $p = .16$ or for left AI, $r = .14$, $p = .48$. These results suggested that the univariate activations of IFJ and AI did not predict differentiation of behavioral performance. However, behavioral switch cost means were negatively correlated with the mean connectivity difference (switch—repetition) of the connections between left IFJ and other regions, $r = -0.50$, $p < .01$ (Figure 5A). By contrast, the corresponding correlation of switch costs with left AI connectivity difference was not statistically reliable, $r = -0.27$, $p = .19$; Figure 5B).

Discussion

In the current study, participants displayed expected performance costs in switching trials compared to repetition trials (i.e.,

slower RTs and lower accuracy). In addition, compared with repetition trials, switching trials resulted in increased activation in DLPFC, AI, ACC, dPMC, IFJ, IPL, IPS, SPL and occipital cortex. Finally, multi-PPI analysis was used to quantify the effective connectivity among these activated regions during switching. Results showed that task switching was associated with increased connectivity within and between two main cognitive control networks, the fronto-parietal and the cingulo-opercular. The left IFJ was found to be a common node in this switching-dependent connectivity pattern, and was correlated with behavioral switch costs. These findings demonstrate that task switching is related to the joint dynamic activity of two cognitive control networks, with at least one common node. These results provide a novel characterization of the large-scale functional network during task switching.

The activated regions lie within a broadly distributed cognitive control network (Cole & Schneider, 2007). This network is activated during task switching, as follows. During task-repetition trials, individuals just need to maintain the previously configured task-set, whereas during task switching trials, individuals must activate a new task-set configuration (Monsell, 2003). The latter involves control processes for the alternate task-set components, including perceptual, attentional, mnemonic and motor processes (Sakai, 2008). The results confirm that regions of frontal and parietal cortex contain some neural substrates of these control processes, and therefore also support task switching (see Ruge et al., 2013). Specifically, in task switching, the DLPFC is thought to play a role in actively maintaining the representations of task rules (Bunge et al., 2005; Crone et al., 2006; Yoshida, Funakoshi, & Ishii, 2010; De Baene et al., 2012), the IPS and posterior SPL are associated with attentional set shifting (Bode & Haynes, 2009; Chiu & Yantis, 2009; Corbetta, Patel, & Shulman, 2008), the dPMC is thought to be involved in learning arbitrary stimulus-motor associations (Abe et al., 2007; Amiez, Kostopoulos, Champod, & Petrides, 2006; Badre & D'Esposito, 2009), and the ACC is associated with adjustments in control over action selection (Hyafil et al., 2009; Liston et al., 2006; Woodward et al., 2008). Notably, the activated regions showed significant left hemispheric dominance, which is consistent with a number of findings that

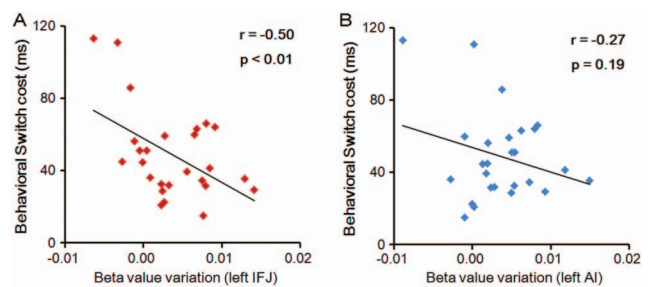


Figure 5. Switch cost correlation relationships of effective connectivity in the left inferior frontal junction (A) and the left anterior insula (B). Scatter plots with lines of best linear fit show the correlation between behavioral switch cost and effective connectivity values. The *x*-axis indicates the mean value of the connections between the left inferior frontal junction (or left anterior insula) and other regions, and the *y*-axis indicates the behavioral switch cost. Each dot represents data for a single subject. See the online article for the color version of this figure.

task-switching preferentially engages left prefrontal and posterior parietal regions (Badre & Wagner, 2006; Braver et al., 2003; Jamadar et al., 2010; Kim et al., 2011; Muhle-Karbe, De Baene, & Brass, 2014). A recent study found that task switching has a general left hemispheric distribution above and beyond specific task requirements (Vallesi, Arbula, Capizzi, Causin, & D'Avella, 2015), further confirming the present finding of predominantly left activation related to task switching. Taken together, the finding that task switching depends on activation in a general cognitive control network provides a justification for subsequent multi-PPI analysis.

Dosenbach et al. (2007) proposed that two anatomically and functionally segregated brain networks support the control of task-sets: the FPN and the CON. The current study found that task switching was associated with increased connectivity within and between regions of these networks. Furthermore, stronger effective connectivity within these networks is associated with better behavioral performance (i.e., smaller switch costs). That is, the higher coactivation of cognitive control networks during task switching is associated with more efficient switching. The CON is thought to underpin the detection of salient events (Menon & Uddin, 2010; Seeley et al., 2007) and to facilitate access to cognitive resources for goal-directed control when a salient cue is detected (Menon, 2011; Menon & Uddin, 2010). In task switching paradigms, the switching cues signal a change which may contain more salience than repetition cues and lead to more activation in the CON. Conversely, the activation of CON might be associated with the detection of switching cues. On the other hand, the FPN is thought to support dynamic (trial-by-trial) cognitive control (Dosenbach et al., 2007; Power & Petersen, 2013) and to serve short-timescale adaptive aspects of cognitive control (Cole et al., 2013; Zanto & Gazzaley, 2013). In the current results, connections among FPN nodes and motor regions might reflect increased demands for integrating trial-by-trial control functions when reconfiguring task-set after seeing a switch cue.

Results showed that the left AI was involved in most of the CON connections. Menon and Uddin (2010) proposed that a fundamental mechanism of control is a transient signal from the AI that engages attentional, working memory and higher order control processes while disengaging other systems that are not immediately task relevant. This proposition is consistent with our finding that the left AI serves as a highly connected node within CON. Intriguingly, although the left AI is well connected, its connectivity strength did not significantly predict behavioral switch costs. In fact, generating a state of heightened physiological awareness for salient stimuli is a general process in cognitive control, and individuals can rapidly enter a sustained state to implement the higher order control functions (Craig, 2009; Critchley & Harrison, 2013; Menon, 2011; Menon & Uddin, 2010). Thus, during task switching, this process is likely necessary, but does not determine the size of switch costs. This implies that CON modulates other regions during switching in a relatively 'all or nothing' manner. However, this speculation remains to be confirmed through additional experimental and analytical approaches.

The present study also found that left IFJ was modulated by CON nodes and interacted with other FPN nodes as well as motor regions. Previous studies have implicated left IFJ in the updating of general task-sets in task switching (e.g., Brass & von Cramon, 2002, 2004; Derrfuss et al., 2005; Kim et al., 2011, 2012; Stelzel

et al., 2011). During task-switching, left IFJ contributes to constructing an integrated representation of the current task goal. Thus, left IFJ might manage task information, and yet its cooperation with other task-set regions in switching trials might be not as close as the cooperation in repetition trials. Consequently, the effective connectivity from left IFJ to other task-set regions may reflect increased demands to ensure effective implementation of the current task-set.

Several recent connectivity studies support this proposition. For instance, Stelzel et al. (2011) found enhanced connectivity between left IFJ and task-specific switching-related regions in different switching contexts (abstract rule switching and hand switching), suggesting that left IFJ is involved in orchestrating various task-related regions when a new task-set must be implemented. Another study reported that stronger resting-state functional connectivity between left IFJ and other switching-related regions is associated with more efficient task switching (Yin, Wang, Pan, Liu, & Chen, 2015). Left IFJ's possible role in mediating other control regions for task-set updating is further supported by the present results: efficiency of the interaction between left IFJ and other regions predicted individual differences in switch costs. Previous behavioral studies have suggested that switch costs result from the reconfiguration of cognitive resources (Meiran, 1996; Monsell, 2003). The present connectivity results suggest that reconfiguring task-set during switching might involve a state-change in connectivity patterns among task-set regions, with the left IFJ serving as a hub of this reconfiguration. Taken together, our findings point toward a pivotal role for the left IFJ in generating a representation of the current task-set and orchestrating other task-set regions when a new task must be performed.

In sum, findings in the current study support the characterization of switching-dependent control as an interaction of at least two networks, FPN and CON (Cocchi et al., 2013; Power & Petersen, 2013). First, PPI analysis reveals connections that are significantly associated with switching, involving many connections among nodes of these networks. Second, mean connectivity change was negatively correlated with individuals' mean behavioral switch costs. Third, activation and connectivity of left IFJ supports previous evidence that this region is intrinsically involved in switching-related control (De Baene et al., 2012; Kim et al., 2011, 2012; Stelzel et al., 2011). The results that the connectivity strength of left AI cannot significantly predict behavioral switch costs imply that these connections might be associated with some basic cognitive functions. Future studies might reveal how each of the specific connections between nodes is associated with specific processes in switching, or with more general cognitive control requirement, such as task difficulty and stimulus congruence.

It is important to acknowledge several limitations of the dataset. First, although multi-PPI analysis is a current method for estimating relative connectivity differences within and between large-scale brain networks (Cocchi et al., 2013), PPI analyses have limited causal interpretability. Future studies using more direct measures of information flow between brain regions and systems would be useful for confirming and elaborating the current findings. Second, given that task-switching requires multiple aspects of cognitive control that overlap with other tasks (e.g., Deák, 2004; Ruge et al., 2013), some of the network connections identified in this dataset are likely involved in other tasks and contexts that require cognitive control. Additional studies will be necessary to

determine how specific the current patterns are to task-switching. Manipulation to shed further light on this could include a wider range of timing and order parameters for switching and nonswitching trials, and a range of difficulty levels and ancillary task demands for both switch and nonswitch trials. Third, and conversely, the current task involved specific task content and demands including reading characters, activating linguistic associations, face processing, and gender classification. It will be important in future work to ensure that the results obtained here generalize to different task-switching tasks involving different stimuli, task domains, and discriminations. Note also that this paradigm imposed both task switches and response switches, but our analysis did not separate effects of these two types of switching. Although some previous work suggests that task switches contribute more than response switches to behavioral switch costs (e.g., Crone, Wendelken, Donohue, & Bunge, 2006; Waszak, Hommel, & Allport, 2003), further studies are needed to determine whether these two types of switches elicit different network activation patterns. Despite these limitations, the current findings indicate that two cognitive control networks work in concert during task switching, and that left IFJ serves as a common region that is pervasively activated in the interaction between the frontoparietal and cingulo-opercular networks during task-switching.

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